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Key Points:

- In highly heterogeneous landscapes local abiotic factors generate shifting limitations to plant productivity through space and time
- Interactions between biogeophysical and biogeochemical factors modulate ecosystem responses to perturbations
- Accelerating snowmelt potentially decouples the timing of snow-water availability from plant water demand in particular vegetation patches

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Ecosystem function in complex mountain terrain: Combining models and long-term observations to advance process-based understanding

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Abstract Abiotic factors structure plant community composition and ecosystem function across many different spatial scales. Often, such variation is considered at regional or global scales, but here we ask whether ecosystem-scale simulations can be used to better understand landscape-level variation that might be particularly important in complex terrain, such as high-elevation mountains. We performed ecosystem-scale simulations by using the Community Land Model (CLM) version 4.5 to better understand how the increased length of growing seasons may impact carbon, water, and energy fluxes in an alpine tundra landscape. The model was forced with meteorological data and validated with observations from the Niwot Ridge Long Term Ecological Research Program site. Our results demonstrate that CLM is capable of reproducing the observed carbon, water, and energy fluxes for discrete vegetation patches across this heterogeneous ecosystem. We subsequently accelerated snowmelt and increased spring and summer air temperatures in order to simulate potential effects of climate change in this region. We found that vegetation communities that were characterized by different snow accumulation dynamics showed divergent biogeochemical responses to a longer growing season. Contrary to expectations, wet meadow ecosystems showed the strongest decreases in plant productivity under extended summer scenarios because of disruptions in hydrologic connectivity. These findings illustrate how Earth system models such as CLM can be used to generate testable hypotheses about the shifting nature of energy, water, and nutrient limitations across space and through time in heterogeneous landscapes; these hypotheses may ultimately guide further experimental work and model development.

Plain Language Summary Projecting ecosystem response to environmental change presents enormous challenges that are critical to understand for multiple stakeholders. These projections are complicated by complex interactions between physical drivers, like temperature and precipitation, and biotic agents like plants, animals, and soil microbes. Using long-term observations from a heterogeneous alpine ecosystem and a state-of-the-art land model, we explore how the physical environment shapes ecosystem function and how the function of this ecosystem may respond to climate change. We found that the land model was able to capture observed water, energy, and carbon fluxes from this well-studied alpine ecosystem, lending credibility to our results. Our simulations also indicated that earlier snowmelt and warmer summertime temperatures might drive divergent plant responses across the landscape. Notably, climate change may decouple the timing of snowmelt that delivers critical water resources from periods when plants experience the greatest water demand, thus altering plant productivity. Additionally, this work raises ecological questions that can be addressed with additional experimentation and/or model development.

1. Introduction

The exposure, sensitivity, and adaptive capacity of ecosystems to climate perturbations are difficult to project [*Beniston*, 2003; *De Lange et al.*, 2010; *Turner et al.*, 2003]. As such, developing the ecological knowledge necessary to understand how environmental change may alter ecosystem function remains an outstanding challenge facing ecosystem and Earth system science. Long-term measurements of natural systems and their response to experimental manipulations provide critical insight into potential ecosystem responses to environmental change [*Hinckley et al.*, 2016; *Sternberg and Yakir*, 2015; *Zhu et al.*, 2016]. For example, results from field manipulations suggest that environmental change generates strong effects on plant community composition that mediate the overall ecosystem response to perturbations [*Davis et al*., 1998; *Farrer et al*., 2015; *Smith et al*., 2009; *Suttle et al*., 2007; *Tylianakis et al*., 2008; *Walker et al*., 2006]. These insights can inform heuristic biogeochemical models that illustrate the temporal dynamics of how moisture, temperature, and nutrient availably may limit plant productivity [*Fan et al*., 2016]; but given their high data requirements, the implementation of such models is only possible in well-studied sites with little spatial heterogeneity. More broadly, these types of ecosystem-scale models provide valuable insights into potential biogeochemical responses to environmental perturbations [*Rastetter et al*., 2013] but have limited capacity to simulate the relevant biogeophysical changes that may ultimately alter ecosystem function.

Within and among ecosystems, abiotic factors—especially related to precipitation—are critical drivers of ecosystem productivity and nutrient cycling [*Austin et al*., 2004; *Fisk et al*., 1998; *Vitousek*, 1984]. This control is readily apparent in mountain ecosystems where microscale to mesoscale topography can drive variability in wind redistribution of snow, and small air temperature differences can result in phase changes from solid to liquid precipitation [*Erickson et al*., 2005; *Knowles et al*., 2006]. These fine-scale physical gradients influence both soil temperature and moisture, generate local heterogeneity in alpine vegetation, and ultimately result in complex landscape- and catchment-scale dynamics [*Billings*, 1973; *Litaor et al*., 2008; *May and Webber*, 1982]. Moreover, long-term observational records suggest that higher-elevation sites are experiencing faster rates of climate change relative to lower elevation ecosystems [*Diaz and Eischeid*, 2007; *McGuire et al*., 2012; *Pepin et al*., 2015; *Williams et al*., 2002]. Given the links between abiotic factors and alpine ecosystem function, this study evaluated the potential ecological responses to climate change across vegetation communities that are characteristic of heterogeneous alpine tundra.

Process-based models that represent fluxes of water, energy, carbon, and nitrogen in an internally consistent manner may provide insights into both abiotic and biotic responses to environmental change. The terrestrial components of Earth System Models (ESMs) integrate insight from multiple scientific disciplines to simulate biogeophysical and biogeochemical processes. Although ESMs are typically applied at global scales [*Arora et al*., 2013], and historically have been developed within the geoscience community, increasingly, this class of models applies ecological understanding to ask biologically relevant questions [*Mao et al*., 2016; *Zaehle et al*., 2014]. Moreover, these terrestrial models provide a cohesive framework to investigate biogeophysical and biogeochemical effects of environmental change on ecosystem processes [*Lombardozzi et al*., 2015]. Here we ask if a global-scale model can represent local-scale patterns of water, energy, and carbon fluxes in a heterogeneous mountain environment for the purpose of generating testable projections of potential ecosystem responses to climate change.

The Niwot Ridge Long Term Ecological Research (LTER) site in Colorado, USA, encompasses a variety of different vegetation communities in an alpine tundra environment. Within this ecosystem, fine-scale differences in snow accumulation produce a soil moisture gradient, with conditions ranging from dry and wind-scoured to persistently wet beneath deep snowbeds. Across this moisture gradient, we hypothesized that abiotic factors would generate shifting limitations to plant productivity, with available precipitation limiting soil moisture and productivity in the dry, wind-scoured sites, growing season length (or energy) limiting productivity in the wet, deep-snow sites, and nitrogen (N) limiting productivity in intermediate sites. To test this hypothesis, we conducted single-point simulations with the Community Land Model (CLM, the terrestrial component of the Community Earth System Model) [*Lawrence et al*., 2011; *Oleson et al*., 2013]. First, we tuned and validated the model to represent a single vegetation community for which we had flux tower data, focusing on biogeophysical fluxes. Second, we synthesized results to examine if the model could simulate general patterns of growing season length and plant productivity across all vegetation communities by using a series of single-point simulations with modified precipitation inputs and soil properties (Table 1). Finally, we applied the model in an ecological framework to look at shifting limitations to plant productivity and their potential response to environmental change.

Observations from the study site and projections of future climate change indicate that alpine tundra ecosystems will experience a longer growing season [*McGuire et al*., 2012; *Pepin et al*., 2015]. We hypothesized that in response to an extended growing season, plant productivity would respond negatively in wind scoured sites (due to increased water limitation), respond positively in snow deposition sites (due to release from energy limitation), and remain stable in intermediate sites. To further investigate the ecosystem responsiveness (or

Table 1. The Alpine Vegetation Communities Considered by This Work and Differences in the Corresponding Data Sets Used in CLM Simulations

Community	Soil Depth (cm)[a]	Water Content at Saturation ($mm^3\ mm^{-3}$)	Snow (% Relative to Observations)[b]
Fellfield (FF)	70	0.22	10, 25 MAM
Dry meadow (DM)	100	0.22	10, 25 MAM
Moist meadow (MM)	130	0.44	100
Wet meadow (WM)	100	0.44	75 + runoff simulated from moist meadow
Snowbed (SB)	70	0.22	200

[a] From *Burns* [1980] and applied in CLM simulations for each vegetation community.

[b] Precipitation inputs were altered when observed air temperature was less than 0°C to approximate observed variation in snow depth among observations on the Saddle research site (Figure 4).

stability) to an extended growing season, we performed several model experiments by increasing spring and summer air temperatures and accelerating snowmelt by decreasing snow albedo. In general, this work illustrates how CLM can be used to generate ecological hypotheses that can ultimately guide future experimental work and model development.

2. Methods

2.1. Site Description

The Niwot Ridge LTER encompasses diverse mountain ecosystems that extend from subalpine forest to high alpine lakes, tundra, and talus in the Front Range of the Rocky Mountains near Boulder, Colorado. Several long-term research areas span a prominent east-west oriented interfluve extending 8 km perpendicular to the Continental Divide, including D-1, which is the highest elevation continuously operating long-term (1953 to Present) weather station in North America at 3750 m above sea level (asl; niwot.colorado.edu). Over this record, long-term warming has been observed during the spring (March-April-May (MAM)) and summer (June-July-August (JJA)) months [*McGuire et al.*, 2012]. Meanwhile, precipitation patterns show high interannual variability and a shift with the Pacific Decadal Oscillation in the late 1970s, and evidence of an increase in wintertime precipitation over the past 60 years at D-1 [*Kittel et al.*, 2015].

Alpine tundra vegetation is structured by mesotopographic variability that governs the wind-driven and topography-oriented snow deposition and redistribution patterns [*Billings*, 1973; *Darrouzet-Nardi et al.*, 2012; *Erickson et al.*, 2005; *Litaor et al.*, 2008; *May and Webber*, 1982; *Walker et al.*, 2001]. The size of individual vegetation patches varies with local topography but roughly covers 0.01–1.0 ha. Specifically, fellfield communities are typically wind-scoured and snow-free in the winter—supporting low statured vegetation with open canopies growing on poorly developed, shallow soils (approximately 40–100 cm deep; all soil depth data from *Burns* [1980]). Dry meadow communities also are windblown over much of the winter but often maintain a thin snow cover and are more productive than fellfield sites, with closed canopies of sedges (e.g., *Kobresia myosuroides*) and diverse forbs growing on more developed, deeper soils (70–110 cm). Moist meadows occur where deeper snow cover allows melt to persist later in the year, thus supporting more diverse and productive communities of grasses (*Deschampsia caespitosa*) and forbs (*Acomastylis rossii*) on yet deeper and more well-developed soils (100–160 cm). Wet meadow communities grow at the bottom of hillslopes and in the local depressions where they receive supplemental runoff from snowmelt-derived surface water from upslope positions (especially late melting snowbeds, described next); consequently, soils (40–160 cm deep) typically stay moist throughout much of the growing season and may experience locally lower soil and air temperatures. Finally, snowbed vegetation occurs where deeper snow accumulates and melts out later in the growing season, producing low-diversity, low-productivity areas that have less well-developed soil (25–90 cm). Without the insulating benefits of consistent snow coverage, fellfield and dry meadow communities experience lower wintertime soil temperatures but longer growing seasons (150–200 days), whereas moist meadow, wet meadow, and snowbed communities are relatively more protected from harsh winter conditions by the accumulation of a consistent snowpack but experience a shorter growing season [*Walker et al.*, 2001].

2.2. Model Forcing and Validation Data

The T-Van (3480 m asl) and Saddle sites (3528 m asl) on Niwot Ridge both include these representative plant communities and are located at a horizontal distance of 420 m from each other (−105.586°E, 40.052°N) in the alpine tundra. At T-Van, the Niwot Ridge LTER also maintains what are believed to be the highest operating eddy covariance towers in North America [*Blanken et al*., 2009; *Knowles et al*., 2012]. The two eddy covariance towers at T-Van have been continuously operating since 2007 and largely sample from wind-scoured fellfield and dry meadow vegetation communities. Given the high spatial heterogeneity of the alpine tundra landscape, small patches of wet meadow vegetation on isolated solifluction lobes are also found within the towers' footprint that may be disproportionately important to the net ecosystem exchange of CO_2 fluxes measured at this site [*Knowles et al*., 2016]. We used the meteorological measurements from T-Van as inputs needed to force CLM simulations for all vegetation communities. These included half-hourly mean horizontal wind speed, air temperature, barometric pressure, and relative humidity. Other measurements from the towers were used to validate simulations of fellfield communities (e.g., net radiation, latent and sensible heat fluxes, soil temperature, and soil moisture).

We used precipitation measurements from the Saddle to force CLM simulations, while measurements of snow depth, plant community composition, and plant productivity [*Bowman and Seastedt*, 2001] were used to more broadly evaluate the representation of different vegetation communities. Continuous climate data collection was established at the Saddle in 1981 [*Litaor et al*., 2008]. Roughly three-quarters of precipitation falls as snow in the alpine tundra on Niwot Ridge [*Knowles et al*., 2015b]. Strong winds redistribute the snow, and this redistribution of snow complicates accurate measurements of wintertime precipitation [*Williams et al*., 1998]. Over the simulation period (calendar years 2008–2013), annual precipitation recorded daily at the Saddle totaled 1030 ± 167 mm yr^{-1} (mean $\pm 1\,\sigma$). These data were corrected for precipitation overcatch due to blowing snow during clear-sky conditions (e.g., during the days following a storm) following *Williams et al*. [1998]. To provide the half-hour precipitation required to run CLM, we proportionally allocated the daily Saddle precipitation measurements to the half-hourly precipitation record from the U.S. Climate Reference Network (USCRN; data from https://www1.ncdc.noaa.gov/pub/data/uscrn/products/subhourly01/; accessed February 2015), measured nearby (4 km) at the lower elevation (3050 m asl) C-1 site. On days when the Saddle record reported measurable precipitation, but the USCRN record did not, we distributed daily precipitation evenly across the day for model simulations. We recognize that in warmer and more rain-dominated systems it may be advisable to concentrate simulated rain events over a shorter period to ensure proper infiltration into soils. Indeed, over our 6 year record approximately one third of the >1500 precipitation events were only recorded at the Saddle; however, only 86 of these (roughly 5%) took place during the growing season. Instead, days when measurable precipitation was only recorded at the Saddle tended to occur in the winter, when the higher-elevation site would record snow events (or blowing snow) that were not recorded at the lower elevation site.

Given the importance of snow in structuring vegetation communities, we altered incoming precipitation and soil characteristics to span the range of snow accumulation and resulting soil moisture conditions for each vegetation community (Table 1). Individual single-point simulations were carried out for each of the five vegetation communities, with the aim of broadly characterizing the variation in abiotic conditions experienced in different landscape positions (Figure 1). Simulations were compared with independent data sets from the Saddle research site that are publically available through the Niwot Ridge LTER [*Bowman and Seastedt*, 2001] (niwot.colorado.edu, accessed July 2015). Since 1982, snow depth data have been manually collected every 1–2 weeks from 88 gridded points spaced at 50 m distance on the Saddle, providing a temporal snapshot of the snowpack evolution across a topographically heterogeneous 17.5 ha landscape. The dominant plant communities have also been also identified at these points [*Spasojevic et al*., 2013], and biomass harvests conducted at the end of the growing season provide an estimate of annual aboveground net primary productivity (ANPP) [*Walker et al*., 1994]. We also used summary estimates of ANPP, belowground net primary productivity and standing plant biomass [*Bowman and Fisk*, 2001] to synthesize the ability of this general, global model to capture local ecosystem heterogeneity across Niwot Ridge. To accomplish this synthesis, we binned these observations by vegetation type and compared results from the five individual point simulations (described below).

Figure 1. Photograph showing part of the Saddle research site with associated vegetation communities including fellfield and dry meadow (foreground), moist and wet meadows (near the research station), and late melting snowbed (background). For comparison inset shows typical wet meadow vegetation at the site. Main photo credit W. Wieder, inset J. Smith.

Finally, the CLM also needs information about incoming shortwave radiation, but given gaps and errors in incoming shortwave radiation measurements collected at the nearby Subnivean laboratory (individual radiation streams are not measured at T-Van), we forced CLM with incoming shortwave radiation measured from the nearby AmeriFlux tower site (US-NR1) in the subalpine forest at C-1 [*Burns et al*., 2016; *Turnipseed et al*., 2002], which showed good agreement with the higher-elevation measurements. All input data were gap-filled by using the R package REddyProc [*Reichstein and Moffat*, 2014]. We also estimated gross primary productivity (GPP) and ecosystem respiration from observational data by using the REddyProc package; briefly, the package uses a sliding window to calculate temperature sensitivities of ecosystem respiration, and subsequently GPP, from short-term data (for additional details see *Reichstein et al*. [2005]). We summed half-hourly data into daily totals for CO_2 fluxes and estimated annual GPP from T-Van observations as the sum of positive daily fluxes during the growing season (here 1 May to 1 October).

2.3. Model Description

Although CLM is typically run at global scales [*Lawrence et al*., 2011], it can also be run in a single-point configuration that approximates the footprint of an eddy covariance tower, for the purpose of more rapidly testing models and/or generating ecological hypotheses [*Bonan et al*., 2012; *Bonan et al*., 2011; *Hudiburg et al*., 2013; *Hou et al*., 2012; *Stöckli et al*., 2008; see also *Dietze et al*., 2011]. The CLM provides global input data sets, but when running simulations for a specific site, site-level modifications are necessary to accurately represent local conditions. Accordingly, we ran a series of single-point simulations of CLM4.5 with active biogeochemistry, which includes vertically resolved soil biogeochemistry [*Koven et al*., 2013]. Single-point simulations do not have a defined spatial resolution, but in five different single-point simulations we modified precipitation inputs and soil properties in order to represent the particular abiotic conditions in each of the tundra vegetation communities (Table 1). In each single-point simulation we used the default parameterization for the arctic C3 grass plant functional type [*Oleson et al*., 2013] with alterations to better represent site characteristics and modification to particular parameters in the model that are described in section 2.4, below.

We spun up all simulations in "accelerated-decomposition" mode for 500 years by cycling over the first four years of forcing data (2008–2011) and allowed C and N pools in soils and vegetation to equilibrate for another 500 years [*Oleson et al*., 2013; *Thornton and Rosenbloom*, 2005]. Control simulations for each vegetation type were conducted over the experimental period (2008–2013) by using observed atmospheric conditions. All simulations were standard, year 2000 cases that were run with fixed CO_2 concentrations (367 ppm CO_2), as well as aerosols and N deposition that are read in from a coarser resolution data set [*Oleson et al*., 2013]. Time invariant N deposition estimates from this forcing data set align well with annual wet and dry N deposition totals observed at the site (0.48 and 0.43 g N m^{-2} yr^{-1}, respectively) [*Mladenov et al*., 2012]. Results were validated with observations at various spatial and temporal scales that included comparing flux tower data from T-Van with fellfield simulations. We assumed that fellfield simulations would best approximate the observed fluxes of net radiation, latent heat flux, sensible heat flux, and GPP at T-Van since the footprint of the T-Van tower is dominated by fellfield vegetation [*Blanken et al*., 2009]. We calculated the monthly evaporative fraction from observations and models by dividing latent heat fluxes by the sum of latent and sensible heat fluxes. Subsequently, we compared results from each of the five single-point simulations intended to represent particular vegetation communities to the mean annual evolution of snow depth and annual estimates of plant productivity to long-term observations from the Saddle research site at Niwot Ridge.

2.4. Site-Specific Configuration

We made several adjustments to match site-specific conditions in our simulations, which included changes to precipitation, soil properties, and vegetation characteristics. Where the model failed to capture observed patterns in soil moisture or plant productivity, we also made several modifications to the parameterizations for soil hydrology and photosynthesis from the default global model. In this section, we describe the adjustments and modifications made to the precipitation inputs and to the representation of soils and vegetation in our point simulations.

To approximate patterns of snow accumulation between vegetation communities, we adjusted incoming precipitation when observed air temperatures were below freezing (summarized in Table 1). While fellfield and dry meadow sites are typically snow-free during the winter, higher-density snow associated with wet spring storms may remain on the ground for several days at a time, especially when wind speeds are lower (J. Knowles, personal observation). Thus, fellfield and dry meadow simulations received 10% of the observed Saddle precipitation under below freezing conditions, except in the spring (MAM) when they received 25% of observed precipitation. Moist meadow and snowbed simulations received 100% and 200% of observed wintertime precipitation, respectively. Snow depth measurements from the Saddle indicate that wet meadow vegetation experiences shallower snow cover than moist meadow vegetation; thus, wet meadow simulations received 75% of observed winter precipitation, but they also received supplemental runoff from moist meadow ecosystems located upslope, which was added to the precipitation input data set for the wet meadow simulations. Atmospheric forcing data are publically available at http://niwot.colorado.edu/data/data/community-land-model-version-4.5-clm4.5-simulations-of-water-energy-and-car.

Although we note high spatial heterogeneity in edaphic properties across plant communities that characterize Niwot Ridge [*Burns*, 1980], all simulations occurred on silt loam soils prescribed with 39% sand and 23% clay [*Seastedt*, 2001]. To better represent mean soil depths for different vegetation communities [*Burns*, 1980] (Table 1), we adjusted aspects of the soil hydrology and the depth to bedrock [*Swenson and Lawrence*, 2015] (Table 1). CLM still lacks a representation of rocks in soils, which are more common in poorly developed soils and can make up a significant fraction of the soil volume [*Burns*, 1980]. To account for the effective decrease in soil porosity due to rocks, we reduced the volumetric soil water at saturation as calculated by the model by 50% for vegetation that typically grows on these poorly developed soils (fellfield, dry meadow, and snowbed). We eliminated subgrid elevation effects on air temperature and snowmelt variability [*Swenson and Lawrence*, 2012] in these point-scale simulations because they are not appropriate for the spatial scale that our simulations approximate (~0.01–1.0 ha.). Finally, in preliminary simulations, surface soils did not dry out as quickly as observations from T-Van suggest; thus, we decreased the dry surface layer resistance to soil evaporation [*Swenson and Lawrence*, 2014] that is calculated by the model by 66% in all simulations (Appendix A).

Finally, we adjusted foliar C:N ratios and C allocation to leaves and fine roots to better match the local observations [*Bowman and Seastedt*, 2001; *Fisk et al*., 1998] (Appendix A). Preliminary simulations showed unrealistic midday declines in summer photosynthesis rates and the unrealistic phenological behavior of plants growing under deep snowpack, requiring additional modification to the code. To produce a better diurnal cycle of GPP, we removed effects of canopy relative humidity on the CLM Ball-Berry equation [*Oleson et al*., 2013]. We also modified the phenological behavior of the model so that plants only began accumulating growing degree days that trigger leaf onset when surface soil temperatures were above 4°C—instead of above 0°C, as in the default model. All CLM output is available at http://niwot.colorado.edu/data/data/community-land-model-version-4.5-clm4.5-simulations-of-water-energy-and-car.

2.5. Experimental Design

After validating model results with observations from the T-Van tower and Saddle sites (section 2.2), we investigated shifting patterns of limitation on plant productivity. In each year, we calculated the total growing season length (defined in the model as the number of days with GPP $>$ 0) for each vegetation community. We also calculated the average soil moisture stress and nitrogen (N) limitation experienced by plants. Briefly, CLM calculates soil water stress as a linear function between zero and one that relates photosynthetic stress to soil matric potential (transpiration beta factor (BTRAN)) [*Oleson et al*., 2013]. Similarly, the model calculates total plant and microbial demand for N and allocates the "available" inorganic N proportionally to these demand terms. Subsequently, the model calculates actual photosynthesis that is realized after accounting for N limitation (fraction of potential GPP (FPG)) [*Oleson et al*., 2013]. Here we subtracted simulated growing season values of BTRAN and FPG from one, so that higher values indicate stronger water stress and N limitation on plant productivity, respectively.

We conducted two parallel experimental simulations to investigate the effect of an extended summer growing season on plant productivity across all five vegetation communities. To simulate these effects, we (1) increased air temperature by 2°C over observations during the spring and summer (1 March to 31 August) and (2) accelerated snowmelt at the end of winter by decreasing snow albedo. Field trials demonstrate that experimentally manipulating snow albedo provides a cost-effective, reliable way to accelerate snowmelt in remote mountain landscapes [*Blankinship et al*., 2014], and pilot studies at Niwot Ridge demonstrate that adding inert black sand to the top of the snowpack in early May can accelerate snowpack by 10–14 days. We replicated this experimental approach by increasing black carbon deposition inputs to the model by 0.3 mg m^{-2} s^{-1} during the month of May. Our motivation for these simulations was to explore potential differences in the abiotic conditions and vegetation response to ongoing environmental change (warming) versus those resulting from proposed experimental manipulations (black sand). We compared extended growing season simulations to control cases by focusing on both the biogeophysical effects (snowmelt, growing season length, soil moisture, and soil temperature) and biogeochemical responses including N limitation and biomass (which integrate changes in productivity and autotrophic respiration) of both experimental scenarios.

3. Results and Discussion

We present our main findings in three sections focusing on model calibration and validation, synthesis, and application. We discuss relevant ecological considerations, describe model strengths and limitations, and identify relevant data gaps. First, we calibrate and validate fellfield vegetation simulations with observations from the T-Van research site. Next, we synthesize observations and simulations to independently compare snow and productivity dynamics across all simulated vegetation communities. Finally, we apply our simulations in an ecological context to determine limitations on plant productivity and their potential shifts under extended growing season simulations.

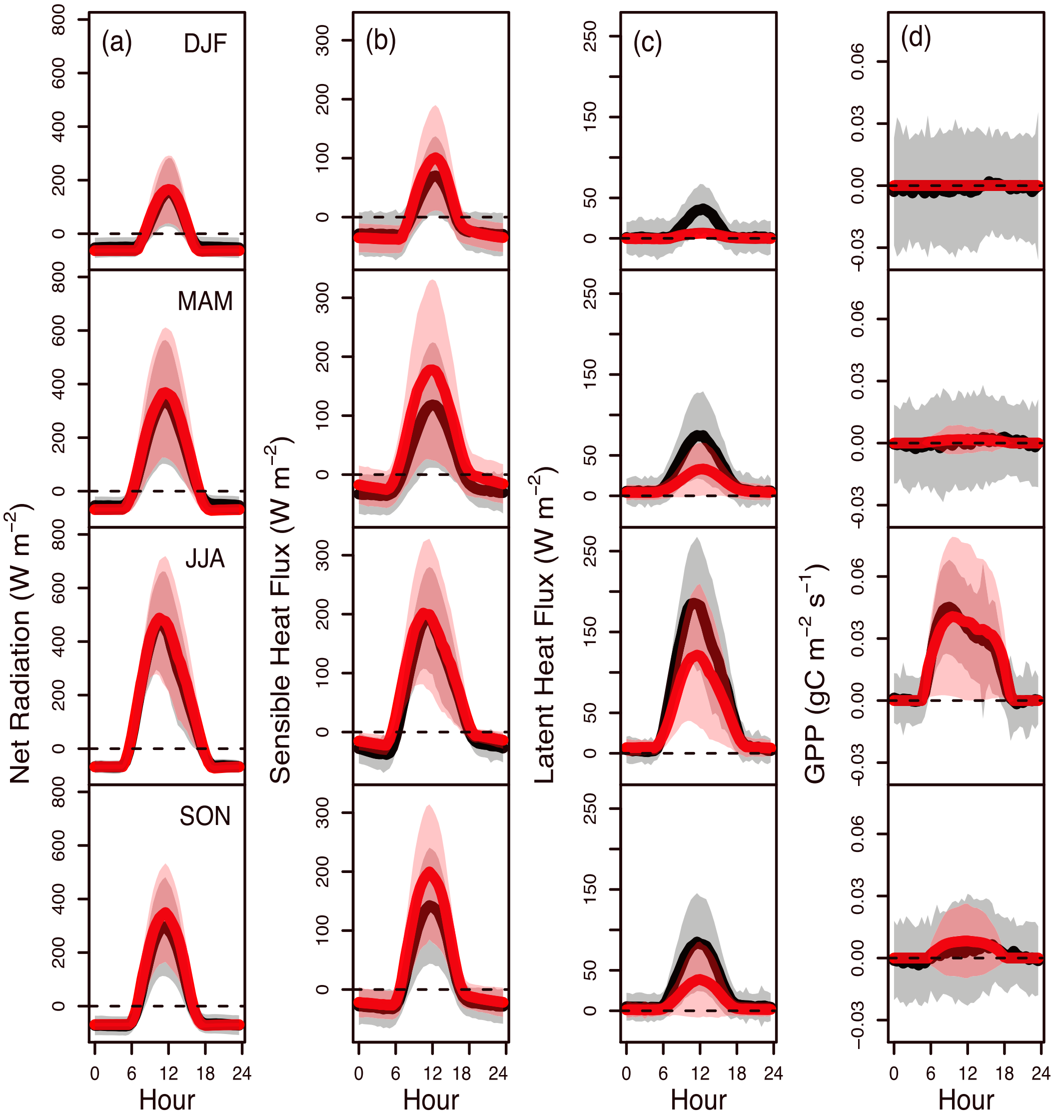

Figure 2. Mean diurnal fluxes (±1σ) from T-Van observations and single-point CLM simulations configured for fellfield vegetation (black and red lines, respectively), showing (a) net radiation, (b) sensible heat flux, (c) latent heat flux, and GPP for each season during the entire study period (2008–2013).

3.1. Model Calibration and Validation: Flux Tower Measurements and Fellfield Simulations

Energy fluxes in the fellfield simulations effectively matched observations from T-Van (Figure 2). Simulated net radiation correlated well with observed values throughout the year ($r = 0.90$), with the highest correlation during the snow-free summer months (JJA; Figure 2a). Although the annual sensible heat fluxes from the model showed good agreement with observations ($r = 0.77$), CLM shows a high bias in sensible heat flux that is balanced by a low bias in the simulated latent heat flux (Figures 2b and 2c, respectively); this was most evident during the spring (MAM). Consequently, CLM underestimated the monthly evaporative fraction during the growing season (1 May to 30 September), which averaged 0.61 ± 0.10 and 0.37 ± 0.18 for observed and modeled values, respectively (mean ± 1σ). Low biases in latent heat fluxes (Figure 2c) were compensated by a high bias in ground heat fluxes simulated by CLM, relative to the T-Van observations (data not shown).

Elsewhere, CLM4.5 simulations show systematic underestimation of the evaporative fraction, and this bias extends to other land models [*Best et al.*, 2015], suggesting that the partitioning of water fluxes to evapotranspiration and runoff may overestimate runoff fluxes. This bias merits consideration as more sophisticated two-dimensional representations of catchment-scale hydrology are developed in models designed to investigate hydrologic landscape connectivity and water resource availability [*Livneh et al.*, 2015]. The challenge may be especially acute in systems with a low leaf area index (LAI), which place extra emphasis on the soil calculations and may explain the biases in simulated ground and latent heat fluxes (Figure 2). On balance, however, our results seem promising when one considers the observational uncertainty related to wintertime precipitation [*Williams et al.*, 1998], incoming solar radiation, and lack of energy budget closure [*Blanken et al.*, 2009; *Knowles et al.*, 2012; *Turnipseed et al.*, 2002].

Our simulations rely on simplifying assumptions made by the application of a global model for these ecosystem-level simulations, with relatively limited information about local edaphic and vegetation characteristics (Table 1 and Appendix A). Despite room for improvement, especially related to partitioning the evaporative fraction of the surface energy balance, these results suggest that CLM broadly captures the daily and intra-annual and interannual variation in energy fluxes for fellfield vegetation on Niwot Ridge. We contend that credibly representing ecosystem responses to environmental change should include representations of the physical environment, but this capability is typically absent from most ecosystem biogeochemistry models.

The ability of CLM to simulate appropriate energy fluxes at T-Van is notable given the model's strong dependence of energy fluxes on leaf area index (LAI). For example, *Bonan et al.* [2011, 2012] prescribed LAI in the single-point simulations over forests that were used to validate the canopy fluxes applied in CLM4.5. This is a more tightly constrained configuration of the model that seeks to isolate biogeophysical representations, especially in summer. By contrast, here we applied simulations with active biogeochemistry that generated prognostic estimates of LAI. Simulated LAI estimates averaged 0.6 during the growing season across all simulated years, which is close to the observed fellfield LAI on Niwot Ridge of 0.87 $m^2\,m^{-2}$ [*Knowles et al.*, 2012]. In "big-leaf" models like CLM, several parameters can adjust LAI including specific leaf area (SLA), plant C allocation, and photosynthesis rates. Given evidence for increased belowground C allocation in alpine and arctic vegetation, we increased C allocation to fine roots in these simulations [*Bowman and Fisk*, 2001; *Fisk et al.*, 1998; *Iversen et al.*, 2015], but we did not adjust parameter values for SLA from the default version of the model (0.030 $m^2\,g^{-1}$ C) [*Oleson et al.*, 2013], although this value may be too high for vegetation at the site [*Spasojevic and Suding*, 2012]. We are not aware of data on maximum rate of carboxylation (V_{cmax}) from alpine vegetation communities at Niwot. We also do not assume any differences in plant physiological traits among vegetation communities. To improve modeled estimates of the energy budget on Niwot Ridge, future work could more carefully investigate the range of values for these parameters observed within and among different plant communities on Niwot Ridge.

The average diurnal cycle of GPP showed fairly good agreement with observations (Figure 2d). Nitrogen limitation of leaf photosynthesis CLM4.5 produces unrealistic declines in GPP throughout the day. Our simulations show some evidence for this behavior in the summer, although not as drastically as in *Ghimire et al.* [2016]. Specifically, estimates of GPP at T-Van totaled 174 ± 49 and 152 ± 37 g C $m^{-2}\,yr^{-1}$ for the model and observations, respectively ($r = 0.86$ for daily GPP averaged over all years; Figure 3a). Given methodological differences in how GPP was calculated, these observed values are slightly higher than estimates (124 ± 14 g C $m^{-2}\,yr^{-1}$) [*Knowles et al.*, 2015a]. Figure 3 shows the mean annual cycle of GPP, soil temperature, and soil moisture (both at 10 cm depth, $r = 0.98$ and 0.71, respectively, for estimates averaged over all years). Collectively, this indicates that CLM adequately matched the seasonal cycle of plant productivity and soil conditions at T-Van. We are encouraged that with modifications, a model like CLM can simulate the diurnal and annual cycles of water, energy, and C fluxes for a unique environment such as alpine fellfield tundra (Figures 2 and 3).

Throughout the growing season, simulated GPP showed a greater sensitivity to soil moisture than the observations suggested (Figure 3). In the fellfield simulations, summertime soil moisture was strongly controlled by summer precipitation. This generated high interannual variability of GPP in the model and low correlation between annual GPP estimates from CLM and T-Van ($p = 0.34$, $r = -0.47$). The mismatch of interannual GPP variability between observations and CLM in the fellfield simulations could reflect the influence of other vegetation communities within the fetch of the T-Van towers, especially small areas of wet meadow vegetation that represent biogeochemical hot spots on the landscape [*Knowles et al.*, 2016]. These areas are likely to be hydrologically buffered from interannual variation in precipitation and may smooth the annual GPP observations.

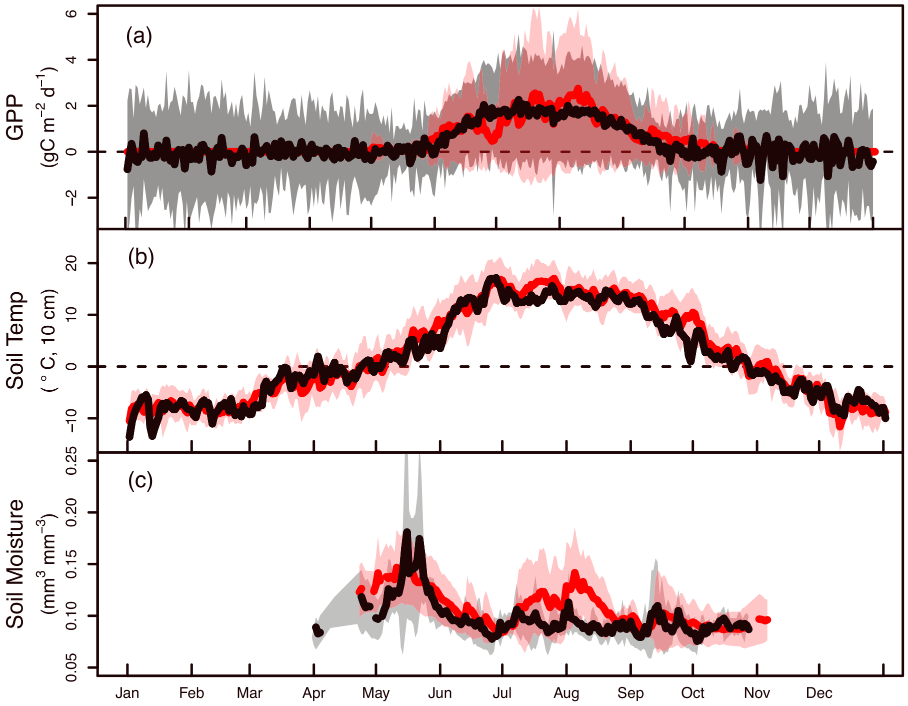

Figure 3. Mean annual cycle (±1σ) of T-Van observations and single-point CLM simulations configured for fellfield vegetation (black and red lines, respectively), showing (a) GPP, (b) soil temperature, and (c) volumetric soil moisture (both 10 cm depth). Results are calculated from daily means over the 6 year study period. Soil moisture results are clipped to periods when observed (or simulated) soil temperature was above freezing, because time domain reflectometry probes do not provide reliable observations in frozen soils.

Alternatively, plant physiology traits in CLM may not be appropriate for local vegetation characteristics at T-Van. The generic parameterization of plant growth strategies for arctic grasses in CLM may afford a more rapid response to favorable growing conditions than fellfield communities actually exhibit. Specifically, alpine plants may express more conservative growth strategies [*Reich*, 2014] in order to survive the fellfield's extreme environmental conditions, which are not represented in the model. New model structures that include plant functional traits [*Fisher et al*., 2015] and plant hydrologic stress [e.g., *Sperry et al*., 2016] are slated for future releases of CLM (D. Kennedy and D. Lawrence, personal communication). Together, these developments offer promising avenues with which to refine the growth strategies exhibited by plants, as well as the hydrologic stress they experience in different environments. Indeed, if environmental change drives indirect shifts in plant community composition [*Farrer et al*., 2015], then indirect effects of environmental change on plant productivity would only be expected if this also drove meaningful shifts in plant physiological traits [*Fisher et al*., 2015]. To our knowledge, there are no data to evaluate this hypothesis from Niwot Ridge or other alpine ecosystems; however, better characterization of plant functional traits is an aim of ongoing measurements at the Niwot Ridge LTER.

Edaphic heterogeneity occurs at (sub) meter scales and strongly influences local hydrological processes; however, CLM typically operates at much coarser resolutions (~10,000 km^2), leading to challenges in accurately representing subgrid variability in numerically tractable ways [*Lee et al*., 2014; *Swenson and Lawrence*, 2012]. Although we apply variable-depth soils in our simulations [*Swenson and Lawrence*, 2015], and take measures to approximate the effect of rocky soils in reducing soil water holding capacity (Table 1), the particular representation of soil hydrology in the model still may not accurately reflect hydrologic dynamics and plant water availability in complex terrain. This issue may be especially acute at the low LAI values (<1 m^2 m^{-2}) that are characteristic of this site. For example, the magnitude of the soil moisture response to summer precipitation suggests that rates of infiltration and retention simulated by CLM may be too high for local edaphic conditions (Figure 3c). Moreover, single-column simulations can only crudely represent the potential effects of landscape connectivity, in particular the supplemental water inputs received from upslope landscape positions (discussed in the section 3.3, below). While current CLM development

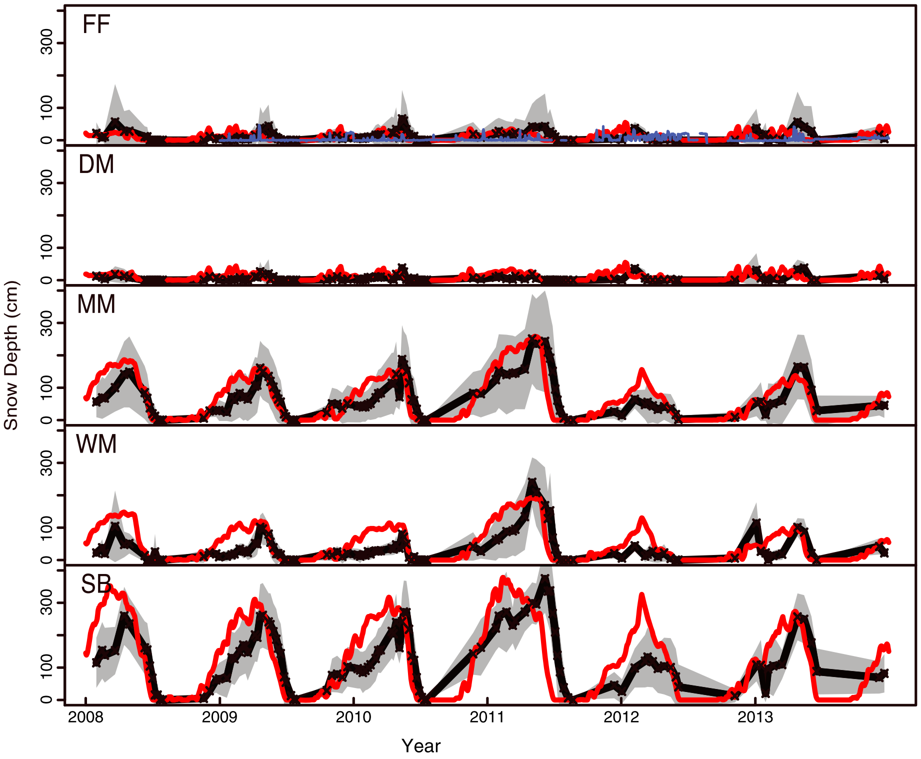

Figure 4. Observed and simulated snow depth from 2008 to 2013 for each of five representative alpine tundra vegetation communities on Niwot Ridge. Biweekly observations from the 88 points in the Saddle research site were measured with snow stakes and averaged for each vegetation community (black line ± 1σ). Starting in 2009, the T-Van towers continuously collected data on snow depth by using an ultrasonic snow depth device, and daily means are shown as the blue line in the top plot. CLM simulations (red line) were forced with alterations to Saddle precipitation observations (summarized in Table 2). Simulations are intended to replicate conditions for fellfield (FF), dry meadow (DM), moist meadow (MM), wet meadow (WM), and snowbed (SB) vegetation communities.

focuses on subgrid representation of soil hydrologic fluxes, the development and application of more site-specific hydrological models may be necessary in order to capture local hydrologic and biogeochemical responses to environmental change, especially related to landscape connectivity. We recognize that in order to address particular site-level questions the development of hillslope hydrology models will require a greater data density to characterize spatial heterogeneity in the physical soil environment and the spatiotemporal heterogeneity of its hydrologic state. This may be more easily accomplished outside of the CLM framework.

3.2. Synthesizing Simulated and Observed Patterns Across Vegetation Communities

As intended, alterations to wintertime precipitation generated maximum snow depth totals that broadly reflected the variation observed both among plant communities and between different years (Figure 4 and Table 2). Good agreement between the timing and rate of snowmelt suggests that the representation of snow physics and energy balance were handled well in the model. In our simulations, the fellfield and dry meadow received just over one third of annual precipitation as snow, developed a thin or intermittent snowpack, and were typically snow-free by late May. This simplified precipitation alteration, designed to approximate the effects of blowing snow, may still underestimate the magnitude of late spring storms that represent an important moisture source to these otherwise snow-free parts of the landscape. By contrast, moist and wet meadows received considerably more snow (Table 2) and developed a consistent ~1 m thick snowpack that persisted until mid-to-late June (Figure 4). Finally, snowbed communities developed a snowpack that was several meters thick and did not melt out until late June or early July. The timing of simulated snowmelt generally followed the observations, with the exception of 2011, when a larger-than-average snowpack melted out too quickly in the model. Although the model was forced to match annual maximum snow depths measured across the Saddle through simple adjustments to wintertime

Table 2. Characterization of Precipitation Inputs and Snow Dynamics for the Five Alpine Vegetation Communities at Niwot Ridge (Mean ± σ)[a]

Community	Rain (mm)	Snow (mm)	Max Snow Depth (cm) CLM	Max Snow Depth (cm) Obs.	Snow Melt Off (Day of Year) CLM	Snow Melt Off (Day of Year) Obs.
Fellfield (FF)	241 ± 71	137 ± 37	40 ± 9	50 ± 11	143 ± 30	164 ± 32
Dry meadow (DM)	241 ± 71	137 ± 37	40 ± 9	29 ± 9	143 ± 30	144 ± 28
Moist meadow (MM)	241 ± 71	790 ± 160	179 ± 40	163 ± 60	175 ± 10	189 ± 23
Wet meadow (WM)	879 ± 235	599 ± 121	137 ± 31	114 ± 67	170 ± 10	170 ± 17
Snowbed (SB)	241 ± 71	1560 ± 330	327 ± 37	259 ± 77	180 ± 10	197 ± 29

[a] Total rain and snow values summarize different precipitation regimes that were used to force the model. Maximum snow depth observations for each vegetation community were averaged at each sampling time, from which maximum annual snow depth was calculated. The maximum annual snow depth for CLM was calculated by using a 5 day running mean. Snow melt off dates are the first snow-free day reported in the model, or the lowest mean snow total observed on the Saddle research site (after maximum snow depth for each year).

precipitation, we made no modifications to snow physics or snow hydrology in CLM4.5—suggesting that the model effectively represented the spatiotemporal variability in snow hydrology that principally structures vegetation communities across Niwot Ridge.

Snowpack determined patterns of plant productivity among vegetation communities in both simulations and observations. For example, as annual snow accumulation increased from fellfield to wet meadow vegetation, plant productivity also increased; however, a short growing season curtailed productivity from the snowbed vegetation communities (Figure 5 and Table 2) [*Bowman and Fisk*, 2001]. Although observations of GPP on Niwot Ridge are limited to fellfield communities, GPP patterns among vegetation communities generally correspond to observed net primary productivity (NPP) and aboveground NPP (ANPP, Figure 5). Even at this LTER site, there are relatively sparse measurements that are relevant to this study taken consistently across all vegetation communities, but annual estimates of ANPP are determined from biomass clippings taken across the Saddle (Figure 5c). These ANPP data clearly show that CLM underestimates ANPP by 30–40 g C m^{-2} yr^{-1} (approximately 35–75%) across all vegetation communities. We note the difficulty in accurately measuring ANPP in the fellfield, given the large amount of long-lived woody vegetation that characterizes the cushion plants in this community. Better model agreement with ANPP observations could be accomplished by modifying plant C allocation patterns toward greater aboveground productivity; however, our choice of root to leaf C allocation seems reasonable (Appendix A). Higher productivity could also be simulated by increasing LAI (via parameter changes to SLA or LMA) or by increasing leaf level photosynthesis rates (e.g., V_{cmax}), although both of these could result in GPP in excess of the field observations (Figure 3a). In sum, there are numerous ways to modify parameters in CLM, but relatively sparse data to inform the most appropriate modifications to the model. Our aim was to determine if the global parameterizations in CLM can adequately capture the local behavior related to growing season length and plant productivity among vegetation communities at Niwot Ridge. Based on results in Figures 4 and 5, we conclude that it can and we utilize these results to focus on shifting patterns of resource limitation among communities and their projected responsiveness to an extended growing season in the future.

3.3. Model Application: Limitations to Plant Productivity and Response to Extended Summer

We hypothesized that the hydrologic and edaphic gradients that we observed (and modeled) over short horizontal distances in this ecosystem would result in different limiting factors on productivity across the corresponding vegetation community gradient. With respect to temperature limitation, soils (0–50 cm) in fellfield and dry meadow ecosystems remained frozen (−5 to −10°C) from December through April (Figure 3b) due to the absence of an insulating snowpack. However, with lower soil moisture and a longer snow free period, the fellfield and dry meadow soils also warmed more quickly in the spring and summer, with soil temperatures (0–50 cm) reaching 15–20°C between June and September. By contrast, soil temperature variability was reduced in the more snow-dominated locations, as evidenced by wintertime soil temperatures (0–50 cm) close to 0°C and summer soil temperatures of 10–15°C. Notably, snowbed soils simulated by CLM remained unfrozen for nearly the whole winter (except for a brief period in the

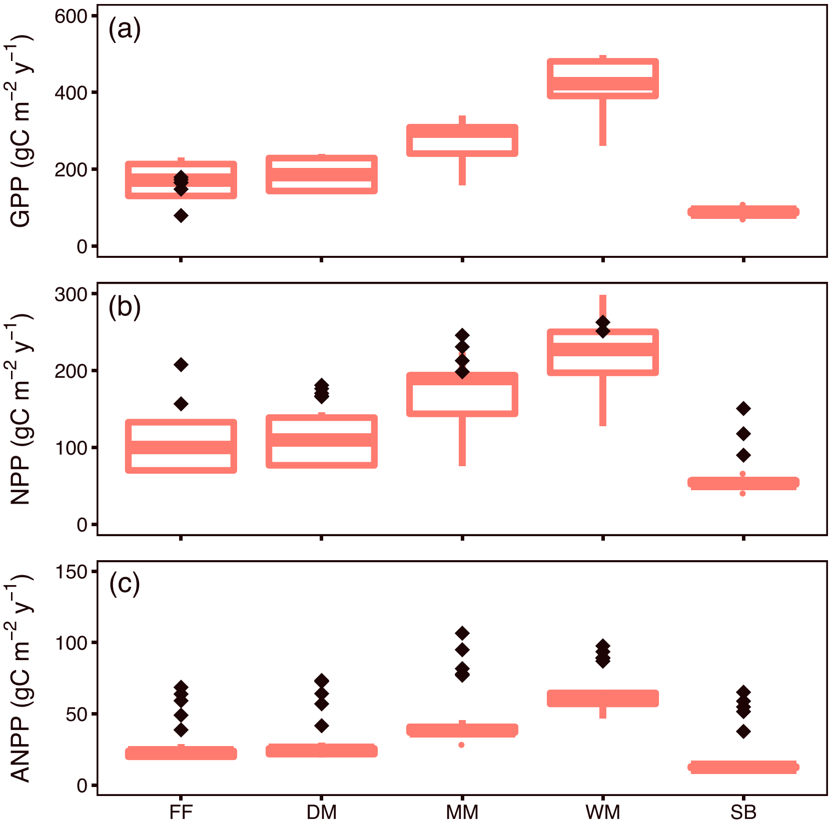

Figure 5. Box-whisker plots showing productivity simulated by CLM and configured to represent alpine vegetation communities at Niwot Ridge (in red median, interquartile range, and absolute range; see Table 1 for abbreviations). Observations (where available) are shown with black diamonds: (a) GPP observations are the sum of half-hourly GPP estimates derived from flux tower measurements at T-Van from 1 May to 30 September. (b) NPP observations are the sum of aboveground and belowground NPP fluxes for Niwot Ridge and other alpine tundra sites summarized by *Bowman and Fisk* [2001]. (c) ANPP observations are the mean for each vegetation community measured by hand clipping vegetation growing in the 88 points of the Saddle research site that were collected from 2008 to 2013 (but not data from 2009).

fall before the development of a snowpack). These results are reasonable and align with limited observations near the study site [*Liptzin et al.*, 2009] and elsewhere [*Hiller et al.*, 2005; *Reinhardt and Odland*, 2013]. Overall, mean annual soil temperatures (10 cm depth) increased substantially with increasing snow depths in CLM simulations (Figure 6a). We interpret these data to signify that temperature limitation to productivity may vary across space and time on Niwot Ridge, with soil temperature chiefly limiting liquid water availability and productivity at dry sites during early spring and late fall periods. In contrast, air and soil temperature may limit productivity in relatively wet areas directly (through growing season length) or indirectly (by slowing rates of soil N mineralization).

Growing season length represents an important control on vegetation productivity in many ecosystems [*Churkina et al.*, 2005; *Fridley et al.*, 2016]. To determine leaf out, the CLM parameterization we used requires the accumulation of growing degree days where soil temperatures (10 cm depth) are greater than 4°C (modified from 0°C in the standard CLM configuration; Appendix A) [*Oleson et al.*, 2013]. This occurred first in fellfield and dry meadow simulations and last for the snowbed community (Table 2). Accordingly, growing season length was closely related to snow accumulation, with the longest growing seasons in fellfield and dry meadow ecosystems (Figure 6b). Conversely, the low productivity in snowbed simulations (Figure 5) resulted from the long-duration snowpack and the very short subsequent growing season (Figure 6b). Although these results are consistent with our expectations for this site, additional data are needed to evaluate the spatiotemporal accuracy of the soil temperature, soil moisture, snow depth, and phenological events from different vegetation communities that were simulated by the model.

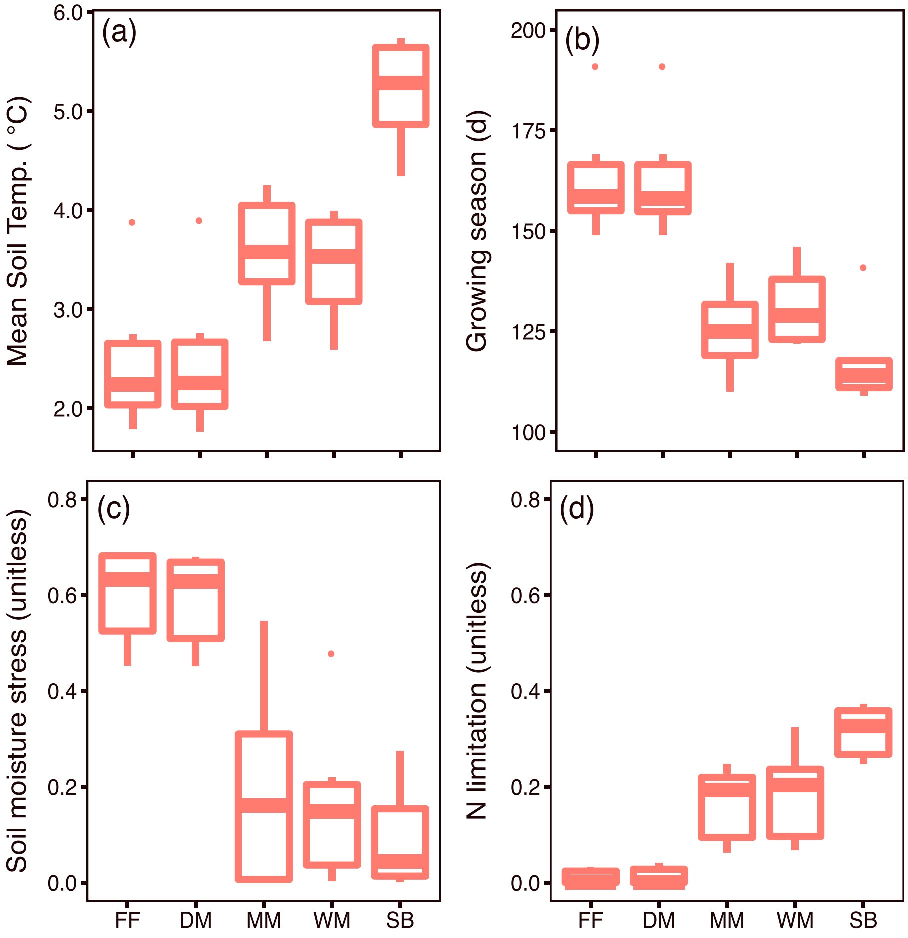

Figure 6. Conditions simulated by CLM, configured to represent alpine vegetation communities at Niwot Ridge (see Table 1 for abbreviations) showing (a) mean annual temperature, (b) growing season length, (c) growing season soil moisture stress, and (d) growing season N limitation. Box-whisker plots show the median, interquartile range, and absolute range of annual values simulated between 2008 and 2013. Higher values for soil moisture stress and N limitation indicate stronger limitation of plant productivity by water and N availability, respectively.

Given the persistence of dry soils, the simulated plant productivity in fellfield and dry meadow communities was strongly water limited (Figure 6c) and rarely experienced N limitation (Figure 6d). By contrast, moist meadow, wet meadows, and snowbed vegetation communities experienced decreasing soil moisture stress and increasing N limitation (Figure 6). The low levels of N limitation in dry meadow simulations contradict long-term findings from experimental manipulations at this site that clearly demonstrate a positive correlation between N enrichment and productivity in dry meadow communities [*Bowman et al*., 1995; *Bowman et al*., 1993; *Bowman et al*., 2006; *Gasarch and Seastedt*, 2016]. We note that despite a large experimental N enrichment, the observed biomass response in dry meadow communities is less than in the moist meadow. This could be and artifact of the experimental protocol, which assumes steady state conditions at present day and prescribes static atmospheric CO_2 concentrations and N deposition rates. Evaluating model response to simulated N enrichment serves as a good test of the assumptions and parameterization of N limitation in models like CLM [*Thomas et al*., 2013; *Thomas et al*., 2015], although thoroughly assessing potential model deficiencies falls outside the scope of this paper.

The mismatch between simulated and observed N limitation in the dry meadow community could arise for several reasons. For example, the simplistic alteration of precipitation inputs that was necessary to capture the redistribution of snow at the site potentially underestimated spring snowmelt pulses and resultant soil moisture dynamics (Figures 3c and 4). Alternatively, assumptions regarding plant physiology in CLM may be inappropriate for alpine vegetation as the model lacks representation of plant water storage capacity and, given the parameterization of rooting depths in the model, may have limited access to deeper soil water. Moreover, the default representation of soil biogeochemistry in CLM may overestimate soil organic matter stocks and inorganic N availability, as simulations were not tuned to observed values [*Fan et al.*, 2016]. As models like CLM become more ecologically realistic, the representation of processes like ecosystem N losses and the temporal partitioning between peak plant and microbial N demand [*Fisk and Schmidt*, 1996] could be important to consider. Indeed, robust evaluation of the modeled response to field data is complicated by the indirect effects of plant community compositional changes in response to environmental manipulations that drive concurrent shifts in plant N and water use efficiency at Niwot Ridge and elsewhere [*Bowman et al*., 1993; *Farrer et al*., 2015; *Sistla et al*., 2013]. Although new tools are coming online to begin addressing these shifts in plant demography and their feedback on terrestrial processes [*Fisher et al*., 2015; *Moorcroft et al*., 2001], typically, these efforts do not focus on arctic or alpine vegetation.

Extended growing season simulations generally had the intended effect of lengthening the growing season and increasing soil moisture stress. Black sand additions accelerated snowmelt and extended the growing season by 2–3 weeks in more snow-dominated ecosystems, but had little effect in fellfield and dry meadow simulations that accumulate thin snowpacks (Figure 7a). In contrast, the 2°C atmospheric warming extended the growing season in all vegetation communities by 1–2 weeks, with the strongest effects in the wet meadow. With earlier snowmelt, all communities experienced proportional increases in soil moisture stress (Figure 7b). Specifically, longer, hotter summers decreased plant biomass in fellfield and dry meadow simulations by exacerbating plant water stress (Figure 7d). These results suggest that fellfield and dry meadow communities may show less responsiveness to accelerated snowmelt in the future, but that they may respond negatively to increased air temperatures and the resultant moisture stress. In contrast, extending the growing season for moist meadow and snowbed communities generally increased productivity despite increases in soil water stress and N limitation, indicating that productivity from these communities may respond positively to a longer growing season. Overall, this work suggests that an extended growing season scenario could potentially decouple the timing of snowmelt from periods of significant plant water demand, which could explain the additional moisture stress and changes in plant productivity evidenced by these simulations. This is perhaps best illustrated by the somewhat unexpected results from the wet meadow simulations.

We hypothesized that wet meadow vegetation would show the least responsiveness to extended summer treatments since it received supplemental water from upslope locations in our experimental design. Our results, however, indicated that the wet meadow showed a strong negative response to the extended growing season scenarios (Figure 7). In the wet meadow simulations, black sand and 2°C warming treatments increased the average growing season length by 15–18 days but decreased mean annual GPP by 16% and 11%, respectively, with comparable declines in LAI and plant biomass (Figures 7d and 8). Plant productivity decreased in extended summer treatments because accelerated snowmelt resulted in higher surface soil temperatures and supplemental water inputs that arrived in advance of plant demand. Because of this temporal decoupling between soil water availability and plant water demand, the wet meadow vegetation ultimately experienced greater soil moisture stress (as opposed to N limitation), resulting in a negative plant productivity and biomass response to extended summer simulations (Figures 7b–7d).

We acknowledge that our results may be a product of assumptions about the timing, sources, and magnitude of supplemental water inputs into wet meadow simulations to a certain extent; however, findings from other sites suggest that these results may be consistent with observations. For example, *Blanken* [2014] studied a high-elevation wetland and found that a single winter drought caused a longer growing season during the subsequent summer. Earlier snowmelt associated with this winter drought increased soil temperature and moisture, but in advance of vegetation demand, as in our extended summer simulations (Figure 8). Even in these relative well-watered systems, observations and models suggest that this results in a shift in energy partitioning to higher sensible heat fluxes, with concurrent declines in LAI and absorbed photosynthetic radiation [*Blanken*, 2014] (Figures 7 and 8). Indeed, observational surveys conclude that particular vegetation responses to climate variability and climate change may result from complex interactions in climate hydrology, nutrient availability, and phenology [*Walker et al*., 1995]. Based on our wet meadow simulations and observations from *Blanken* [2014], we conclude that a loss

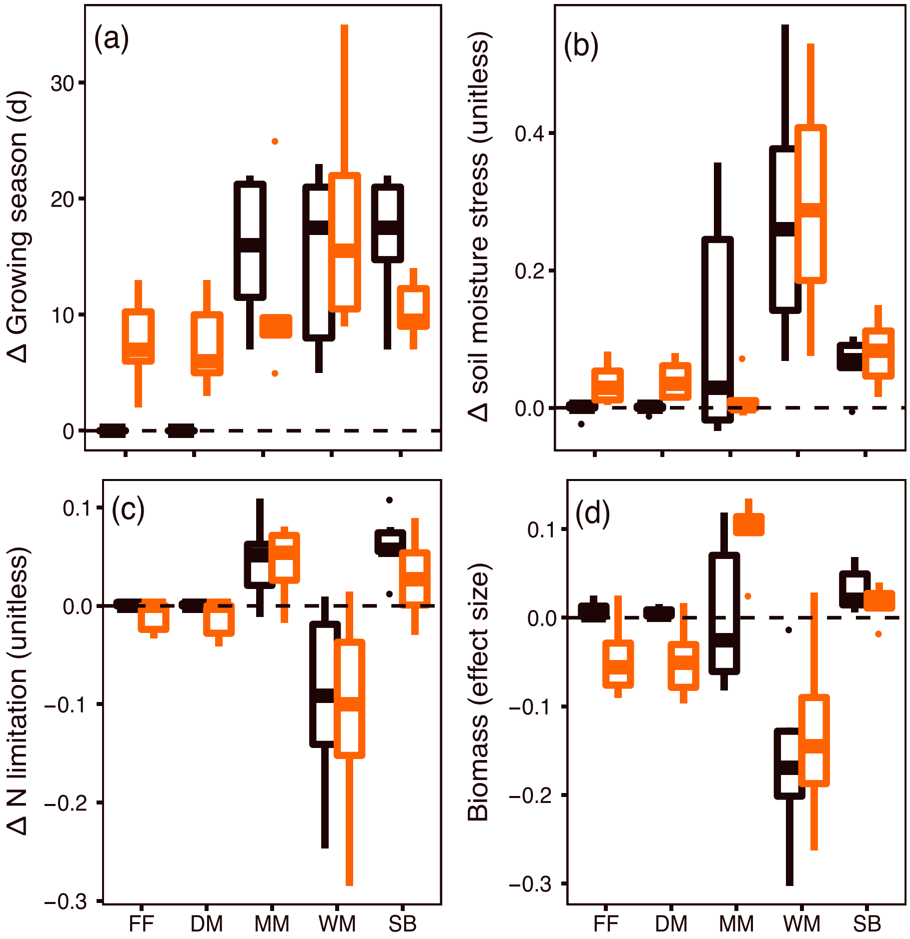

Figure 7. Changes for extended growing season simulations that included accelerated snowmelt, achieved by adding black carbon to the snow surface in May, and atmospheric warming, which is represented by increasing air temperature 2°C above observations from 1 March through 31 August (black and orange box-whisker plots, respectively). Panels show changes (relative to control simulations) for (a) growing season length (defined as GPP > 0), (b) annual growing season soil moisture stress, (c) annual growing season N limitation, and (d) total plant biomass. Figures 7a–7c show simple differences between experimental treatments and control simulations for each year. Given differences in initial plant biomass for each vegetation community, we calculated an effect size [ln(treatment/control)] for annual biomass totals in Figure 7d. Vegetation communities abbreviated as in Table 1.

of hydrological connectivity between alpine tundra plant communities may be expected to accompany higher summer temperatures in the future. Thus, future work could represent watershed-scale hydrological connectivity in a more sophisticated manner to better understand where alpine vegetation may be vulnerable to an extended growing season.

Beyond emphasizing the spatial connectivity among vegetation patches, our results suggest that an extended growing season scenario has the potential to modify temporal resource connectivity. For example, consistent subnivean temperatures provide ideal conditions for microbial activity that is important for both C and N cycling in the alpine tundra [*Brooks et al.*, 1996; *Knowles et al.*, 2016; *Lipson et al.*, 2000; *Liptzin et al.*, 2009]. Moreover, snowmelt marks an abrupt change in soil microbial biomass, community composition, and soil biogeochemical dynamics [*Brooks et al.*, 1998; *Lipson et al.*, 2002; *Schadt et al.*, 2003]. Since plant N acquisition during snowmelt appears to be an important source of N for alpine vegetation [*Bilbrough et al.*, 2000; *Lipson et al.*, 1999], the temporal dynamics of biogeophysical and biogeochemical fluxes could be disrupted by earlier snowmelt. In our simulations, the acceleration of spring snowmelt exposed vegetation and surface soils to freezing temperatures, greater diurnal temperature fluctuations, and accelerated desiccation with variable implications across the soil moisture and

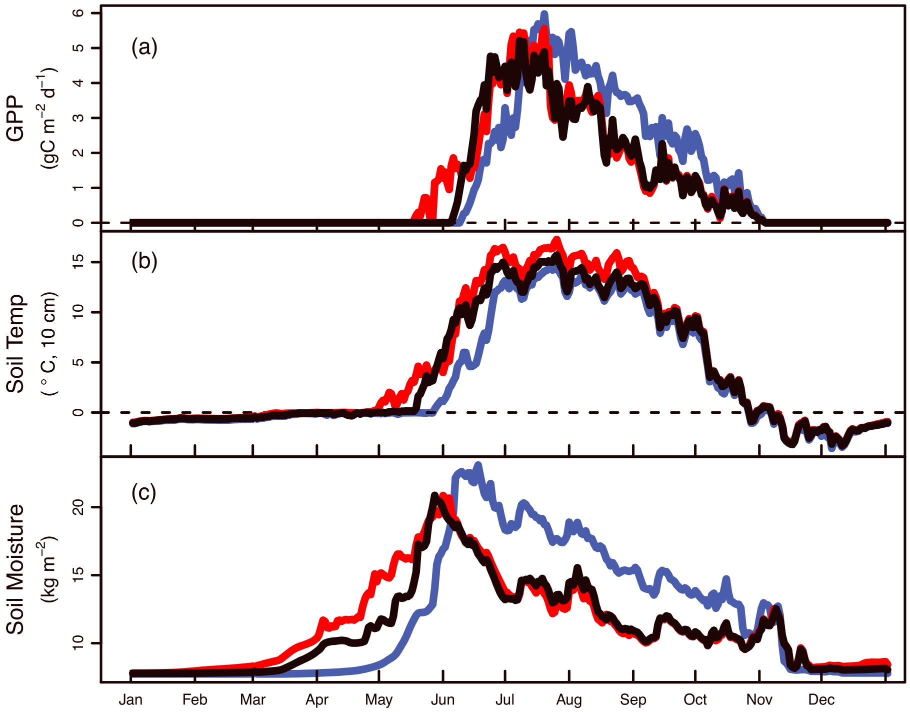

Figure 8. Mean annual cycle of CLM simulations configured for wet meadow vegetation showing daily (a) GPP, (b) soil temperature, and (c) soil moisture (both from the third soil layer simulated by CLM, 10 cm depth). Results are calculated from daily means over the 6 year study period for control (blue), 2°C warming (red), and black sand (black) simulations.

vegetation gradients on Niwot Ridge. Testing the hypotheses generated by this work with observations, manipulations, and models will build understanding of the ecosystem-scale response to expected environmental perturbations that are complicated by spatial heterogeneity and complex terrain.

4. Conclusion

With modifications to vegetation characteristics and soil hydrology parameterizations, the Community Land Model was able to capture observed spatiotemporal patterns of energy, water, and C fluxes at multiple scales across five distinct alpine tundra vegetation communities (Figures 2–5). Although running CLM requires relatively high-frequency meteorological data, the results leverage biogeophysical and biogeochemical representations of snow, soil, and vegetation processes that are not common in typical hydrology, ecosystem, or biogeochemical models. Moreover, areas where the model fails, or does not produce expected results, can generate ecological questions that can be addressed with additional experimentation and/or model development. Direct and indirect effects of perturbations can alter community composition and ecosystem function at multiple levels of organization. Models like CLM, however, need information about these perturbations to ultimately alter plant physiological traits like stomatal conductance, C allocation, or N use efficiency—which in turn affect ecosystem function. For example, does weaker-than-expected N limitation in dry meadow simulations (Figure 6) suggest that CLM may omit or simplify factors controlling plant access, uptake, and storage of water and N? What parts of the tundra share hydrological connections, when are those connections likely to broken, and what are the implications of disrupting those connections on the ecosystem-level responsiveness to environmental change (Figure 7)? Finally, how may earlier snowmelt decouple microbial and plant activity and influence the timing and magnitude of nutrient retention, limitation, and export from terrestrial ecosystems? To address these complex questions, interdisciplinary approaches and diverse tools are required. We hope that the lines of ecological inquiry incited by this work will help to ensure that future modeling efforts more accurately capture the nuanced effects of environmental change on biogeochemical and biogeophysical processes.

Table A1. Modifications to Model Parameters

Parameter	Default Value	Modified Value	Reference
Soil resistance scalar	15	5	*Swenson and Lawrence* [2014]
Leaf C:N ratio	25	32	*Bowman and Fisk* [2001] and *Fisk et al.* [1998]
Fine root:leaf ratio	1	2	*Bowman and Fisk* [2001] and *Fisk et al.* [1998]
Minimum growing degree day temperature	0°C	4°C	*Oleson et al.* [2013]

Appendix A: Parameter Modifications

Simulations used default parameterizations from CLM4.5 described in *Oleson et al.* [2013]. Table A1 describes the modifications we made for all single-point simulations to represent alpine tundra ecosystems in this study.

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