



Productivity of Montane Meadows in a Warming World: Evidence from an Elevation Gradient and a Warming Experiment

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PRODUCTIVITY OF MONTANE MEADOWS IN A WARMING WORLD:
EVIDENCE FROM AN ELEVATION GRADIENT AND A WARMING EXPERIMENT

by

Amanda Nicole Henderson

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This thesis has been approved on the date shown below:

Brian J. Enquist
Professor of Ecology and Evolutionary Biology

December 16, 2016
Date

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ABSTRACT

Climate change is expected to disproportionately impact high elevation ecosystems by disrupting current temperature and precipitation regimes. The future carbon balance of these systems is uncertain, given the interplay between longer growing season length and the potential for increased drought. Currently, the most robust inferences about ecosystem responses to changing climate come from the integration of experimental and observational methods. In this thesis, I utilize evidence from a warming experiment and an elevational gradient to gain insights into how aspects of ecosystem productivity and community functional composition change in response to the abiotic environment. First, I show that ecosystem productivity was similar in the heated and ambient treatment groups of the warming experiment. Net ecosystem productivity (NEP) was similar between treatments with only slightly increased NEP in the early season in the heated treatment. Important leaf functional traits (leaf mass per area, LMA; leaf dry matter content, LDMC) shifted with heating in directions associated with higher productivity, both at the community level and within species. While these results are counterintuitive, potential insight was provided by a soil cooling effect found in the heated plots in the early season. Second, I investigate ecosystem productivity across spatial and temporal gradients using phenology cameras. I show strong relationships between greenness indices generated from camera images and on-the-ground measurements of gross primary productivity (GPP). I also used changes in greenness indices early season to infer green-up rates, and found a strong pattern of increasing green-up rate with increasing elevation. Together, these studies highlight the importance of comparing experimental and gradient methods to assess how different spatial and temporal scales influence our conclusions about the effect of climate change on ecosystems.

INTRODUCTION

The carbon balance of terrestrial plant communities is one of the main regulators of atmospheric CO₂ via carbon sequestration in plant tissues, and subsequently in soil reservoirs. Rates of photosynthesis and respiration of ecosystems will likely be altered globally by the effects of climate change. Great uncertainty remains in how the general patterns of increased temperature and CO₂ will affect the carbon balance of different regions. In particular, increased temperature is expected to increase growing season lengths, metabolic rates, and nitrogen mineralization rates thereby increasing productivity, especially at high latitudes and altitudes (Friend *et al.*, 2014). However, water and nutrient limitations create the potential for lower productivity (Reich *et al.*, 2014), and potentially for net carbon losses to the atmosphere. The largest projected changes in growing season length are expected to occur in the mountainous regions of the western United States, accompanied by decreases in snowpack, earlier snowmelt, and earlier associated runoff (Walsh *et al.*, 2014). These changes may have substantial impacts on ecosystem carbon dynamics and whether high elevation areas remain carbon sinks or become carbon sources.

To try to predict the effect of climate change on ecosystem function, scientists have employed three different approaches: experimental manipulations, long-term observation, and space-for-time inferences. Experimental warming is often viewed as the most rigorous of the methods due to increased control over abiotic and other potentially confounding factors. However, community and ecosystem responses to warming often differ between short and long time-scales (Harte *et al.*, 2015; Andresen *et al.*, 2016), but extending experimental manipulations out over several decades is often impractical. A space-for-time substitution can be used to address the spatial and temporal scales more relevant to ecosystem climate change responses.

Within a region, natural abiotic gradients (often associated with elevation) can be exploited to gain insight about future climate scenarios (Sundqvist *et al.*, 2013). This method is complicated by uncertainty about how species and whole ecosystems will track a rapidly changing environment in comparison to historical changes. The use of temporal gradients (long-term monitoring) suffers from similar complications, where patterns observed now or in the recent past may not apply to future conditions. While all of these methods have their known issues, there has recently been a call for investigating these approaches in combination in order to make more robust predictions across different spatial and temporal scales (Elmendorf *et al.*, 2015; Rustad 2008; Dunne *et al.*, 2004).

In this study, I assess the effects of a changing climate on montane meadow ecosystems by combining a long-term artificial warming experiment with spatial and temporal gradient-based methods (Saleska *et al.*, 2002). The warming experiment was initiated in 1991 at the Rocky Mountain Biological Laboratory (RMBL), and allows for insights about future community structure and function under the projected conditions of earlier snowmelt and increased temperature, as compared to adjacent ambient conditions (Harte & Shaw, 1995). I draw on the rich history of research associated with this experiment to inform my predictions of current carbon dynamics and functional composition (Harte & Shaw, 1995; Saleska *et al.*, 1999; Price & Waser, 2000, de Valpine & Harte, 2001; Harte *et al.*, 2015). In addition, I employ sites along an elevational gradient in a watershed adjacent to RMBL spanning nearly 1000 m elevation and over 40 km aerial distance, as well as temporal variation from the growing seasons of 2012 to 2015.

With the warming experiment, I assessed the effect of over 20 years of continuous warming on ecosystem productivity and community functional composition. I tested to see if

instantaneous rates of photosynthesis and respiration decreased in the heated plots based on previous findings showing that the heating treatment increased soil temperature, decreased soil moisture and increased shrub abundance. I further tested if any differences between the treatments led to changes in the overall carbon balance. Concurrently, I measured plant functional traits associated with productivity (leaf mass per area, LMA; leaf dry matter content, LDMC; and leaf thickness, LT) (Wright *et al.*, 2004) at the community and species level. Heating did not cause large disparities in ecosystem productivity, and the small differences observed were ultimately not substantial enough to indicate growing season effects. However, there were very strong trait shifts observed in the communities and within species in both treatments. In both the case of small differences in productivity and large trait shifts, the patterns I observed were opposite of my prediction. A potential explanation for this discrepancy was a soil cooling effect observed in the heated plots during the early growing season. These results highlight the importance of future work investigating the specific abiotic effects achieved by the warming experiment.

Next, I assessed the value of near-surface remote sensing for monitoring productivity over temporal and elevational gradients. I used phenology cameras, “phenocams”, to capture multiple images per day at five sites during the 2012-2015 growing seasons. From these images I calculated greenness indices (green chromatic coordinate, GCC; and greenness excess index, GEI) to assess phenological changes in landscape greenness and their implications for landscape productivity rates (Richardson *et al.* 2007). The greenness indices showed clear differences within a growing season, among sites, and among years. I found strong relationships between both GEI and GCC and productivity rates. Finally, I found a strong positive elevational pattern in how rapidly green-up occurred, as well as a strong association between green-up and biomass

accumulation. This study confirmed the utility of phenocams for monitoring productivity, and in addition, tested hypotheses about abiotic controls on ecosystem productivity across spatial and temporal gradients.

Considering key components of both studies, we see contrasting conclusions between the studies employing the two methods. Specifically, we found with the elevation gradient that the abiotic conditions characteristic of lower elevation sites (increased temperature, decreased precipitation, longer growing season length) led to lower productivity rates. With the warming experiment, the heating treatment was intended to achieve conditions analogous to lower elevation. However I found similar, or slightly increased productivity in the heated compared to the ambient plots. While this result contradicts our expectations and our findings from the elevation gradient, I also found a soil temperature cooling effect present in the heated plots early season. If this was a true and consistent feature of the soil microclimate, then the experimental heating may not have had the intended effect, although further investigation is needed to fully assess this concern.

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APPENDIX A:

The effect of experimental warming on functional traits and ecosystem
productivity in a montane meadow

Abstract:

Climate warming is expected to influence the species and functional composition of communities, and influence ecosystem function. One means of predicting the future of montane communities is to combine experimental manipulations that match potential climate scenarios with measurements of ecosystem-level fluxes and trait composition of communities. In this study, we examine the effects of more than 20 years of experimental warming on ecosystem function and functional traits of a montane meadow in the Rocky Mountains. We find little evidence for differences in instantaneous rates of productivity between ambient and heated plots. While we observed small increases in early season net ecosystem productivity (NEP) in the heated plots, these differences decreased with progression of the growing season. Importantly, we found strong evidence for inter- and intraspecific shifts in several important functional traits. However, many of these shifts were opposite of our expectation, which had been based on the assumption that the heating treatment created consistently warmer and drier conditions. A potential explanation for this discrepancy was a prominent unexpected effect of experimental warming on soil temperature. Heated plots experienced warmer nighttime temperatures but cooler daytime temperatures resulting in less diurnal variation in soil temperature than control plots. Our results (i) point to need for future work to assess how experimental warming methods can also modify soil microclimate and influence productivity and functional traits; (ii) highlight the challenges of accurately manipulating the effect of temperature on whole-community and ecosystem-level processes; and (iii) point to the importance of potentially rapid plastic responses of trait composition in response to a directionally changing environment.

Introduction:

Increasing temperature and other effects associated with global climate change have begun to accelerate, and are expected to disproportionately impact high-altitude and high-latitude systems (IPCC 2013). These changes can have large implications for ecosystem carbon dynamics. Increased warming may disproportionately increase soil respiration in relation to total plant photosynthesis (Heimann & Reichstein, 2008; Bond-Lamberty & Thomson, 2010; Yvon-Durocher *et al.*, 2012). However, it is difficult to predict the outcome of temperature on carbon balance because of the complex interaction of factors influencing rates of photosynthesis and soil respiration (Luo *et al.*, 2008; Moyano *et al.*, 2013; Sharp *et al.*, 2013). If carbon uptake from photosynthesis is outpaced by carbon release from respiration, the end result will be a positive feedback of a net carbon release to the atmosphere (Davidson & Janssens, 2006; Luo, 2007). In the Intermountain West, warming is expected to cause decreased winter snowpack and earlier snowmelt, which will likely lead to less available soil moisture during the summer and fall (Barnett *et al.*, 2006; Regonda *et al.*, 2005; Foster *et al.*, 2016). These changes have the potential to greatly alter the balance of ecosystem carbon fluxes in montane meadows (Sloat *et al.*, 2015).

To address the uncertainties associated with predicting ecosystem carbon balance, it is necessary to monitor the effects of warming over a relatively long time scale. The warming experiment at the Rocky Mountain Biological Laboratory has been implemented for 23 years, providing a long-term record of the effects of warming. Early effects of warming were changes in the functional composition of the communities with a decrease in forb biomass and increase in shrub biomass (Harte & Shaw, 1995). These shifts could have significant implications for ecosystem carbon balance because shrubs tend to be much less productive than forbs.

Saleska *et al.* (1999) measured ecosystem carbon balance on the warming meadow in 1993 and 1994, two and three years after the initiation of experimental warming. They found that the main effect of experimental warming, earlier snow melt, caused advanced initiation of carbon uptake in both years, and an overall reduced net carbon uptake in 1993. Furthermore, increased shrub biomass had a direct negative effect on carbon uptake in both years (Saleska *et al.* 1999). This finding led to the conclusion that as long as warming continued to cause shrubs to replace forb species, carbon uptake would decrease compared to ambient conditions. A recent study looking back at biomass shifts from 1991 to 2013 shows that heating did indeed continue to increase shrub biomass, and decrease forb biomass, relative to control plots (which were themselves changing due to long-term climate trends (Harte *et al.*, 2015).

In this system, it is likely that shifts in vegetation composition have been driven by both changes in species abundance as well as by a difference in the traits expressed by the remaining species. Plant functional traits are a simple, species-blind way to characterize various life-history strategies within communities (McGill *et al.*, 2006; Violle *et al.*, 2007). The functional characteristics of individual plants tend to shift along climate gradients and can influence ecosystem carbon dynamics (Reich, 2014). Highly productive environments tend to select for plants characterized by unique traits that characterize higher growth rates including greater photosynthetic capacity, shorter leaf lifespan and lower carbon and higher nutrient concentrations (Westoby *et al.*, 2002, Reich *et al.*, 2003, Wright *et al.*, 2004, Shipley *et al.*, 2006, Reich, 2014). In contrast, lower productivity environments are characterized by plants with longer lifespans, higher dry matter content but higher carbon and lower nutrient concentrations (Grime, 2006; Reich, 2014). These functional shifts are reflected in key leaf functional traits such as leaf mass per unit area (LMA), which is comprised of both leaf thickness (LT) and the

dry matter content (LDMC) (Westoby *et al.*, 2002; Reich *et al.*, 2003; Wright *et al.*, 2004; Shipley *et al.*, 2006; Reich, 2014).

Recently, researchers investigating the effect of warming on functional traits have utilized species-based approaches including concentrating on focal species (Hudson *et al.*, 2010; Yang *et al.*, 2011) and have employed using species trait means to explore global patterns of responses to warming (Gornish & Prather, 2014). While these approaches have yielded important insights into how a rapidly changing climate can influence species-level trait composition they neglect the community context. An alternative approach that can better link traits to ecosystem functioning is to assess the distribution of traits within a community (Webb *et al.*, 2010). Quantifying shifts in community-level trait distributions can better assess how shifts in climate on growth strategies then ramifies to influence ecosystem function (Enquist *et al.*, 2015). In this study, we focus on assessing directional shifts in community trait distributions in response to warming utilizing community weighted mean (CWM) trait values (Garnier *et al.*, 2004). The CWM is based on the Mass Ratio Hypothesis (Grime, 1998), which predicts that the traits of dominant species will have greater contributions to productivity. Specifically, we investigated functional traits that have close links to productivity, including LMA and LDMC (Pontes *et al.*, 2007) as well as LT, which has important links to litter quality (De Deyn *et al.*, 2008).

We address the following questions: 1) How does long-term experimental warming affect instantaneous rates of whole-community photosynthesis and respiration, and does heating have an overall effect on ecosystem carbon balance? 2) Has experimental warming caused directional shifts in community weighted functional traits? Do observed trait shifts influence productivity as predicted by trait-based theory? 3) Do community trait responses to warming reflect mainly inter- or intraspecific shifts?

Methods:

Study site

The site of the warming experiment is a montane meadow located at the Rocky Mountain Biological Laboratory, Gunnison, CO, USA (lat 38°57'29''; long -106°59'22''). The region sits within the geographic and elevational boundary between subalpine meadow and Great Basin sagebrush steppe. Vegetation in these meadows consists of low shrubs, long-lived perennial forbs, and graminoid species.

The experimental design consists of 10, 3 x 10 m plots, with each plot spanning a small elevation gradient from dry ridge to moist swale. Five of the 10 plots are warmed by overhead infrared radiators running continuously, with a downward heat flux of 15 watts m⁻² between 1991 and 1993, and 22 watts m⁻² from 1993 to present (Harte & Shaw, 1995). Each plot is divided into three zones: upper (dry), middle, and lower (moist). This study was conducted exclusively in the dry upper zone of the plots, with a measurement area of 75 x 75 cm. The biomass of these meadow communities is dominated by sagebrush (*Artimisia tridentata*), long-lived perennial herb species (*Erigeron speciosus*, *Helianthella quinquenervis*), with some graminoid species (*Festuca thurberi*, *Achnatherum spp.*) (de Valpine & Harte 2001; Rudgers *et al.*, 2014).

CO₂ flux measurements

We measured whole ecosystem carbon exchange during the growing season of 2013 following the design described by Saleska *et al.* (1999). Each plot area was temporarily enclosed using a 235 L clear Plexiglas chamber measuring 42 cm in height and 75 cm to a side. To enclose the measurement area without crushing surrounding plants, the chamber was supported using an aluminum frame ~15 cm off the ground, supported by four metal stakes with plastic platforms holding the frame. The metal stakes were driven into the soil at the beginning of the

summer, and only adjusted if necessary to improve stability. We attached plastic skirting material fully around the perimeter of the aluminum frame. Prior to each measurement period we installed and rebalanced the frame and carefully placed the plastic skirting around adjacent plants. Frames and skirts were never in place for more than 36 h.

The Plexiglas chamber was equipped with a LiCor 7500 infrared gas analyzer (Lincoln, NE) and two small fans, all mounted to the inside top of chamber. Before each measurement, ambient CO₂ levels were measured for 30 s with the chamber on its side, open to the environment. The chamber was then placed on the frame to create a relatively leak-free system in which carbon and water flux was measured for 60 s. Belowground respiration was measured using a LiCor 6400 with soil respiration attachment (Lincoln, NE). Measurements were taken on bare ground to avoid the disturbance associated with installing semi-permanent PVC rings.

Whole ecosystem carbon flux measurements were taken at between 900 and 1100 in the morning to assess peak photosynthesis, and between 2100 and 2200 at night to assess peak nighttime respiration rates. Flux measurements began approximately one week after all plots were free of snow cover (May 22), and extended into the late portion of the growing season (August 18) for a total of 6 measurements.

At the beginning of the growing season, we also installed ibutton temperature data loggers (OnSet, Bourne, MA) in the soil of each plot at a depth of 10 cm. Placement was determined based on multiple criteria, including distance from plant stems and rocks. We measured soil moisture using a soil moisture gauge (Hydrosense, Campbell Scientific, Logan, UT) at the time of every carbon flux measurement.

Community composition and functional trait sampling

Community composition and biomass were monitored concurrently with carbon flux measurements. We measured maximum plant height in the four corners of each measurement area. Cover was estimated by functional type (shrub, forb, graminoid, and bare) with a 75 x 75 cm quadrat with 5 cm² grid cells. Functional types were assigned within each grid cell based on >50% green vegetation presence. In the case of grid cells with two or more functional types (e.g., high presence of both shrub and forb), the cell was assigned based on higher presence. We estimated species cover once mid-summer using the same methodology, but defining each grid cell by dominant species instead of plant functional type. Utilizing a previously developed model, we utilized our measurements of vegetation cover and height to estimate aboveground biomass ($R^2 = 0.78$, $P < 0.0001$) (Lamanna, 2012).

We collected leaves for functional trait measurements from species in both treatments within two weeks of peak growth, which was visually assessed based on the initiation of flowering. Thus, collection dates varied on a plot and species basis, with timing most influenced by the plot-specific-snowmelt dynamics. We collected leaf traits for every species that had >5% presence in the species-based cover estimates, resulting in 3-5 leaves per species per plot with leaves coming from different individuals. This collection design captured inter- and intra-specific trait variation, but no intra-individual trait variation. Leaf trait protocols followed Pérez-Harguindeguy *et al.* (2013), and fresh leaves were collected, weighed, scanned, and measured for thickness within a 2 h period. Leaves were then dried for >48 h at 65 °C before weighed again. Traits measured include leaf mass per area (LMA gm⁻²), leaf dry matter content (LDMC gg⁻¹), and leaf thickness (LT mm).

Modeling carbon exchange

We fit mixed-effect models with day of year as a random effect and utilized the data exploration ‘dredge’ function in the MuMIn package of R (Barton, 2015) to evaluate the relative importance of different explanatory fixed effects and develop a predictive model. We fit a global model with all possible fixed effects and evaluated all possible models using AICc. Because this process did not result in a small number of ‘best’ models, we utilized model averaging with the MuMIn package to estimate average fixed effect coefficients based on all models within delta 2 AICc. We also calculated marginal and conditional R^2 values (R^2_{marg} , R^2_{cond}) for each component model in order to assess overall model utility.

Separate model competition was performed for NEP, nighttime whole-ecosystem respiration (R_{eco}), daytime soil respiration (R_{day}), and nighttime soil respiration (R_{night}). All global models started with the same fixed effects, including abiotic (soil moisture, leaf temperature, soil temperature, total solar flux), community composition (plant height, shrub biomass, herb biomass, graminoid biomass), and community weighted mean (CWM) functional traits (LMA, LDMC, LT).

In all cases, the absolute value of the dependent variable (NEP, R_{eco} , R_{day} , R_{night}) was log10 transformed to address problematic heteroscedasticity, and to improve normality. We logit transformed soil moisture as it was measured as a percentage. Cover percentages were converted to grams of biomass for each functional type, and thus did not require logit transformation. We calculated CWM trait values for all leaf traits based on the dominance of each species, where dominance was estimated via a combination of cover and average height.

Results:

Abiotic effects of heating

The majority of heated plots experienced first instance of bare ground around March 30 (day 89), and continued to receive intermittent short-term snow cover until mid-May. Snowmelt on the southernmost heated plot lagged substantially, and bare ground did not appear until May 2 (day 122). Ambient plots melted over a span of two weeks from April 27 to May 12 (day 117 to 132), with melt occurring directionally from north to south.

As also observed in previously in this experiment (Saleska *et al.*, 1999), we found that the average daily soil temperature on heated plots was actually *cooler* during early to middle parts of the growing season (Fig 1a). This time corresponds to when plants were actively growing and producing leaves. Breaking this pattern down by hour showed that during the early portion of the growing season, heated plots were warmer overnight but cooler during the day (Fig 1b). Thus, warmed plots were actually more thermally buffered, experiencing warmer nighttime temperatures and cooler daytime temperatures.

Growing season carbon exchange

We found differences in daytime instantaneous fluxes between heated and ambient plots, but only early in the growing season (Fig. 2). The total growing season productivity did show a trend toward higher rates of both NEP and respiration in the heated plots (Fig.2). Consistent with earlier work, the greatest carbon flux differences between warmed and control plots were observed in the few weeks right after snowmelt (Saleska *et al.* 1999). There is also an indication that warming increased NEP very early in the growing season. However, this difference subsequently disappears and NEP values were similar throughout the rest of the growing season (Fig. 2).

Timing of first flux measurement did not allow for directly observing the compensation point when NEP switched from negative (respiration dominating signal) to positive (photosynthesis dominating signal). However, extrapolating from the loess fit indicates this shift occurred at approximately DOY 130, May 10. NEP steadily increased early season towards a mid-season productivity peak around DOY 165, June 14. Visual assessment of the Loess smooth suggests higher rates of NEP in the heated plots in the ramp-up towards the productivity peak, but the difference was only significant at the second time-point, DOY 151 (Wilcoxon rank-sum, $W=3$, $p=0.0556$).

Daytime soil respiration rates did not change much with the progression of the growing season until a slight increase in respiration late in the season (DOY 230). There was a persistent trend for heated plots to have higher rates of respiration (more negative values) throughout the growing season, but the difference was slight with DOY 193 the only marginally significant time-point (Wilcoxon rank-sum, $W=21$, $p=0.0952$) (Fig. 2).

Nighttime R_{eco} did not show a distinct growing season pattern, except for a slight peak at DOY 151 in the heated treatment only, indicating higher nighttime ecosystem respiration in the heated plots (Wilcoxon rank-sum, $W=22$, $p=0.0556$) (Fig. 2). Other than this small peak, R_{eco} remained fairly constant through the most of the growing season, then increased late in the season. Heated plots experienced higher respiration rates, but only early in the season (Wilcoxon rank-sum, $W_{DOY\ 141} = 21$, $p_{DOY\ 141} = 0.0952$; $W_{DOY\ 151} = 24$, $p_{DOY\ 151} = 0.0159$), likely due to earlier snowmelt in most of the heated plots.

We calculated the cumulative effect of carbon fluxes over the course of the growing season in order to assess how small productivity disparities between treatment groups might accumulate over time. Positive NEP over the first three time-points indicate higher carbon uptake

in the heated plots; while concurrently, negative R_{eco} indicate higher whole-ecosystem nighttime carbon release in the heated plots (Fig 3). These patterns taken together point toward higher overall carbon exchange in the heated plots early season, up to the observed productivity peak. After that point, there was no discernible non-zero difference in carbon exchange rates, which was likely due to the combination of rate convergence as well as increased uncertainty due to the additive nature of cumulative error.

Functional trait shifts

We observed significant and directional shifts in community weighted functional traits. The heating treatment caused decreased CWM LMA (Wilcoxon rank-sum, $W = 21$, $p\text{-value} = 0.0952$), decreased CWM LDMC (Wilcoxon rank-sum, $W = 23$, $p\text{-value} = 0.03175$), and increased CWM LT (Wilcoxon rank-sum, $W = 4$, $p\text{-value} = 0.09524$) (Fig 4). Together, these results do not support the expectation that traits in heated plots would shift toward lower productivity due to more xeric conditions. Instead, the observed trait shifts are consistent with a shift to more productive traits.

Of the five species with sufficient coverage in both treatments, four significantly followed the trend of decreased community LMA in the heated plots (Wilcoxon rank-sum; *A. tridentata*, $W = 653$, $p\text{-value} = 0.003433$; *H. quinquenervis*, $W = 93$, $p\text{-value} = 0.0043$; *L. lanszwertii*, $W = 130$, $p\text{-value} = 0.06094$; *P. hippiana*, $W = 79$, $p\text{-value} = 0.08154$). With LDMC, only *A. tridentata* followed the community pattern of decreased LDMC in heated plots (Wilcoxon rank-sum, $W = 592.5$, $p\text{-value} = 0.04343$), indicating that the community-level trait shift was primarily driven by *A. tridentata*. Two species, *A. tridentata* (Wilcoxon rank-sum, $W = 199.5$, $p\text{-value} = 0.0005069$) and *E. umbellatum* (Wilcoxon rank-sum, $W = 13$, $p\text{-value} = 0.006121$), displayed the community pattern of increased leaf thickness in the heated treatment

(Fig 5). Together, these results indicate that the community level trait shift was more nuanced at the intraspecific level, with some indication that intraspecific trait shifts were more uniform for LMA but not for LDMC and LT.

Mixed-effect models

Results of model selection using mixed effect models with DOY as a random effect show that plant height, shrub biomass, and soil moisture had the largest positive effect on ecosystem productivity (based on a combination of z-score and importance values) (Table 1). Traits followed the expected directionality with negative effects on productivity for LMA and LT, and positive effect on productivity for LDMC. Together, these results are consistent with trait-based theory showing the importance of plant size and carbon economy traits as strong predictors of variation in ecosystem functioning. Overall, the component models explained a range of variation from 14.25 to 31.3% in NEP from fixed effects alone (marginal R^2), and 41.54 to 65.1% of variation in NEP from fixed and random effects together (conditional R^2). Fitting a simple mixed-effect model explaining NEP with the treatment as the only fixed effect and day of year as the random effect, we are able to explain very little variation ($R^2_{\text{marg}} = 0.018$, $R^2_{\text{cond}} = 0.188$).

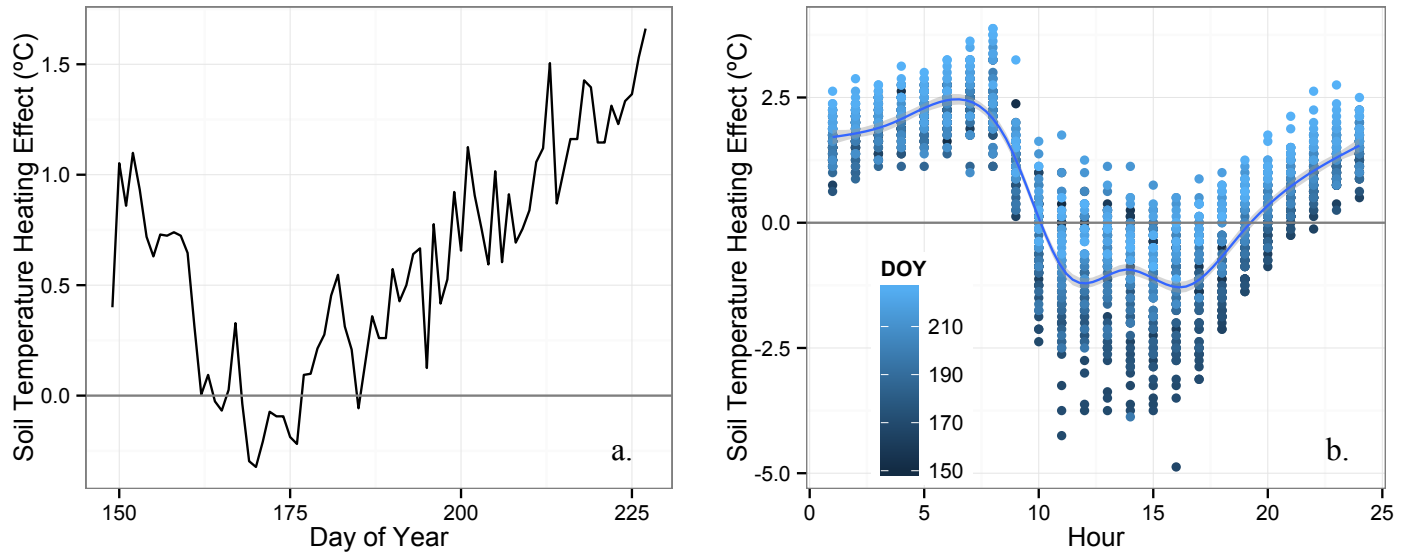


Figure 1. Difference in soil temperature (°C) between heated and ambient plots, averaged daily (a) and broken down by hour of the day (b) with dark-to-light blue gradient showing day of year. Positive values indicate warmer temperatures in the heated plots. Experimental warming increased soil temperature on average early and late in the year. However, this effect mainly reflects warmer nighttime soil temperatures, as during the daytime experimental plots actually have cooler soil temperatures than control plots. As a result, experimentally warmed plots experience less diurnal variance in soil temperatures than the control plots.

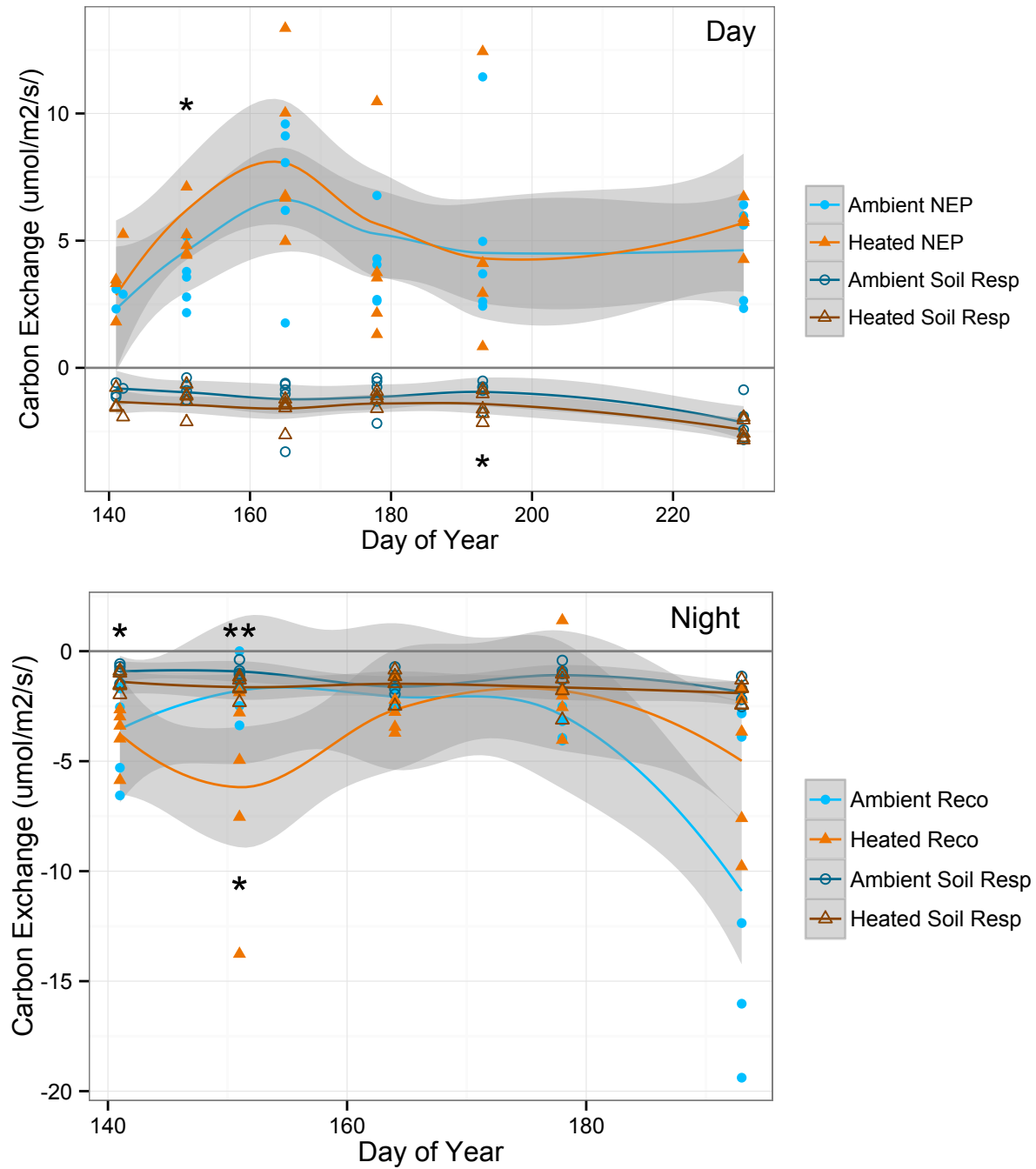


Figure 2. Growing season carbon exchange dynamics from daytime measurements (ca 10:00), and nighttime measurements (ca 22:00) in 2013. Heated plots are represented in orange lines and triangle symbols with NEP = light orange, filled triangles, and Soil Resp = dark orange, open triangles. Ambient plots are represented in blue lines and circles symbols with NEP = light blue, filled circles, and Soil Resp = dark blue, open circles. Asterisks indicate significant differences within a single time-point based on two-sided Wilcoxon rank-sum tests. Significance symbols for NEP are placed above the light orange and light blue lines for day and below the light orange and light blue for night (and vice versa for Soil Resp). Significance codes: * $p < 0.1$, ** $p < 0.05$.

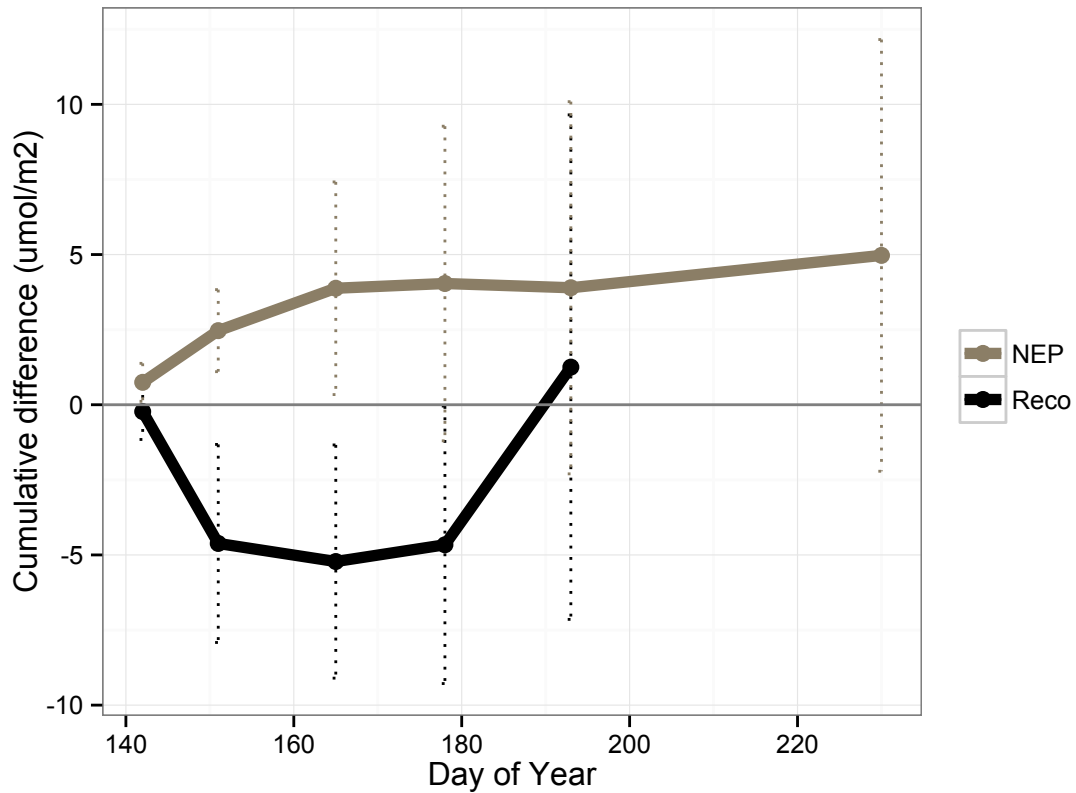


Figure 3. Cumulative differences in carbon exchange rates between heated and ambient plots over the course of the growing season. Positive values for daytime NEP (brown line) indicate higher carbon uptake in the heated plots. More negative values for R_{eco} (black line) indicate higher carbon release in the heated plots. Error bars are SE, and are additive over time. The only statistically significant difference in cumulative NEP and Reco occurred early in the growing season (between DOY ~150 and ~170) with warmed plots having increased fluxes of NEP and R_{eco} . There was a trend for higher cumulative NEP throughout the entire growing season in heated plots, but because of the large SE the differences were not statistically significant.

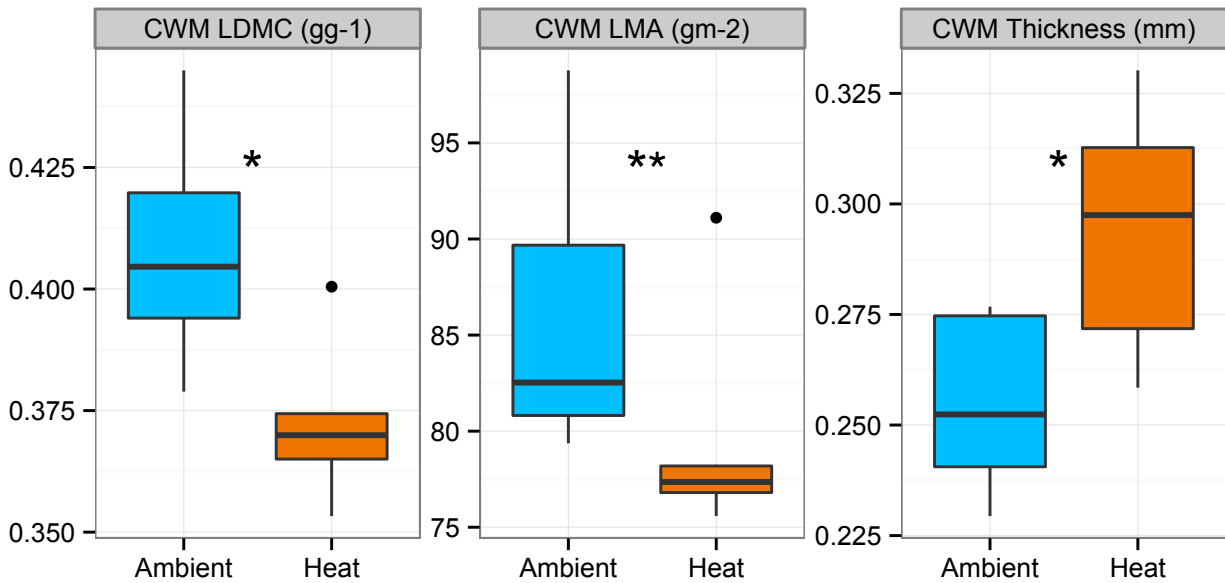


Figure 4. Community weighted mean trait values for leaf dry matter content (LDMC), leaf mass per area (LMA), and leaf thickness (LT). Significance codes: * $p < 0.1$, ** $p < 0.05$. In contrast to expectations, experimentally warmed plots are characterized by leaves with lower LDMC and LMA but increased LT.

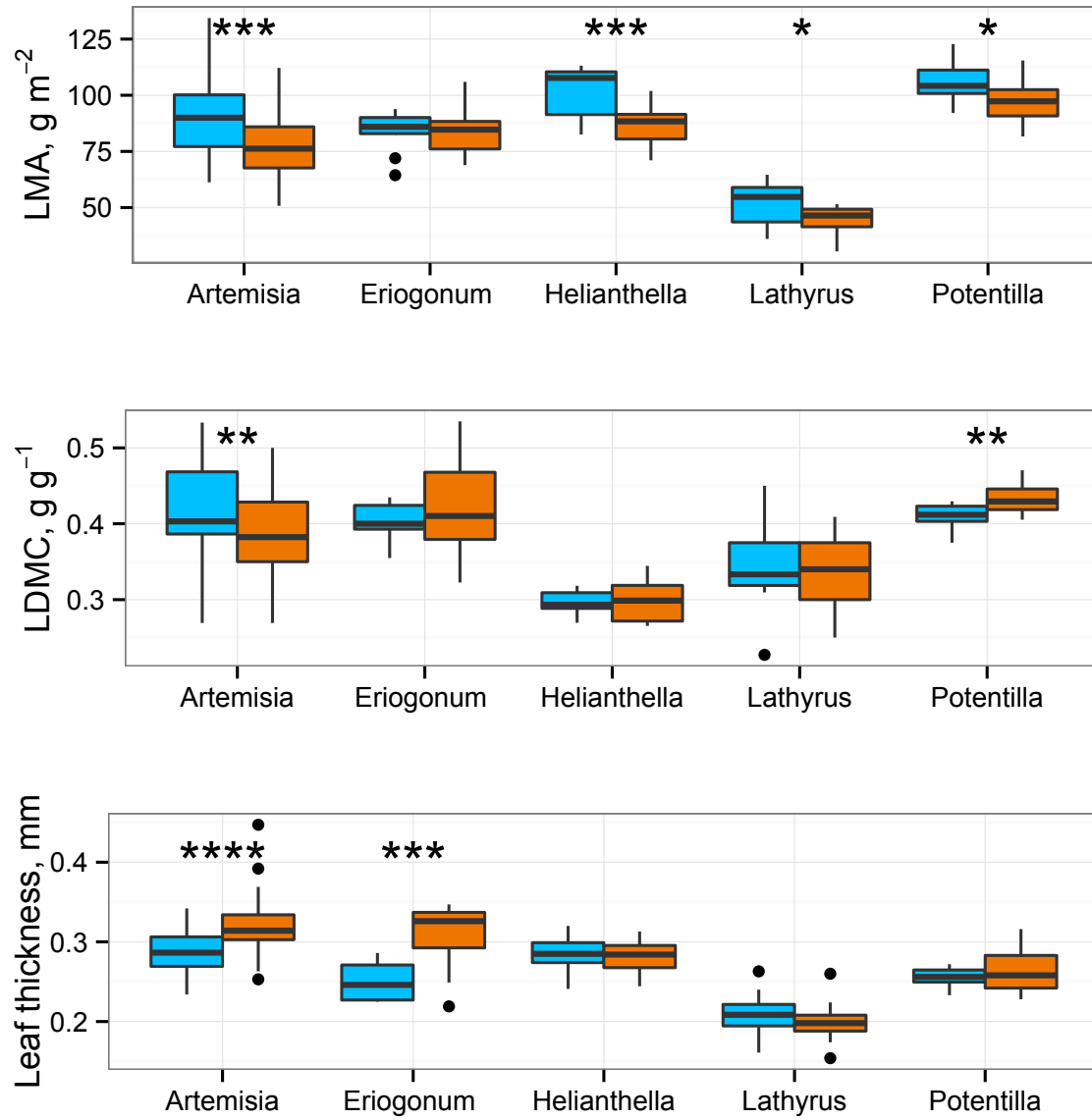


Figure 5. Species level trait differences, where light blue = ambient plots and light orange = heated plots. Species are *Artemisia tridentata* ($n_a = 20$, $n_h = 45$), *Eriogonum umbellatum* var. *aureum* ($n_a = 9$, $n_h = 11$), *Helianthella quinquenervis* ($n_a = 9$, $n_h = 12$), *Lathyrus lanszwertii* var. *leucanthus* ($n_a = 14$, $n_h = 13$), and *Potentilla hippiana* ($n_a = 17$, $n_h = 9$). Significance codes: * $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$, **** $p < 0.001$.

Table 1. Averaged model coefficients for daytime Net Ecosystem Productivity (NEP) and daytime soil respiration within delta 2 AICc. Importance estimates based on the number of component models containing variable. All models are linear mixed-effects models with day of year as a random effect. NEP and soil respiration were both log10 transformed to improve normality and heteroscedasticity. Soil moisture was logit transformed and height was log10 transformed.

		Ave Coef	SE	Z	P	Import	Sign. Code
NEP	Intercept	-0.2598	0.5247	0.4950	0.6205		
	Soil Temp	0.0049	0.0122	0.3990	0.6898	1	
	Soil Moisture	0.1126	0.0577	1.9510	0.0511	0.71	*
	Leaf Temp	0.0127	0.0084	1.5060	0.1322	0.3	
	Mean Height	0.3132	0.1518	2.0640	0.0391	0.96	**
	Shrub Bio	0.0002	0.0001	2.5920	0.0095	0.04	***
	Grass Bio	-0.0043	0.0023	1.8470	0.0648	0.51	*
	CWM LMA	-0.0081	0.0044	1.8490	0.0644	0.16	*
	CWM LDMC	2.1150	1.3620	1.5530	0.1204	0.39	
	CWM LT	-2.8700	1.8010	1.5940	0.1110	0.2	
Soil Resp	Intercept	-0.2737	0.3101	0.8830	0.3775		
	Soil Moisture	0.0839	0.0378	2.2200	0.0264	0.57	**
	Leaf Temperature	0.0139	0.0051	2.7090	0.0068	0.86	***
	Mean Height	0.1795	0.1072	1.6750	0.0939	0.66	*
	CWM Thickness	-1.2692	1.4319	0.8860	0.3754	0.10	

Discussion:

While we find little evidence for major shifts in rates of productivity and respiration caused by experimental heating our results also indicate that small differences between experimental treatments may accumulate over time to potentially cause shifts in the carbon balance. On the one hand, these conclusions are similar to other results showing experimental effects of warming on ecosystem functioning (Saleska *et al.* 1999; Saleska *et al.*, 2002; de Valpine *et al.* 2001; Harte *et al.*, 2015). On the other hand, the differences between experimental and control plots we observed were opposite than expected. We observed a trend toward *higher* cumulative rates of carbon flux in the heated treatment, whereas Saleska *et al.* (1999) found higher rates in heated plots only in the early season followed by significantly reduced rates in heated plots. Their results showed an overall *decrease* in carbon uptake in the warmed plots due to heating (Saleska *et al.*, 1999). These discrepancies may reflect either changes in community functional composition that have occurred in the 20-year span between measurements (Harte *et al.*, 2015), or could be due to differences in methodology. If our observations do reflect true shifts in the traits of plants within the heated plots, then it would indicate that the observed productivity of heated and ambient plots might be converging. Continued monitoring will be crucial to disentangle the trajectories of productivity rates and overall carbon balance under ambient and experimentally warmed conditions.

We found strong evidence of treatment-induced directional changes in both community- and species-level traits. Both LMA and LDMC tend to follow strategy tradeoffs associated with the leaf economic spectrum, where higher LMA and LDMC indicate lower productivity (Wright *et al.*, 2004). Strategy tradeoffs are also highly linked to the abiotic environment, with harsher conditions (e.g., high temperature, low moisture) generally leading to less productive, but longer

lasting leaves (Reich, 2014). However, the direction of trait shifts observed in this study was opposite of this expectation, assuming that the heated treatment did induce harsher conditions compared to ambient. At the community level, LMA and LDMC exhibited lower values in the heated treatment compared to ambient. In contrast, we expected LMA and LDMC to increase in response to warming. This expectation is based on global patterns of trait covariation found by Wright *et al.* (2005) showing increased LMA in hot, dry, and high irradiance conditions, and global patterns in leaf tissue density found by Niinemets (2001) showing increased density (similar to LDMC) with decreased precipitation. LT was the only trait that changed in accordance with our expectations, with higher LT in the heated communities (Niinemets, 2001). Our findings are in contrast with a 4-year warming study that found increased LDMC at the community level with warming (Cantarel *et al.*, 2013), and a 16-year warming study that found species-specific decreases in SLA (reciprocal of LMA therefore equivalent to increased LMA) with warming (Hudson *et al.*, 2010). Similar to our result, Yang *et al.* (2011) found decreased LMA in an alpine sedge in response to two years of warming.

Different patterns between community and species shifts emerge for the three traits. The strong decrease in CWM LMA remained robust at the species level, with four of the five species occurring frequently in both treatments mirroring the community trend. Species-level LT was also consistent with the community trend, but only in two out of the five species. Importantly, only one species (*A. tridentata*) demonstrated decreased LDMC, indicating that the community shift in LDMC may have been driven by *A. tridentata* or by species that did not commonly occur in both treatments. These results highlight the importance of assessing trait shifts of whole communities, while simultaneously considering trait variability within species.

In our attempts to explain variation in net ecosystem productivity or NEP with abiotic factors, vegetation composition, and community traits, we found that models including variables from all of the categories usually did a better job of explaining productivity. This highlights the complex interplay of the environment and community structure on ecosystem function. However, we also found that little variation in NEP could be explained by the treatment effect alone. This indicates that while traits, community composition, and abiotic variables explain ecosystem productivity well; treatment group identity did not explain variation in these factors. This could be due to the large amount of variation present between plots both between and within treatment groups. The plots in this warming experiment are oriented along a north-south line with a slight arc in the ridge causing an average 4°-aspect difference between each plot, resulting in more southern exposure for plots on the northern end of the layout (Saleska *et al.*, 1999). Due to these aspect differences and some shading effects, snowmelt dates varied greatly within treatment group. Heated plots experienced a 33-day span between first and last plot to melt, and ambient plots experienced a 15-day difference.

The abiotic conditions present during this study provide a potential means of evaluating our observed counterintuitive productivity and trait differences between experimental plots. More specifically, the effect of the heating treatment during the 2013 growing season may have been different from the original intention of the experiment. We found that soils were actually cooler in the heated plots compared to ambient during the early growing season, with the largest cooling effect observed during the middle of the day. The heated plots generally melt well in advance of the surrounding areas, leading to patches of bare ground surrounded by snowpack. This had the potential to effectively provide a reservoir of melt water from the surrounding snow accessible to plant species with extensive root systems (e.g., *A. tridentata*). This effect, paired

with more buffered soil temperature in the early season (perhaps caused by increased cover along with increased cooling effect via soil water evaporation), might have led to conditions that were not actually warmer, at least early in season when plant growth and leaf expansion rates were higher.

The observed cooling of the soil is consistent with earlier findings of Harte *et al.* (1995) who found that in the more wet portions of the warmed plot that warmed plot soil was cooler. They attributed this difference to the observed increase in plant cover in the warmed plots. The increased in cover is thought to have then led to shading of soil and hence a cooling. In their original paper, they did not see a soil cooling effect in the upper zone where we focused our measurements. Our observed soil cooling results may be consistent with their proposed mechanism. Since the original study (Harte *et al.*, 1995) there has been an increase in shrub cover in the heated and ambient plots in the upper zone where we worked (Harte *et al.* 2015). An increase in shrub cover may provide a mechanism for the observed increase in soil cooling, as shrubs would lead to more shading of soil. Another potential explanation is that increases in shrub cover may have led to an increase in hydraulic lift of deeper soil water from the deeper-rooted shrubs. Hydraulic redistribution would result in more moist soil that could lead to more cooling due to latent heat from evaporation. Together, differences in vegetation cover and hydraulic lift may potentially lead to cooler soils. Future work should assess these linkages in more detail than our data permit.

Our results yield two important insights. First, the methods used in the experimental warming treatment appear to have led to conditions that buffer extreme temperatures and that have actually cooled soil temperatures by several °C during the most productive time of the growing season. These results generate important questions about how to experimentally warm

communities and ecosystems most effectively to simulate the effects of a warmer world. We are currently making more detailed measurements of soil temperature and soil moisture to further document and explain the observed soil temperature differences found in this study. Coupling these data with current measurements of plant functional traits at both the community and species level will allow us to better understand how plants respond to warming, and how these responses might influence future persistence and success. Second, our results underscore that plant communities can respond relatively rapidly at the inter- and intraspecific level to changes in their abiotic environment. As the plant species in the experiment are long-lived perennials the observed shift in community composition is likely the result of plastic within individual shifts and not the result of differential survivorship and mortality based on traits.

In conclusion, our results indicate that long-term experimental warming has indeed influenced the structure and functioning of a high elevation meadow but that the observed changes have been counterintuitive. The observed shifts in ecosystem fluxes underscore the importance of species trait responses to climate but also point to the importance of non intuitive responses due to experimental design. Our results point to need for future work to assess how experimental warming methods can also modify soil microclimate and influence on productivity and functional traits. They also highlight the challenges of accurately manipulating the effect of temperature on whole-community and ecosystem-level processes. Further, our results point to the importance of potentially rapid plastic responses of trait composition in response to a directionally changing environment. Monitoring the traits of individual species in conjunction with community trait patterns may generate insight into the future success of species, and resulting community composition by comparing species trait means and variability to the community trait distribution (Enquist *et al.*, 2015; Sides *et al.*, 2014).

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APPENDIX B:

Digital repeat photography accurately captures instantaneous, growing season, and interannual variability in CO₂ flux and productivity of Montane and Subalpine ecosystems.

Abstract:

High elevation systems exhibit a large degree of variation in productivity both spatially and between growing seasons. With increased uncertainty about how changing climate conditions will impact productivity and carbon balance of montane and subalpine ecosystems, there is a need for monitoring of growing season carbon dynamics both locally and across environmental gradients. Near-surface remote sensing utilizing phenocams has emerged as an effective tool for detecting and quantifying phenological events and ecosystem productivity. We utilize the greenness excess index (GEI) and the green chromatic coordinate (GCC) generated from repeat digital photography to estimate ecosystem productivity instantaneously and over the course of the growing season (May - September) from 2012 through 2015. We show that we are able to effectively visualize and quantify growing season productivity utilizing greenness indices, with a large portion of instantaneous gross primary productivity (GPP) explained by GEI ($R^2 = 0.623$). Importantly, when explaining GPP with multiple variables included in models, greenness indices remain highly important, indicating that the indices capture physiologically relevant information. Additionally, strong associations between greenness indices and productivity allow us to utilize GEI and GCC to assess ecologically important aspects of the growing season, including green-up rates and cumulative productivity. We conclude that phenology cameras produce information relevant to ecosystem processes and can be utilized for monitoring of growing season dynamics.

Introduction:

Global climate change is expected to impact high elevation and high latitude ecological systems before other areas, and will likely have a greater effect on species' success and survival (IPCC 2013). Already, climate scientists are observing changes in temperature and precipitation regimes, and a trend towards greater variability (Karl *et al.*, 2009; Francis & Vavrus, 2012; Walsh *et al.*, 2014). In particular, the Intermountain West is expected to experience warmer temperatures mainly in the summer, and decreased precipitation during late spring and summer (Lukas *et al.* 2014; Meixner *et al.*, 2016). Projections of reductions in late winter and spring snowpack and subsequent reductions in runoff and soil moisture pose increased risks to water supplies and ecosystem functioning (Cayan *et al.*, 2010). Recent studies in high elevation, water limited ecosystems have found that early snowmelt combined with the disruption of precipitation regimes results in decreased streamflow (Hidalgo *et al.*, 2009) and reduced ecosystem productivity (Hu *et al.* 2010; Sloat *et al.* 2015).

Scientists have taken a multi-pronged approach in order to predict the fate of potentially vulnerable high-elevation ecosystems. Small-scale manipulative experiments in conjunction with larger-scale monitoring over elevation have generated several insights on how climate change influences montane ecosystems (Harte & Shaw 1995; Dunne *et al.* 2004; Sloat *et al.* 2015; Alatalo *et al.*, 2016). These insights provide crucial information for modeling efforts attempting to predict future biotic and abiotic conditions in high elevation ecosystems (van Bodegom *et al.*, 2014; Yang *et al.*, 2016). However, currently manipulative and observational investigations of productivity remain resource-intensive due to upfront investment, ongoing effort, or both.

In reaction to the need for more extensive monitoring with less overall investment, recent attention has been given to digital repeat photography using relatively inexpensive mounted

cameras, or “phenocams” (Richardson *et al.* 2009; Brown *et al.* 2016). Scientists have begun to develop methods for using this simple technology to track important phenological changes in vegetation and their implications for ecosystem carbon balance (Richardson *et al.* 2009; Ahrends *et al.* 2009; Toomey *et al.* 2015). Information provided by phenocams can be used to provide a middle ground between larger scale remote sensing techniques (loss of local detail, both spatially and temporally) and place-based observations (potential for bias, difficult to standardize, and time intensive). Phenocams also provide flexibility in application between long-term monitoring and shorter-term experiment based questions.

Phenocams for vegetation monitoring are currently most commonly used in forest canopies (Richardson *et al.* 2009; Saitoh *et al.* 2012; Sonnentag *et al.*, 2012; Keenan *et al.* 2014), with some extensions into grasslands and crop fields (Toomey *et al.* 2015). Most studies aiming to connect information from phenocams to ecosystem productivity have employed data from eddy flux towers, which have the benefit of capturing carbon fluxes continuously year-round at the landscape level. Consequently, this methodology is still spatially relatively large-scale, which has the benefit of consolidating information over large swaths of homogenous vegetation, but which could pose difficulties in more heterogeneous environments (Schmid & Lloyd, 1999). While it is possible to isolate the effect of specific vegetation types within a mosaic of vegetation using the eddy covariance tower method (Göckede *et al.*, 2004), the most accurate and unbiased estimates of carbon exchange occur in homogenous vegetation (Baldocchi 2003). This is especially important in montane and subalpine ecosystems where the landscape can be described as a mosaic of meadow, mesic willow, aspen, and coniferous forest with vegetation shifts occurring at relatively small scales. This study extends the current approach of combining

phenocam observations and carbon flux measurements by adapting it for use at small scales, making it more relevant for place-based questions.

We used measurements of ecosystem productivity and greenness indices from phenocam observations to assess the ability to quantify ecosystem carbon flux and biomass productivity using near surface remote sensing. We quantified the strength of correlations between greenness indices and gross primary productivity (GPP) across an elevational gradient in the Rocky Mountains of Colorado, with sites spanning from the lower montane to the subalpine. Specifically we look at the green chromatic coordinate (GCC) and greenness excess index (GEI) as potential predictors of ecosystem productivity at instantaneous and growing season timescales.

Methods:

Study system:

We monitored five sites (originally established in 2002) along an elevational gradient spanning 2475-3380 m asl in Gunnison County, CO, from 2012 through 2015. The lowest elevation site is arid and shrub dominated, and the sites extend into the subalpine, with an average of 200 m elevation difference between sites. All sites consist of forb, low shrub, and graminoid functional groups, with generally decreasing occurrence of shrubs with increasing elevation.

Each site is approximately 50 m² with five 1.3 m² plots that were monitored during the early to peak growing season from 2012 to 2015. Plots were placed haphazardly each growing season and measured for below- and aboveground instantaneous carbon fluxes, species composition, biomass estimates, and abiotic factors (air, leaf, and soil temperature, soil gravimetric water content, soil carbon content).

Biomass estimation:

Biomass was estimated during each year of the study using a model developed to assess aboveground biomass non-destructively using vegetation height and functional group percent cover ($R^2 = 0.78$, $p < 0.0001$) (Lamanna, 2012). We measured plant height and functional cover 3-5 times per site per growing season to capture on-the-ground biomass and growth dynamics at a finer time scale than we can achieve with instantaneous measures of NEP.

Instantaneous carbon flux measurements:

The general design and measurement of net ecosystem productivity (NEP) follow Jasoni *et al.* (2005), with modifications designed to make the carbon flux measurement system highly mobile. We enclosed the 1.3 m² plot area in a cube made of a semi-translucent tarpaulin material that allowed 70% of PAR (Shelter Systems, Menlo Park, CA), and a PVC frame for structural stability. A single open face of the cube was placed over the plot, and an attached canvas skirt was secured to the ground using a chain. This design results in the ability to enclose small areas of vegetation with relatively few leaks for short periods of time. We measured the concentration of CO₂ and H₂O within this space with a LiCor 7500 infrared gas analyzer (Lincoln, NE) placed within or above the vegetation canopy on a tripod, along with two fans circulating air around the sensor.

Daytime NEP was measured at each site between 0900 and 1100 under clear sky conditions two days during the growing season: ‘early’ season during the green-up period, and ‘peak’ season when most of the dominant species had reached their ultimate growth and were flowering. Each NEP calculation consisted of an initial sample of ambient CO₂ levels for 30 s (plot not enclosed by cube), immediately followed by a 90 s measurement of the rate of change of CO₂ (plot enclosed by cube, and secured with chain to prevent leaks).

Belowground carbon flux was measured at the soil surface with PVC collars sunk into bare soil using a LI-6400 with soil respiration attachment (Lincoln, NE). We measured soil efflux at two soil collars per plot, during the same 0900-1100 timeframe as NEP. The contribution of belowground respiration to the whole-ecosystem flux (NEP) was estimated to be the average of these two measurements weighted by the percent bare ground occurring in the plot. Accounting for the belowground contribution allowed us to estimate gross primary productivity (GPP) from our direct measurements of NEP.

Camera design:

At each site, one phenology camera (Wingscapes, Calera, AL) was mounted 1.5 m above the ground on a metal T-stake with N to NE orientation and at a 35° downward angle in order to capture the 50 m² site. Cameras were present at all sites for the majority of the growing season from 2012-2015, and programmed to capture an image every 10 min between 0900 and 1600 (timeframe later truncated for analysis to 1000 to 1500 to reduce incidence of sun glare and shading) with 4 MP total image size. There was a moderate failure rate, mostly due to complications caused by variable early season access as well as factors associated with working on public land – including camera theft, and damage and movement caused by livestock. Camera age also emerged as a limitation in the late season of 2015.

Image processing:

All images were visually inspected in order to purge the image collection of extraneous subject matter (presence of humans or animals, extreme camera angle change). Images that were outside of 2 standard deviations of the mean total brightness were also eliminated to further reduce extremes produced by sun glare and cloudy or rainy days.

We used MATLAB to extract raw digital numbers (DN) for red (R), green (G) and blue (B) channel intensities, and to calculate two greenness indices that have been previously shown to capture growing season phenology and productivity (Richardson *et al.*, 2007). The first index is the proportion of green compared to total brightness, also known as the green chromatic coordinate, $G/(R+G+B)$, hereafter referred to as GCC. By putting the value of the green channel in the context of total brightness, the index is partially buffered from day to day variation in brightness present within our threshold. The second index is a measure of the differentiation of G from R and B, calculated as $2G-(R+B)$ and notated as greenness excess index (GEI). This index helps our understanding of green (productive) biomass by enhancing the green component and minimizing the red and blue components (Richardson *et al.* 2007; Woebbecke *et al.* 1995). Daily averages of both indices were calculated, and used for further analyses.

Statistical analysis and modeling:

Overall patterns of greenness indices between sites and between years were assessed using the non-parametric Kruskal-Wallis test and associated post-hoc comparisons.

We used a single predictor linear regression to model the effectiveness of the two greenness indices for predicting GPP. For each site, we averaged our plot-level measurements of GPP to approximate a site-level value. The values for GCC and GEI used in this analysis were extracted as daily averages from the same day as the carbon flux measurements. For a more complete model utilizing greenness indices, we fit a multiple regression model with biomass ($\log_{10}$ transformed), shrub cover (arcsin square root transformed), and GCC. GCC was found to be a better predictor in multiple regression models than GEI as determined by amount of variation in GPP explained.

To integrate the relationship between ecosystem greenness and productivity over the course of the growing season, we calculated cumulative daily instantaneous rate of GPP utilizing the equation from the GEI simple linear regression model (Figure 2b). In this case, GEI was used in favor of GCC based on the higher percentage of variation explained in the single predictor models (GEI: $R^2 = 0.623$; GCC: $R^2 = 0.578$). For this visualization, prediction uncertainty was also cumulative based on the model error (SE=2.75).

We produced a further application of the greenness indices in order to estimate the rate of early season growth. In high elevation systems with short growing seasons and very little standing biomass at the time of snowmelt, green-up rate is a major determinant of success. We assessed green-up rate as the daily rate of change in the greenness indices between snowmelt ($G \sim 0$) and peak growth (maximum G). We then correlated this rate with elevation, as well as the biomass accumulation rate (measured as the daily rate of change in grams aboveground biomass between two measurement periods, usually early and peak).

Finally, we explored different multiple regression models to assess our ability to explain and predict GPP utilizing easily measured variables, and importantly, evaluate whether greenness indices aid us in this effort. We used biomass, shrub cover and greenness indices as the base predictors in our model, assuming that the combination of these three factors would be our best proxy for the density of photosynthetic machinery per site. We also assumed that productivity rates would be highly dependent on abiotic conditions (PAR, temperature, available moisture), but after investigating these as potential factors in the model we found them to be poor predictors. This is most likely because the abiotic conditions at the time of GPP measurement are typically close to optimal due to aspects of our protocol. Model assessment included analysis of the relative importance of each variable utilizing the lmg method in the

relaimpo R package, which partitions the R^2 by averaging over different orderings of the variables and with importance metrics scaled to 100% of total R^2 (Groemping 2006; Lindeman *et al.*, 1980).

Results:

The sites in this study followed clear patterns of decreasing temperature and increasing precipitation with elevation that were consistent across years (Table 1). The 2012 growing season was characterized by an exceptionally early melt, and a hot and dry early summer. Conditions in 2013 were fairly similar, although less severe on most accounts. In contrast, 2014 and 2015 were generally wetter and cooler with later snowmelt. 2014 had consistently late melt across elevation, whereas 2015 had more variance in melt dates (Table 1).

We found clear differentiation in growing season dynamics based on site (elevation) as well as year. Mean greenness values were different across elevational sites overall (Kruskal-Wallis, GEI: $\chi^2=886.05$, $df=4$, $p<0.0001$; GCC: $\chi^2=787.80$, $df=3$, $p<0.0001$), and all pair-wise post-hoc comparisons were significantly different ($p<0.0001$), except for the comparison between the two highest elevation sites. Greenness indices were similarly different between the four years of the study (Kruskal-Wallis, GEI: $\chi^2=234.38$, $df=3$, $p<0.0001$; GCC: $\chi^2=235.25$, $df=3$, $p<0.0001$). All pair-wise post-hoc comparisons were significantly different ($p<0.0001$) from each other, except for the comparison between 2012-2013 (GEI) and 2014-2015 (GEI and GCC). Overall, we found higher season-long greenness at the two highest elevation sites most years with some exceptions, notably 2710 m in 2015 (Fig 1).

As predictors of landscape level productivity, both greenness indices did well at characterizing the variation in instantaneous carbon flux measurements. We utilized on-the-

ground instantaneous measurements of GPP within five plots at each site, and used the average of these values to describe the productivity of the site. Between the two indices in single predictor models, GEI explained variation in GPP slightly better (Fig 2. GCC: $R^2 = 0.578$, and GEI: $R^2 = 0.623$). This was likely due to the higher sensitivity of GEI to the green signal, which in this context we assume to represent photosynthetic material (leaves and green stems).

We employed the relationship observed between GPP and GEI to integrate our estimates of productivity over a portion of the growing season at daily intervals. Each daily average GEI value was converted to an approximation of GPP, using the simple linear regression model $GPP = 3.14 + 0.14 * GEI$ (Fig 2b). With this method, we were able to visualize how small differences in instantaneous rates of carbon flux could accumulate quickly over the course of the growing season. Even with the timeframe truncated to the first 40 d of each camera record, we saw very high productivity rates at the high elevation sites (3115 and 3380 m) indicating rapid growth (Fig 3). This method also highlighted the importance of capturing a record of greenness over the entire growing season. The length of active growth varied greatly over the elevation gradient, and the overall productivity of some sites was underestimated (the arid, shrub dominated 2475 m site in particular) without taking into account the full time they were active.

Green-up rate increased with elevation (Fig 4a, $R^2 = 0.736$), indicating a stronger response to the start of the growing season at higher elevations (where growing seasons were shorter). In addition, this pattern suggests a fundamental difference in growth rates based on the relatively strong correlation between the rate of green-up and the rate of biomass accumulation (Fig 4b, $R^2=0.604$). It is important to note that the relationship between green-up rate and biomass accumulation rate was not a 1:1 relationship, indicating that greenness indices captured additional information not directly related to biomass production.

In order to better predict productivity at the landscape level, we modeled GPP with greenness indices as well as aspects of plant composition. Despite performing better in the single predictor models, GEI was slightly worse than GCC in the context of multiple variables. The final model explained 75.3% of the variation found in GPP utilizing log10 transformed biomass, arcsine square root transformed shrub percent cover, and untransformed GCC:

$$GPP = -26 + (11.61 * Biomass) - (7.74 * Shrub Cover) + (24.97 * GCC)$$

Analysis of the relative importance of each factor to the overall R^2 showed nearly equal contribution but highest for GCC (Biomass: 31.1, Shrub Cover: 29.2, GCC: 39.6).

Table 1. Environmental variables for the five elevations from 2012 to 2015. Precipitation and average temperature acquired from PRISM 4km grid cells interpolated to exact location. Snowmelt dates were estimated as the first day of consistent soil temperature $< 0^{\circ}\text{C}$, measured with site-specific soil temperature sensors (HOBO data logger and temperature sensor, Onset).

Year	Elevation	May - Aug Precipitation (cm)	May - Aug Temperature ($^{\circ}\text{C}$)	Snowmelt (Day of year)
2012	2475m	14.12	14.76	75
	2710m	14.40	13.14	84
	2815m	14.33	13.04	99
	3115m	15.21	11.75	121
	3380m	15.32	11.64	135
	Avg:	14.68	12.87	102.8
2013	2475m	15.77	13.90	83
	2710m	17.81	12.24	93
	2815m	18.21	12.14	112
	3115m	23.72	10.79	145
	3380m	23.95	10.67	157
	Avg:	19.89	11.95	118
2014	2475m	15.27	12.97	115
	2710m	16.89	11.44	125
	2815m	17.48	11.33	140
	3115m	26.92	9.87	153
	3380m	27.13	9.76	169
	Avg:	20.74	11.07	140.4
2015	2475m	22.45	12.89	81
	2710m	28.07	11.15	82
	2815m	28.45	11.09	127
	3115m	40.69	9.93	150
	3380m	40.67	9.82	164
	Avg:	32.07	10.98	120.8

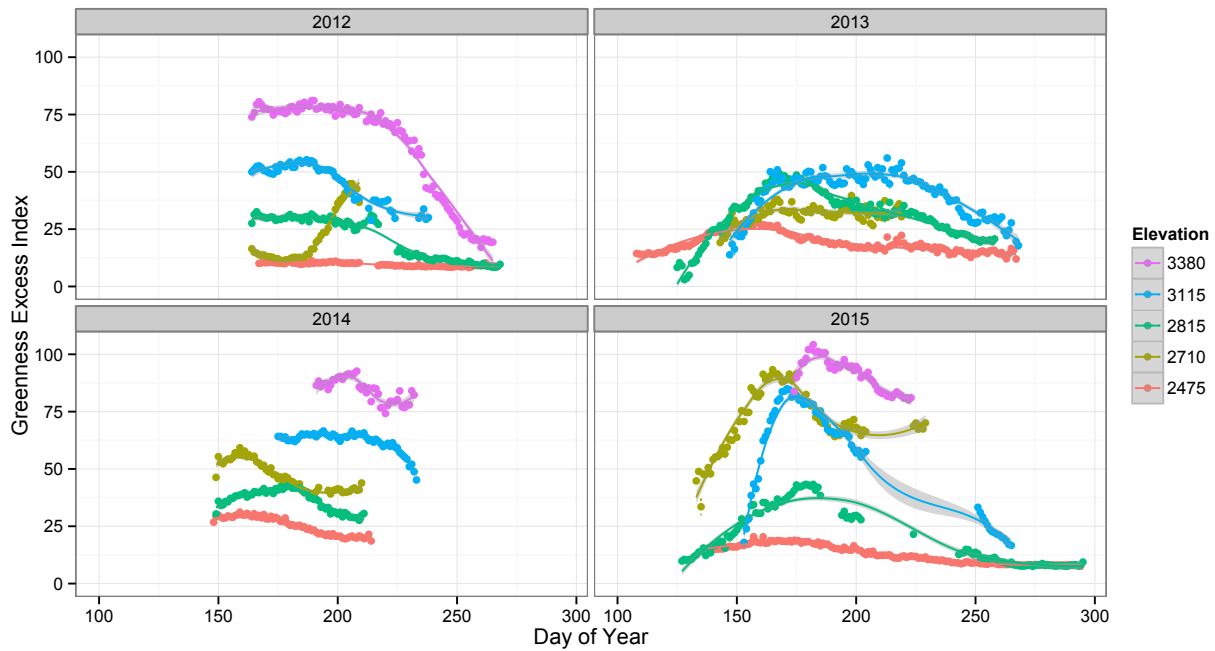


Figure 1. Growing season Greenness Excess Index (GEI) for five sites along an elevation gradient for 2012 – 2015. Notes about data record completeness by year: 2012) cameras deployed mid-season; 2710m site truncated due to damage by cattle. 2013) no data at 3380m due to camera theft. 2014) green-up period missed at high elevation due to site access; cameras removed before true end of growing season to avoid cattle. 2015) gaps between day of year ~200-250 at 2710m, 2815m, and 3115m due to cattle; 3380m truncated due to camera theft.

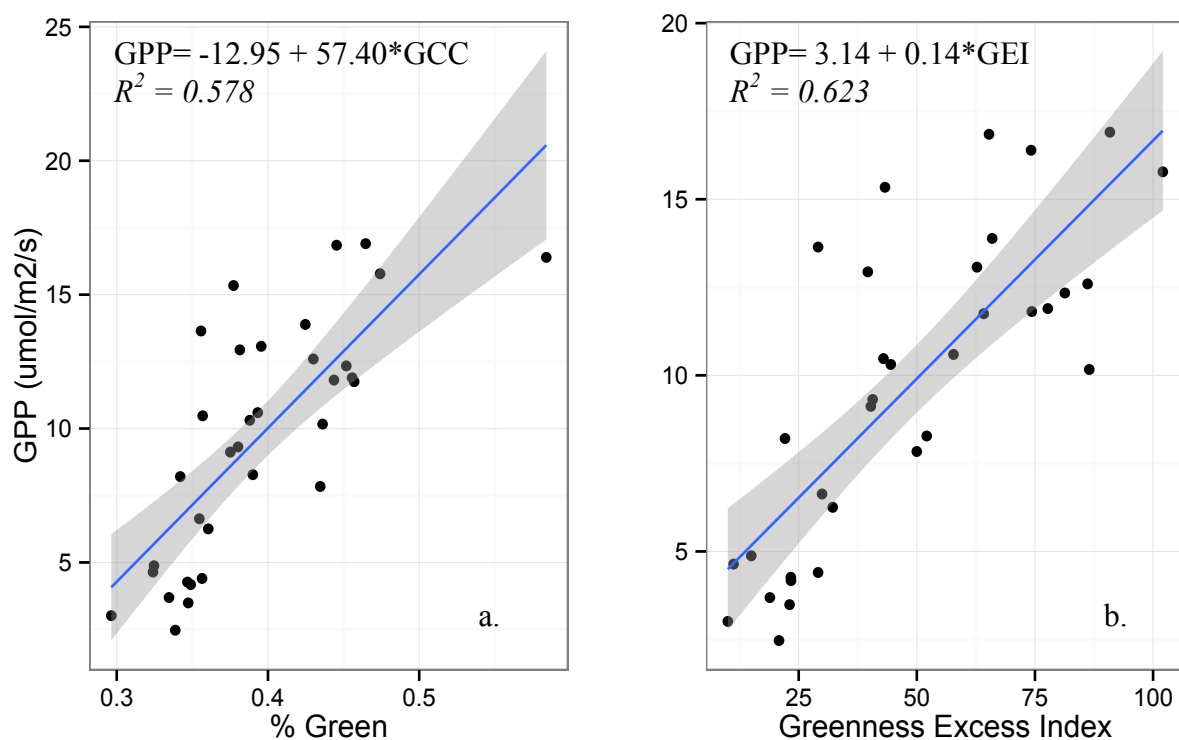


Figure 2. Simple linear regressions estimating Gross Primary Productivity (GPP) by a) Green Chromatic Coordinate (GCC) and b) Greenness Excess Index (GEI). GPP values were measured twice per site per year as daytime instantaneous NEP corrected for the negative contribution of soil respiration. Same-day averages of greenness indices were calculated corresponding to days when GPP was measured.

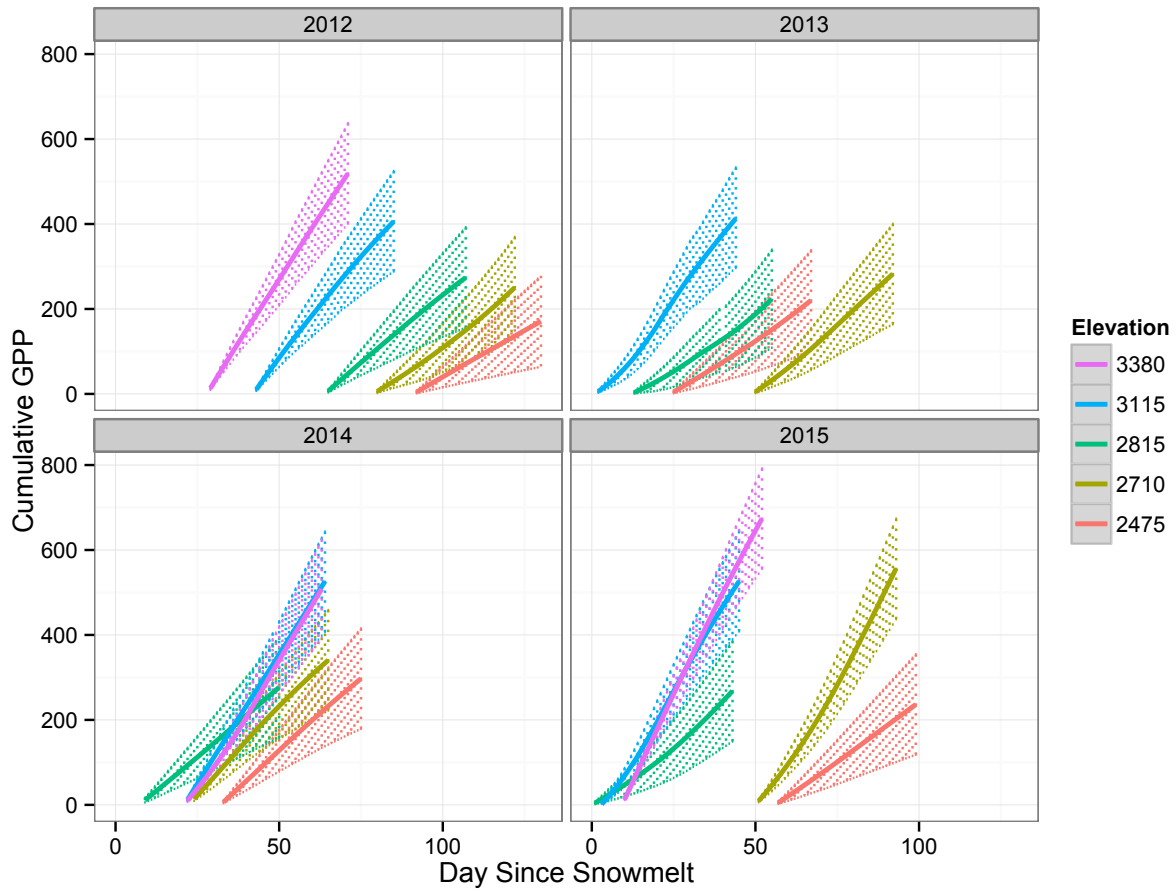


Figure 3. Estimate of cumulative instantaneous GPP ($\mu\text{molC m}^{-2} \text{s}^{-1}$) over a span of the first 40 days of camera operation (40 days is the shortest duration of camera operation). Daily GPP values were generated using the relationship between GPP and GEI described in Fig. 2b. Uncertainty is displayed as the cumulative model error.

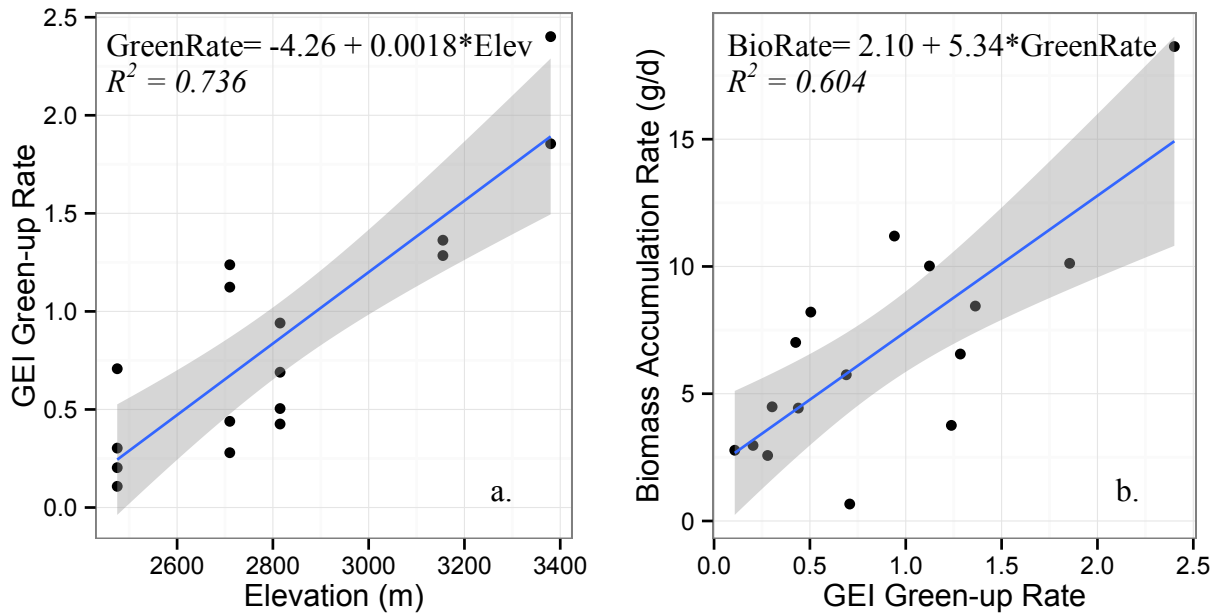


Figure 4. (a) Elevational relationship observed in the daily rate of change of GEI from snowmelt (GEI $\sim$ 0) to peak greenness (maximum GEI). Missing data (n=4) due to data record not capturing true ‘peak’. (b) Relationship between green-up rate described in (a) and biomass accumulation rate, estimated as daily rate of change between early and peak biomass measurements.

Discussion:

Using phenocams, we were able to visualize and quantify greenness patterns within growing seasons as well as across sites and years. Important aspects of productivity dynamics were clearly detected, including peak growth and rate of early season growth. In comparison, on-the-ground visual identification of these dynamics is possible, but remains subjective and difficult to compare year-to-year. This method allowed us to identify a clear elevational greenness pattern that remained fairly consistent between years, with some deviations occurring at mid-elevation sites. There was also high variability for some elevations amount years (timing and magnitude of peak greenness), usually at higher elevations, but also at the 2710 m site. The elevations with the least variability among years (2475 m and 2815 m) were also the locations with the highest site-wide shrub abundance. These patterns suggest that the high elevation, low shrub cover sites may be more vulnerable to extreme events (drought, low winter snowpack) which are more likely to occur according to climate change predictions (IPCC 2013).

Both of the greenness indices examined here, GEI and GCC, were successful predictors of productivity, explaining 62.3% and 57.8% of variation in site-level GPP respectively in single predictor models. This is remarkable given the simple methodology and associated sources of variation, including imperfect matching of camera field of view and productivity measurement areas. The remaining variation in GPP unexplained by the greenness indices is likely due in part to error associated with the methodology, but also confounding visual factors. In particular, peak flowering usually occurred concurrently with our measurements of peak growth at many sites. Therefore, flowers were always a larger visual factor at the peak measurement of GPP, and when we fit separate regression models for the early and peak groups, the early measurement period had a much stronger relationship between the greenness indices and GPP (GEI: $R^2 = 0.78$,

$p < 0.0001$; GCC: $R^2 = 0.65$, $p < 0.0001$) compared to peak (GEI: $R^2 = 0.59$, $p < 0.0001$; GCC: $R^2 = 0.55$, $p < 0.0001$). Thus, much of the residual variation associated with the original single predictor models may have stemmed from the peak season data. Methods have been developed for automated flower counts from digital repeat photography (Adamsen *et al.*, 2000; Crimmins & Crimmins, 2008). This technique could probably be extended to calibrate of the flower color effect on estimates of productivity.

In addition to acting as effective single predictors of GPP, greenness indices continued to provide ecologically relevant information when included in multivariate models explaining GPP. Our final model included GCC, biomass, and shrub cover to explain 75.3% of variation in GPP, with relatively equal contributions to variation explained from each factor. This model offers the possibility of an accurate and uncomplicated method for widespread productivity monitoring that only requires phenocams and relatively simple vegetation surveys. There are still uncertainties that need to be addressed in order to refine our understanding of the relationship between camera-based greenness indices and ecosystem productivity. For example, Yang *et al.* (2014) found a mismatch in the timing of peak forest canopy GCC and peak leaf chlorophyll concentrations (peak GCC occurring before peak chlorophyll), and perhaps as a consequence, several studies have found productivity measures to lag temporally behind greenness indices (Richardson *et al.*, 2007; Richardson *et al.*, 2009; Toomey *et al.*, 2015).

A simple extension of the relationship between greenness indices and productivity is to convert daily average GEI (or GCC) into daily GPP using the equation from the simple linear regression model. With this method, we were able to integrate GPP over the course of a growing season, similar to eddy covariance but without the large investment in multiple flux towers. In this case, we begin to see an elevational pattern in the rate of early season productivity based on

the difference in slopes. Higher elevation sites tended to outstrip lower elevation sites in cumulative productivity when limited to this timeframe. Of course, this ignores the fact that lower elevation sites have longer active growing seasons and their lower daily productivity can accumulate over a longer period of time. This highlights the importance of future work focusing on year round imaging in order to capture full growing season productivity. A full accounting of the growing season would help us assess whether longer growing seasons at lower elevations ultimately catch up to the rapid green-up and high productivity observed for short durations at higher elevation sites. Analysis of cumulative productivity based on camera derived greenness indices is a promising step toward estimating growing season carbon dynamics.

We further investigated the different green-up rates across elevation by estimating a daily rate of change in greenness indices between snowmelt and the observed peak greenness. We found further evidence for increased growth rates at higher elevation. These results support the hypothesis that the short and variable growing season typical of high elevation sites favors specific traits and physiologies associated with higher growth rates (Kerkhoff *et al.*, 2005; Enquist *et al.*, 2007). Inter-annual variation in precipitation was also greatest at the two high elevation sites, underscoring the close relationship between productivity and the interplay of growing season length and soil moisture (Berdanier & Klein, 2011). Testing these GEI-derived green-up rates against aboveground biomass accumulation rates showed a relatively strong correlation, indicating greenness indices can be used to estimate growth rates during the period of rapid, early season green-up.

Near-surface remote sensing using phenocams provides ecologically relevant information, including the timing and rate of green-up and estimates of growing season productivity. The scale and resolution of phenological data generated by cameras can act as a

bridge between on-the-ground observations and measurements and satellite derived vegetation indices. Further efforts toward greater linkages between near-surface and satellite remote sensing will be important to better inform and ground truth regional and global models of phenology and productivity (Fisher *et al.*, 2006; Hufkens *et al.*, 2012). In particular, the temporal and spatial resolution of productivity available with phenocam monitoring can fill the current gap in local detail not present in even the highest frequency and resolution satellite data. This study highlights the potential for using phenocams to monitor growing season carbon dynamics in local and experimental contexts.

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