



Surveys up on the ridge with Mountain Research Experience participants. Credit: Alex Rose

NWT LTER VII

Long-term Research on the Dynamics of High-Elevation Ecosystems:
A Framework to Understand Ecological Responsiveness to Climate Change

**Year 5 Annual Report
2020 - 2021**

In LTER VII, our overarching goal is to better understand where and when climate change results in ecological change, and to elucidate the mechanisms that lead to both sensitivity and buffering in ecological systems. Our objectives are to (a) continue to characterize how ecosystems are changing with climate variation, (b) test hypotheses about the underlying drivers of this variation, and (c) use this information to enhance forecasting and management in mountain areas.

We have framed our work by extending two bodies of ecological theory. First, we utilize work aimed at predicting vulnerability to climate change at regional scales, which emphasizes that response is a function of the magnitude of climate change experienced (exposure), the intrinsic ability to tolerate a given amount of change (sensitivity), and the degree to which elements can shift in response to the change (adaptive capacity) (Dawson et al. 2011, Dickinson et al. 2014). We extend these ideas to spatial variation at the landscape scale, where complex terrain (Q1, below) and biophysical effects of biota (Q2) modulate climate, creating a heterogeneous backdrop of resource supply changing both over the course of the growing season and across years due to climate variation. Second, we utilize work focused on responses to changing temporal variation as well as spatial connectivity across landscape positions, outlining how responsiveness to different patterns of temporal (Q3) or spatial (Q4) variability aggregates to other levels (e.g., population to community, patch to catchment). We extend these ideas to how integration, interaction, and connection buffer or amplify responsiveness. We specifically designed our work to address four questions:

Q1) SHIFTING LIMITATIONS. How do terrain-related differences in exposure, by shifting the limiting resources and abiotic stressors, affect ecological response? We expect that complex terrain, by altering the magnitude of climate exposure experienced at a location, will shift how climate variation impacts the relative supply of different resources and the occurrence or frequency of stress. These shifts will result in both positive and negative responses, depending on the strength and nature of the limitations, and influence process rates across levels of organization, including at the ecosystem (productivity), community (species turnover) and population (abundance, recruitment) levels.

Q2) BIOTIC INFLUENCE. How do structure-forming biota attenuate climate exposure to influence ecological response? We also expect that biota can influence climate exposure through effects on the physical environment. Because these effects will occur at a relatively fine scale, we expect that structure-forming biota will increase heterogeneity within a habitat, influence the number of species able to coexist, and create micro-refugia in the face of a changing climate.

Q3) ADAPTATION STRATEGIES. How do different strategies for managing temporal variability and uncertainty at the organism and population levels aggregate to influence community and ecosystem processes? We expect that terrain- and biota-related differences in exposure, in addition to modulating average conditions (Q1 and Q2), will influence environmental variability and predictability. Species' sensitivities reflect evolutionarily constrained responses to past climate, and constraints at the organism and population levels should be reflected in community and ecosystem responses.

Q4) CATCHMENT INTEGRATION. How do responses across space aggregate to affect catchment response? Water quality and quantity leaving a catchment represents an integrated signal of the biotic and abiotic processes occurring along flow paths. We expect that shifts in hydrological connectivity along these paths (where some areas of the catchment may contribute in some years but not in others) should influence net water quality and quantity. Our fourth hypothesis represents a critical line of thinking for LTER VII because it links much of the fine-scale work in terrestrial sphere with the aquatic through water quality and quantity. To make this linkage, we are working to scale up to the catchment scale – integrating spatial heterogeneity in response emphasized in the previous hypotheses – and then relating these dynamics to catchment-wide responses that we know influence the lake ecosystems: water discharge, nutrient export, and DOM inputs. This inquiry also enables a longer-term linkage by incorporating vegetation/land cover change at the catchment scale.

We have unified our investigations of ecological responsiveness by focusing on a specific aspect of climatic change in these high-elevation snow-governed ecosystems: the **EXTENSION OF SUMMER** (Fig. 1). Winter snow cover has been noted as one of the fastest changing climate features globally (Vaughan et al. 2013). Across Colorado, snowmelt timing has advanced approximately three weeks since the 1970s (Clow 2010), with a longer and hotter snow-free period.

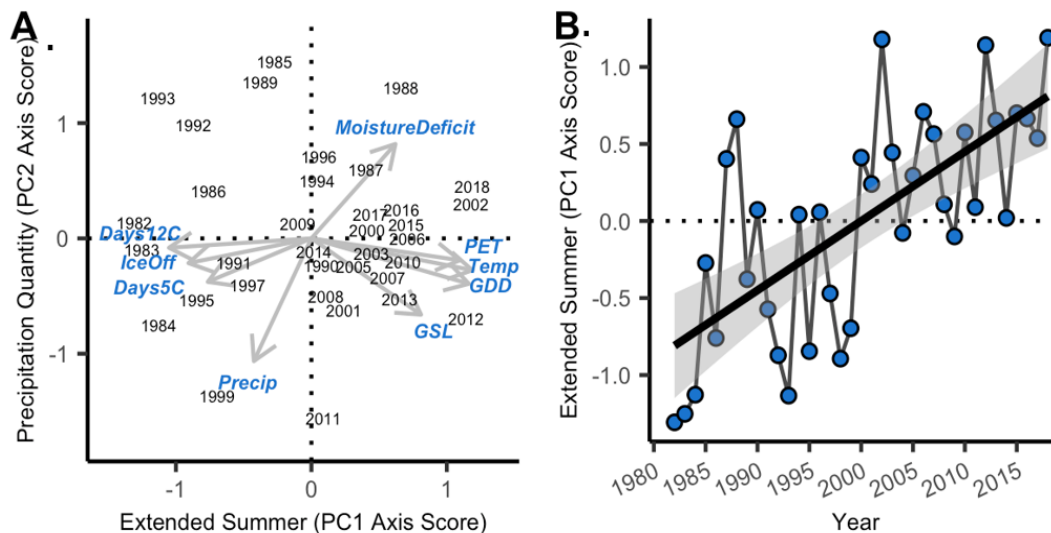


Figure 1. Climate at NWT is changing towards longer and warmer growing seasons, a trend we call “extended summer.” (A) Climate conditions in multivariate space as summarized by principal component analysis using data from Niwot Ridge Saddle and Green Lake 4. Over 50% of year to year variation is described by climate characteristics (blue text) related to extended summers (PC1): high summer potential evapotranspiration and warmer mean summer temperature, advanced start to the growing season (days to a five-day running max temp of 5C or 12C) and lake ice-off in the Green Lake 4, a long growing season and high number of growing degree days. Variables related to the amount of summer precipitation and moisture deficit describe the second axis (PC2) and capture almost 20% of yearly variation. GDD is the growing degree days (base 5°C), GSL is defined as the growing season length, where the boundaries for the season are defined by 3 consecutive days where the minimum temperature is below -3°C. (B) Since the start of the NWT program, extended summer has significantly increased ($\beta = 0.04$, $adj-R^2 = 0.49$, $p << 0.001$) with much inter-annual variation. Years 2002, 2012, and 2018 were years that particularly characterized this phenomenon. Data sources: knb-lter-nwt.405; knb-lter-nwt.413; knb-lter-nwt.416; knb-lter-nwt.106

One key hurdle in most empirical statistical models and many process-based models is the assumption of stationarity: that the current relationships among system components will hold in the future. Indeed, this is an underlying assumption of the multivariate analysis we use to describe the suite of climate variables that contribute to the extended summer trend at NWT (**Fig. 1**). In a now published work, we evaluated this assumption by asking whether relationships among these key characteristics are stationary across the 37-year time series. Bueno de Mesquita et al (2020) investigated temporal trends within our extended summer metric and found a breakpoint in correlation between temperature and growing season length (**Fig. 2**) in the early 1990s at NWT. Prior to the early 90s, temperature (measured as growing-degree days - GDD) and growing season length (GSL) were coupled (a hot summer meant a long summer) but in more recent decades, this relationship has broken down. We suspect this decoupling is related to continued warming but with no associated decrease of snowpack at NWT.

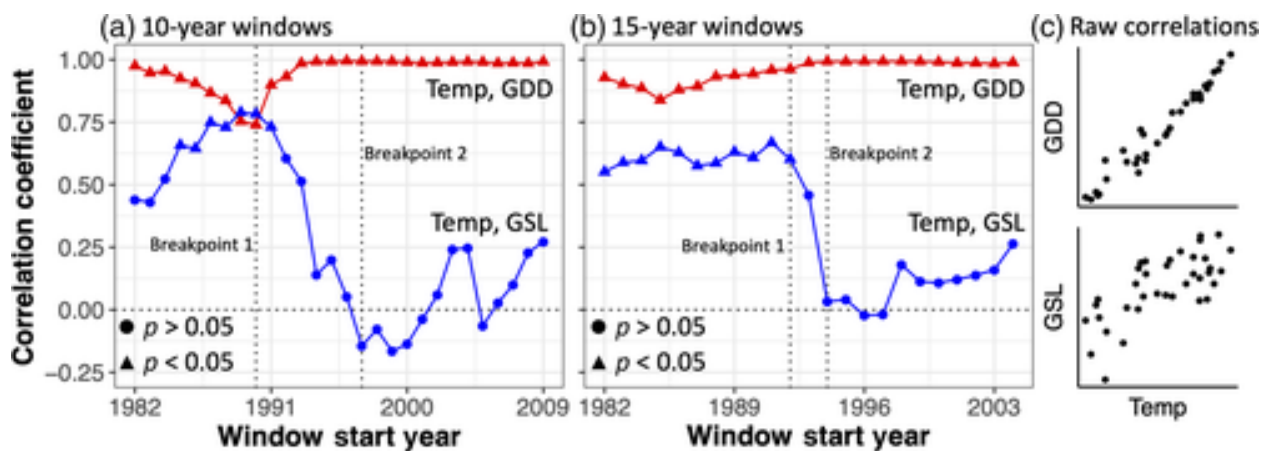


Figure 2. Moving window correlation analyses between mean summer temperature and either growing degree days or growing season length for (a) 10-year windows ($n = 28$) and (b) 15-year windows ($n = 23$). Panel (c) shows raw scatterplots between temperature and GSL and temperature and GDD from 1982 to 2018. Correlation coefficients are Pearson r values, and the significance of the correlations in (a) and (b) are represented by either triangles (significant, $p < 0.05$) or circles (not significant, $p > 0.05$).

In the following sections, we detail our accomplishments and our next steps towards meeting or stated objectives for each of our four main research question. Our structure follows the order of the work plan in our proposal, with sections on outreach and information management following the sections on research.

1. SHIFTING LIMITATIONS. How do terrain-related differences in climate exposure affect ecological response?

In our first hypothesis, we proposed that complex terrain, by altering the magnitude of climate response at a location, will shift how climate variation impacts the relative availability of different resources and the occurrence or frequency of stress. To test this idea, we proposed a series of studies using observed patterns in long-term datasets (**A**), modeling (**B**), and experimentation (**C**) for LTER VII. Here, we detail our expectations and progress to date for each in the following sections.

A. Continued monitoring of tundra, forests, chickadees, pikas, pollinators, streams, and lakes. Across a broad range of ecological systems, we have examined ecological responses to changing climate conditions at NWT. While correlational, this step leverages patterns in our

long-term data to confirm and guide expectations. It also highlights the varied responses across landscape position, organism, and level of organization.

Alpine tundra. We have continued to follow tundra plant production and compositional change in established tundra (88-plot saddle grid) as well as in sensor network in the Saddle Catchment. In the saddle grid, we previously found that production in the established tundra exhibits little response to extended summer climate conditions. In year 5, we examined if the mechanisms underlying the biodiversity-production relationship (mass-ratio effects or niche complementarity) and found that these mechanisms change dynamically with changing climate (increasing GDD). Using Structural Equation Modeling (SEM) that examine functional trait patterns on the saddle grid, we found that mass-ratio effects are the dominant mechanism that maintain production across all years, but that their strength generally decreases with increasing GDD. Concurrently, niche complementarity effects remain relatively weak across all years and the snow becomes less important with increasing GDD (**Fig. 3A**). Critically these key biotic and abiotic drivers of the biodiversity ecosystem function relationship weaken (explain less variance in productivity) as GDD increase (**Fig. 3B**) suggesting decoupling or change in the drivers of the biodiversity-ecosystem functioning relationship as GDD increases (**Fig. 3**; Huxley et al, in prep).

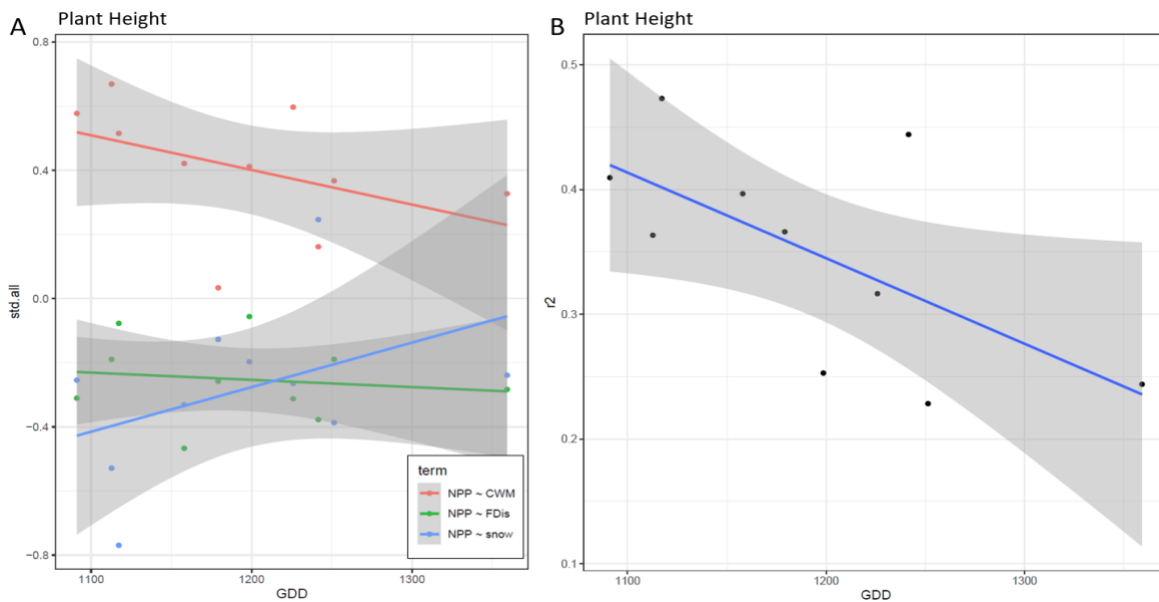


Figure 3. (A) Path coefficients from SEMs for snow depth, community weight mean height (CWM) and functional dispersion of height (FDis) regressed against growing degree days (GDD). (B) The amount of variation (r -squared) in NPP explained by the SEMs in (A) decreases with increasing GDD.

We also began analyzing vegetation responses in multi-year experiments where we have manipulated resources and environmental conditions to test our expectation about how limitations shift in extended summer years. We found that years with extended summer conditions correlate with lower biomass and plant cover, higher species richness, and shifts in species composition towards more opportunistic, nitrophilic species. (Bueno de Mesquita et al, in prep). We have also expanded our monitoring to examine the drivers of variation in potentially sensitive terricolous lichen across the saddle plots. These initial detailed surveys will provide a baseline for repeated sampling in the future.

Following encouragement for within-site synthesis at our mid-term site review, we have initiated a synthesis project focused on functional responses to environmental change across experiments at Niwot Ridge. The overarching goal of our synthesis is to ask: 1) do functional traits predict species response to environmental change, and 2) do these responses scale up to influence changes in community composition and biodiversity? We are using data from eight NWT datasets that have manipulated some combination of nutrient availability, temperature, and/or snow depth (NutNet Plots, 2-4-6 Plots, ITEX plots, Snowfence plots, CoDom plots, Fert 20-10 plots, historical ITEX plots, Snowbed plots) to ask 1) which species are constantly changing, 2) are those changes predicted by plant functional traits, and 3) do our experiments predict changes in the long-term monitoring plots? We began data synthesis in Spring 2020, but a planned in-person workshop and progress on analyzing the data were delayed until 2021 due to the pandemic. Since reinitiating this project, we have found wide variation in species responses. Using a response ratio approach that accounts for species' responses to natural climatic variation, we found that much of the variation among species in responses to our experimental treatments is explained by plant functional traits. For example, species with higher leaf dry matter content tend to increase in response to N addition, while species with higher tissue N tend to increase in response to the combination of added snow and warming (**Fig. 4**).

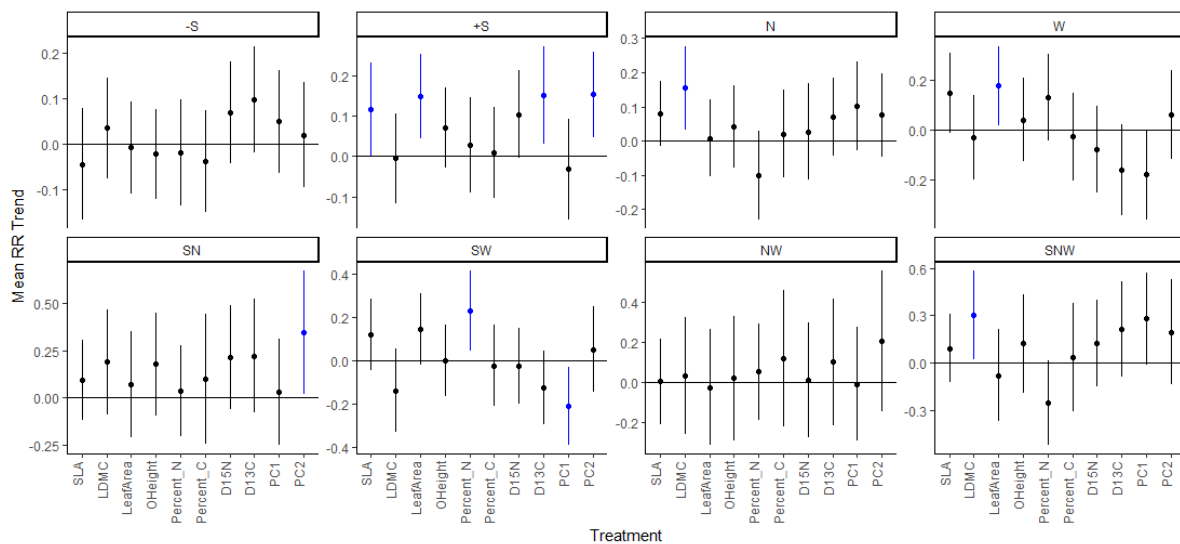


Figure 4. Functional traits predict some species response to experimental treatments (-S snow reduction, +S snow addition, N nitrogen addition, W warming, SN snow and nitrogen addition, SW snow addition and warming, NW nitrogen addition and warming, SNW snow and nitrogen additions and warming). Blue points represent traits that significantly predict changes in response ratios. Positive value indicates that species are increasing in response to experimental treatments and a negative value indicates that species are declining in response to experimental treatments.

In a synthesis of data from the International Tundra Experiment (ITEX) covering 18 sites (including NWT) and 46 open-top chamber warming experiments across Arctic, sub-Arctic, and alpine ecosystems on six plant phenophases (green up, flowering, end of flowering, fruiting, seed dispersal, and leaf senescence), Collins et al (2021) demonstrated that reproductive phenophases shifted in response to experimental warming with a greater magnitude than vegetative phenophases, with warming delaying senescence (**Fig. 5**). The advancement of reproductive seasons and lengthening of growing seasons may have significant consequences for trophic interactions and ecosystem function across the tundra.

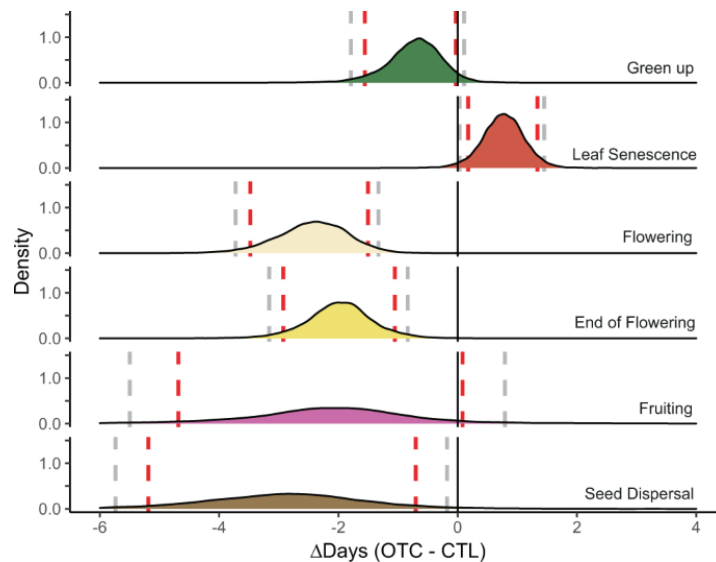


Figure 5. Density plots of modeled estimates of treatment effects for the difference (in days) in phenophase timing for plants growing in OTC versus control (CTL) plots across a data synthesis of 18 sites and 46 OTC warming experiments. Estimates are shown on the x axis and phenophases are plotted vertically including data from all sites, years, and species. Black vertical lines denote zero difference (no change) in the timing of phenology between OTC and CTL plots while red and gray dashed lines denote the 90% and 95% Bayesian credible intervals, respectively. Peaks to the left of black lines indicate an advancement, while peaks to the right of black lines indicate a delay, of that phenophase in response to warming.

Tundra plant populations. In a previous reporting year, we initiated studies that track species survival and recruitment to better understand population-level responses and species turnover dynamics. To date, we have established 20 0.25 x 0.25m observational plots in dry meadow. We planned to establish 20 more plots in moist meadow and resample the dry meadow plots in 2022. In the existing 20 dry meadow plots we have tagged and mapped 4,907 individuals across 32 species. In the short term, we are currently exploring 2 questions: 1) how do soil resources and spatial structure interact to structure communities; and 2) what is the role of the foundational species *Silene acaulis* in influencing species coexistence? Over the long term we plan to track recruitment and survival of all individuals each year to begin to examine how interannual climate variability influences tundra plant population dynamics beyond our community abundance measures.

Pika. We focus on the American pika (*Ochotona princeps*) as a model species for studying climate sensitivity in small, herbivorous mammals exploiting sub-surface habitats. We expect loss of sub-surface ice, increasingly warm temperatures during the period of juvenile dispersal, and cold events in the absence of insulating snowpack will all be aspects of extended summer conditions detrimental to pika populations and many other species in this guild. Over the past year, we have continued a mark-resight study of pika demography and the pika habitat occupancy survey that was established in 2016. With the support of an NSF Graduate Research Fellowship, a student on the project moved from a masters to a Ph.D. program to focus on dynamic occupancy modeling of the NWT pika survey data and test a model of pika response to climate that we developed for nearby Rocky Mountain National Park (ROMO). She has made

great progress in her modeling skills this year and is currently completing a preliminary analysis of community-science data on pika occupancy in ROMO. Our community-science partnership with ROMO, the Denver Zoo, and Rocky Mountain Wild was strengthened in 2021 by additional National Park Service funding for her analysis and by a nearly two-fold increase in the number of volunteers certified (>400) to collect these data in ROMO and elsewhere through the Colorado Pika Project, as featured in National Geographic (<https://www.nationalgeographic.com/animals/article/american-pika-sounds-alarm-for-global-warming>).

We had several publications involving NWT pika populations in the past year, including one by our recent MS student exploring patterns of seasonal stress in pikas at NWT (Whipple et al. 2021, with two undergraduate coauthors), and a synthetic study of genetic patterns demonstrating recent range-wide contractions in pika population size (Klingler et al. 2021, with a doctoral student lead author). Four papers are in preparation (three led by students) addressing spatial patterns in pika stress metrics, range-wide occupancy, and local range retraction on Niwot Ridge. The latter paper is led by two students who graduated *summa cum laude* based on honors theses investigating this range retraction. We also obtained support from the Environmental Data Initiative for a summer 2021 Fellow who developed a flexible pipeline for publishing NWT talus temperature data to EDI and published several such datasets from our growing network of collaborators investigating pika habitat dynamics.

Chickadee. We have monitored the population dynamics of a small bird, the Mountain Chickadee (*Poecile gambeli*), for three years in collaboration with Dr. Scott Taylor. We are now monitoring 400 nest boxes that have been installed along an elevational gradient that includes Niwot Ridge and will allow us to determine the relationship between breeding success of this boreal specialist and forest productivity. We are also monitoring interactions between the Mountain Chickadee and a close relative, the Black-capped Chickadee (*P. atricapillus*), which hybridize at low frequencies where they co-occur. We expect that extended summer conditions will alter the distributions of both species, via both direct climate effects as well as indirect effects via changes in sub-alpine forest food resources.

Subalpine forest. In our original proposal, we predicted that extended summer conditions would intensify soil moisture limitation in subalpine forest and reduce seedling establishment and increase tree mortality. Indeed, we found that extended summer conditions reduced seedling establishment (Andrus et al. 2018b), and that most recruitment events occurred during cool, wet summers. We have continued monitoring the NWT permanent forest plots in Year 5 and recent analyses have shown that extended summer conditions also increased rates of tree mortality (Andrus et al. 2021). While we observed detrimental effects of warmer climate conditions on tree seedling establishment and mortality, aboveground live tree biomass has increased in NWT permanent plots from 1982-2016 (Chai et al. 2018), a trend we suspect is primarily driven by slow stand development following stand-initiating fires over a century ago.

Pollinators: In the summer of 2021, Dr. Adrian Carper (CU Boulder), Dr. Julian Resasco (CU Boulder), and Dr. Warren Sconiers (University of the Ozarks) began a new effort to characterize the pollinator community across Niwot Ridge by surveying pollinators at each site with a Black Sand experimental plot (Soddie, Trough, Saddle, East Knoll, Lefty, and Audubon) using bee bowls (Shapiro et al. 2014) and blue vane traps (Kimoto et al. 2012). At each site, we established

a 35m transect with 6 bee bowls evenly spaced along the transect and one van trap at each end. We sampled pollinators three times over the summer growing season: 5th July, 27th July, and 16th August 2021. All specimens from the first two samples have been processed and pinned and the final collection will be pinned by the end of December. After each sample is labeled, sorted, and identified to the lowest possible taxon, we will summarize pollinator communities, compare pollinator abundance, richness, and diversity among sites and across the growing season. We will characterize differences in pollinator communities using ordination, including taxonomic and functional traits of pollinators as potential drivers of community differentiation. All collections will be stored at the CU Boulder Museum of Natural History and will be available to be transferred to the Mountain Research Station on loan at any time.

In these same sites, Dr. Warren Sconiers has also started a project examining the diversity of insect pollinators and arthropods across Niwot Ridge to determine if there is a relationship between changing plant species composition and traits, and insect pollinator and other arthropod diversity with changing climate. This work will evaluate if these changes occur mechanistically through changes in plant nectar nutrients (carbohydrates, amino acids), pollen nutrients (amino acid profiles), and nectar/plant allelochemicals.

Tundra carbon flux. Temporal analysis of the first seven years of alpine flux data indicates the potential for increasing alpine carbon emissions with time. Together with respiration of aged soil carbon from solifluction lobes associated with discontinuous permafrost, this also supports a paradigm of permafrost thaw associated with warming air temperatures that may be relaxing limitations on subsurface winter biological activity (Knowles et al. 2019). This is the longest continuous alpine eddy covariance dataset in the world, and the first to suggest an alpine analog to the well-established arctic tundra permafrost warming feedback to climate change.

Alpine Streams and Ponds. In summer of 2021, Dr. Dan Preston (CSU) surveyed nine stream locations in the Niwot Ridge LTER along an elevational gradient from below treeline to the outflow of the Arikaree Glacier, near the Continental Divide. Their analyses of these data will address how variation in elevation (3221 to 3719 meters), water sources (glacial melt, snowmelt, and lake outflows), and corresponding environmental factors (e.g., temperature and hydrology) affect community structure of stream periphyton and aquatic macroinvertebrates. Additionally, the Anderson lab at UC Riverside sampled macroinvertebrate communities in smaller ponds in and near the Boulder Creek Watershed to explore whether community composition is influenced by elevation, environmental factors, and connectivity to other freshwater bodies.

Alpine Lakes. We hypothesized that the effects of extended summer conditions in lake ecosystems will be mediated by shifts in physical limitations, including longer ice-free periods and warmer surface waters, as well as increases in terrestrial DOM inputs from shifts in terrestrial vegetation as warming causes increased shrub encroachment into catchments. In Year 5, we addressed these hypotheses through analyses of a 36-year lake ice dataset (1983-2018) on alpine lakes (>3000 m ASL) from the Green Lakes Valley, Colorado (GLV) (Christianson et al. 2021). In addition, we continued our long-term measurements of alpine lakes (Green Lake 1 and 4) and enhanced our understanding of seasonal mechanism through continuous, year-round measurements of physical and biological data via an in-situ sensor array in GL4.

Long Term Lake Surveys. In Year 5, we evaluated long-term lake ice data from Green Lake 4 and surrounding alpine lakes (Green Lakes 1-5). Since 1968, ice clearance date has been recorded in Green Lake 4 (GL4), while ice clearance and formation date have been recorded throughout the GLV since 1982. Based on weekly to biweekly observations throughout spring and fall, ice formation and clearance dates were classified visually as when each lake was 100% covered or cleared of ice, respectively. Ice thickness has also been measured since 1982 in GL4 (Caine 2018). To better understand the large-scale implications of our data were compared trends in ice cover duration (ice-covered days) with an available database on Northern Hemisphere lakes (1983–2013) (Benson et al. 2000). Since 1983 the ice-free period in the GLV has increased by an average of 24 days, due to both earlier ice-off (9-day average advance in ice-off date) and especially a 15-day average later ice-on (Fig. 6), in addition spring ice thickness on GL4 decreased at a rate of 0.88 cm yr⁻¹ (Fig 4) (Christianson et al. 2021). By comparison, ice-cover duration in the GLV is decreasing ~ 50% faster than Northern Hemisphere lakes (n = 215), which translates to a ~ 2.5 times increase in open water duration in the GLV than the average of the Northern Hemisphere lakes (Fig. 7).

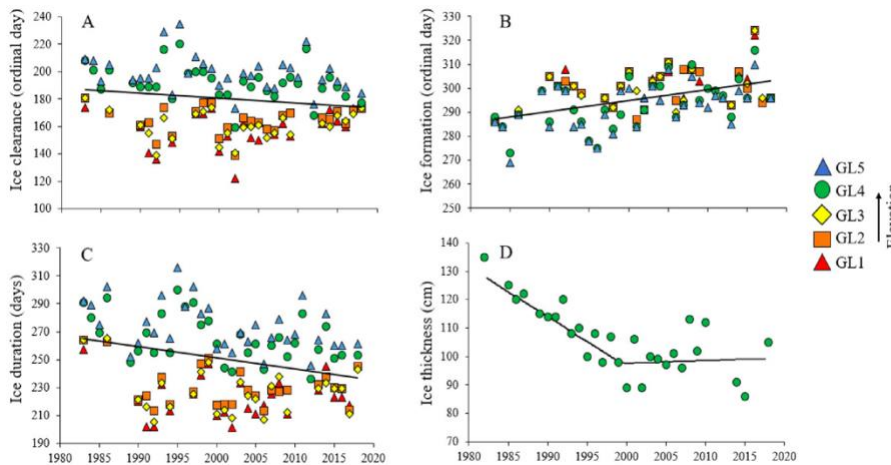
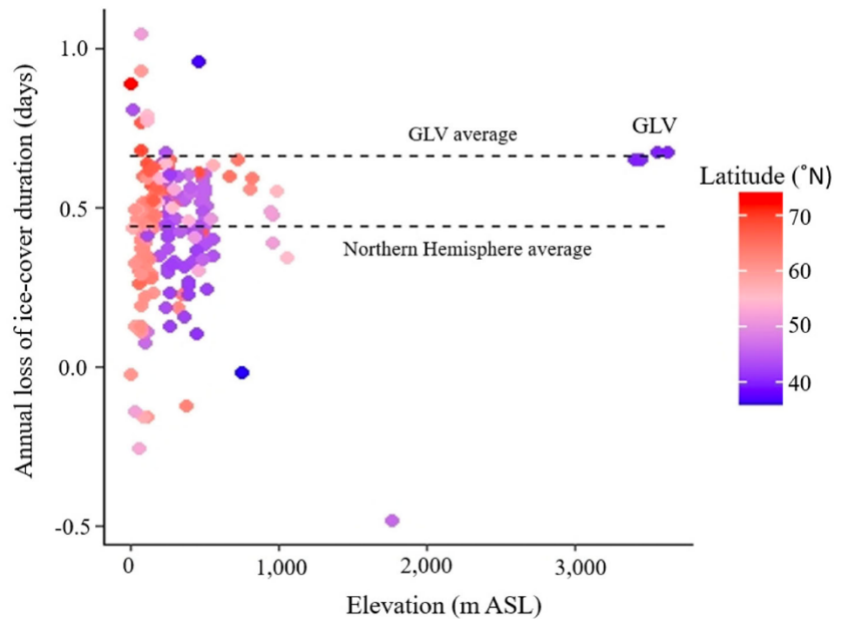


Figure 6. Ice clearance (A) and ice formation (B) ordinal dates, as well as ice-cover duration (C) among Green Lakes 1–5 (elevation: 3425–3620 m ASL) in the Green Lakes Valley, Colorado from 1983 to 2018. Annual maximum ice thickness in Green Lake 4 from 1982 to 2018 is also included (D). A linear trend is shown for all plots except ice thickness, for which was fit with a break-point analysis demonstrating a break point in 2000.

Figure 7. Estimates from a random slope model representing the number of days per year decrease in ice-cover duration for each lake in the Northern Hemisphere dataset as well as for the Green Lakes Valley, Colorado: GLV from 1983 to 2013, with each lake’s latitude and elevation shown for comparison. Note that lakes in the GLV are the highest elevation but nearly the lowest latitude lakes, while generally, the highest latitude lakes of the Northern Hemisphere dataset are among the lowest elevation.



Zooplankton Phenology. In the previous reporting year, we investigated how changes in lake ice phenology impact the biotic communities of alpine lakes (Loria et al. 2020, (Fig. 8). Mapping the intra-annual phenology of abiotic and biotic functions in GL4 provides valuable insight into mechanisms that drive limitations and food-web dynamics and how these might change under extended summer conditions. Our results suggest that shifting limitations due to longer summers are likely to elicit changes in these communities that could have widespread implications for alpine lake systems. We are continuing our investigation of how extended summer conditions influence planktonic communities and lake food webs through ongoing long-term surveys at three alpine lakes in addition to experimental manipulations.

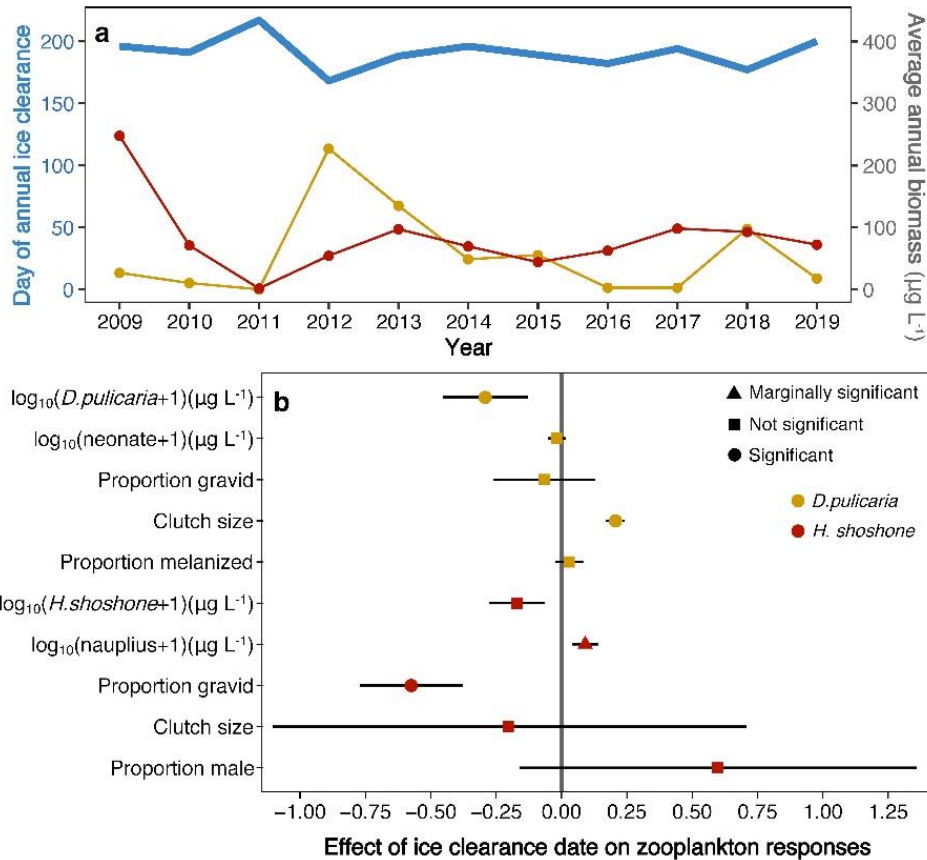


Figure 8. a) The interannual variation in ice phenology and average zooplankton biomass for *D. pulicaria* and *H. shoshone*. Ice-clearance date is depicted in blue. (b) The effect of ice clearance date on each of the following response variables: standardized biomass (g/L) of $\log_{10}(D. pulicaria+1)$, $\log_{10}(\text{neonate}+1)$, $\log_{10}(H. shoshone+1)$, and $\log_{10}(\text{nauplius}+1)$; the proportion of gravid adult zooplankton; clutch size for gravid individuals; and for *D. pulicaria*, the proportion melanized; and for the proportion of male *H. shoshone* based on individual generalized linear mixed-effects models for ice clearance date occurred (scaled). Points thus represent the beta coefficients, where shape refers to a significant relationship for each zooplankton response and the horizontal bars intersecting each point represent the standard error. Loria et al., 2020.

In-situ Sensor Measurements. We deployed a sensor array in GL4 in 2018 to continuously measure biotic and abiotic parameters throughout the water column at 30-minute increments year-round. GL4 is about 13 meters deep and the array design includes eight temperature sensors (RBR solo), three dissolved oxygen (DO) sensors (PME miniDOT), one photosynthetically active radiation (PAR) sensor (PME miniPAR), and one chlorophyll-a sensor (PME Cyclops-7), distributed throughout the water column. We now have four full years of continuous data and are

currently processing and analyzing the data. Preliminary analysis of sensor data indicates that GL4 is mostly polymictic (mixing several times throughout the summer season) and we predict that warmer temperatures and an extended growing season could reduce mixing frequency. Increases in the strength and duration of stratification influence the availability and distribution of nutrients and oxygen and subsequently the behavior of biota. The data collected from our sensory array will provide us with an in-depth understanding of intra-annual (seasonal) dynamics and interannual variability of physical and biological parameters including spatial heterogeneity throughout the lake water column. Compiling this information with our long-term biotic data will provide insight into the linkages of abiotic and biotic processes and how these processes respond to intra-annual variability and long-term change. After some modifications and maintenance this winter, the sensor array will be re-deployed in GL4 as soon as ice out occurs.

B. Modeling studies to explore limitation across space and time on Niwot Ridge.

Modeling Terrestrial Processes. In Year 5 we continued to refine the workflow and development of input data processing and parameter sensitivity tests with the Community Land Model, version 5 (CLM5; Lawrence et al. 2019). The data pipeline uses NWT data as the foundation for modeling studies that can inform additional analyses and forecasts to address NWT hypotheses (e.g. changes in soil moisture in different landscape positions with extended summer). Major accomplishments related to this work include scripts that facilitated the publication of T-Van flux tower data (https://github.com/NWTIter/tvan_L1) to the AmeriFlux data portal (new AmeriFlux sites [US-NR3](#) and [US-NR4](#)). We have also continued improving and updating additional scripts to augment, filter, and gap fill the atmospheric forcing data that are needed to run CLM (https://github.com/NWTIter/NWT_CLM).

In Year 5, we continued working on developing Niwot-specific parameterizations for different vegetation communities across the Saddle. This includes modifications of leaf traits based on community weighted means measured across the Saddle grid and well as validation of simulated results with flux data from T-Van and snow depth measurements from the Saddle grid (Wieder et al. 2017; **Fig. 9**). We are currently integrating soil moisture and temperature measurements from the sensor network into our analyses because these data provide critical insights into changes in the soil moisture state across different alpine vegetation communities. The sensor network array is now generating data that will inform modeling approaches in the next 2-3 years with high resolution (in time and space) data. In our prior modeling work we had to rely on incomplete or infilled data to drive key aspects of the modeling (for example, soil moisture), and the emerging dataset will allow us to revisit these earlier assumptions and revise our modeling accordingly. Moving forward, we are investigating ways to revise the phenology parameterization of the model using phenocam data, implementing the representative hillslope model across the Saddle, and beginning to evaluate potential biotic and abiotic effects of shrub expansion in alpine tundra.

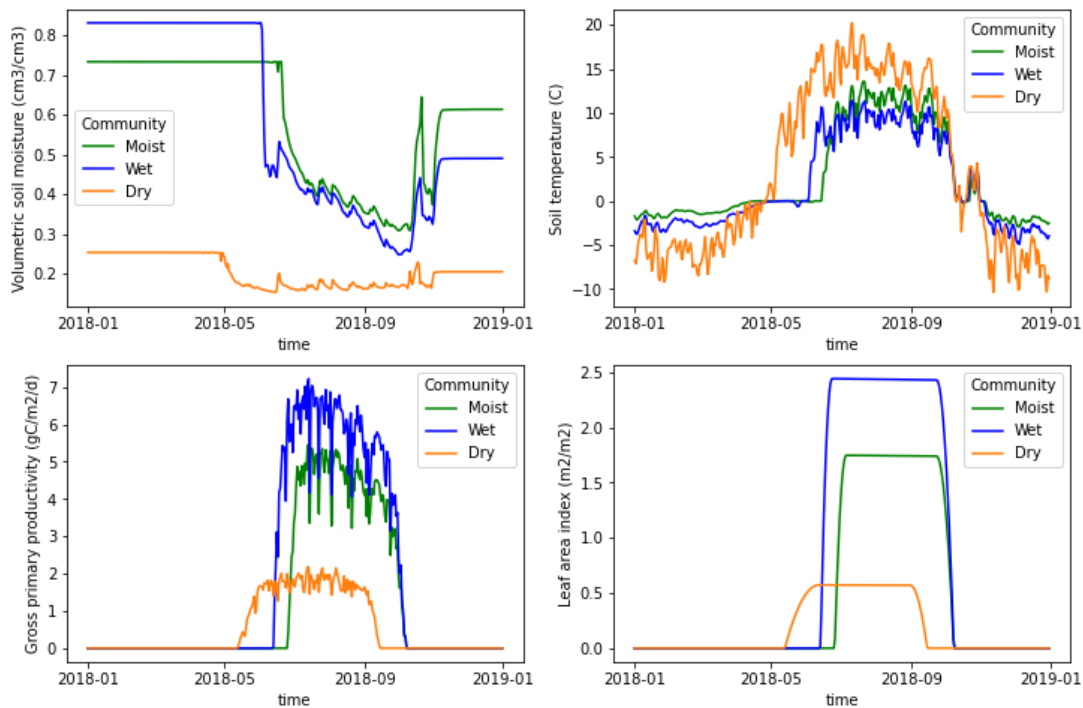


Figure 9. Seasonal variation in soil moisture, soil temperature, productivity and leaf area index that are simulated for moist, wet, and dry meadow simulations (green, blue, and orange lines, respectively) in the Saddle by the Community Land Model, version 5 (CLM5) in single point simulations at Niwot Ridge Simulations with CLM5 forced with atmospheric inputs collected from the T-Van towers and Saddle meteorological station.

Modeling hydrologic and lake processes. As described in the original proposal, we are creating a spatially explicit modeling system for the lakes within Niwot Ridge by utilizing a one-dimensional mechanistic lake model, the General Lake Model (v.3). This model uses empirical long-term buoy data collected from Green Lake 4 for model calibration and validation. Our progress on this model has shown promise in accurately modeling physical lake processes. Thus, this modeling effort will expand our knowledge of the controls on physical lake conditions while also informing our complementary studies, including experimental manipulations and long-term observations, to better understand the drivers of dynamic ecological processes.

C. New cross-cutting terrestrial and aquatic experiments. We have established two large multi-investigator experiments – a terrestrial and an aquatic – to explicitly test our predictions for responses to extended summer climate conditions.

Tundra manipulation of growing season length. Tundra manipulation of growing season length. We are currently in the fourth year of our “black sand” experiment where we manipulate growing season length. We manipulate the length of the growing season by applying a thin layer of black sand to the snow surface in early spring to reduce snow albedo and enhance melt rates without concurrently affecting snowpack depth (after Blankinship et al. 2014). Snow measurements in this experiment continue to confirm that the black sand treatment increases the albedo and speeds snowmelt, with variable effects on soil moisture. We have continued measurements of species composition in a series of subplots and transects within each plot as

well as measurements of soil temperature, nutrient availability, and moisture. We have continued the summer warming treatment using ITEX chambers within both treatment and control plots, enabling us to look at the interactive effects of early snowmelt and warming.

Our initial analyses suggest modest responses of the plant community (in terms of taxonomic and functional composition) to our manipulations so far, indicating and that we need to monitor these plots for several more years to document compositional responses. Plant phenology has been responsive to the experimental manipulations but is highly variable across species. We have also continued monitoring pollinator visitation in both control and extended growing season plots and found that pollinators respond to early snow melt, but that the impact is mediated by landscape position.

Manipulation of aquatic growing season length and DOM. Year 5 marked the second and final year of our mesocosm experiment in the Green Lakes watershed. The objective of this project is to test how earlier ice-off on lakes and increased dissolved organic material (DOM) associated with encroachment of terrestrial plants in the alpine watershed interact to affect aquatic food webs. While we had to modify our proposed methodology due to logistical challenges, we launched our “megacosm” experiment in the fall of 2019 and successfully completed our second full summer season of experimentation and sampling in the summer of Year 5.

This experiment involves the use of large-volume mesocosms (2600 L, 2.5-meter diameter, 0.66-meter depth) that are deployed inside the watershed property and can be manipulated more directly with higher replication relative to in-lake manipulations (which are not allowed by the watershed authority). We call these “megacosms” because the tanks are significantly larger in both volume and surface area than what is commonly used for mesocosm experiments. Although megacosms cannot capture the full complexity of biotic and abiotic interactions unfolding within lake ecosystems, we use them here as one of several lines of investigation (alongside long-term data, comparative sampling over an elevation gradient, and ecosystem modeling) to specifically address interactions in a simplified food web involving phytoplankton and zooplankton. Over Years 1-3, we carefully developed and refined methods through a series of pilot studies in which we confirmed that we could effectively advance ice-out timing and increase average daily temperature by varying the color of mesocosm tanks (black vs beige, i.e., via changes in albedo). We also determined, through analysis of pilot data, that treatment with willow leaf packs significantly increases DOM concentration in treated tanks. These comprehensive pilot studies collectively set the stage for the larger manipulation experiment that finished its second full season in Year 5.

In the fall of 2019, we established 20, 2600L mesocosms at Sandy Corner, a gravel clearing in the Green Lakes watershed at 3300 m ASL (40.042289, -105.584006). Tanks were left to naturally fill with snow over the winter, and after the spring thaw, megacosms were sufficiently full of water. The manipulation is a 2 x 2 randomized block design, in which we manipulate earlier ice-out (black vs. beige tank color), increased DOM (willow leaf pack added yes/no), and their interaction (**Fig. 10**). The experiment includes 5 replicates per treatment for 20 total megacosms. Blocks of four tanks are grouped based on physical location on the landscape to account for variations in slope and wind exposure. The first year of manipulation was hindered by an exceptionally hot and dry summer, which lowered water levels in the megacosms precipitously and prompted us to supplement using water from a nearby stream.

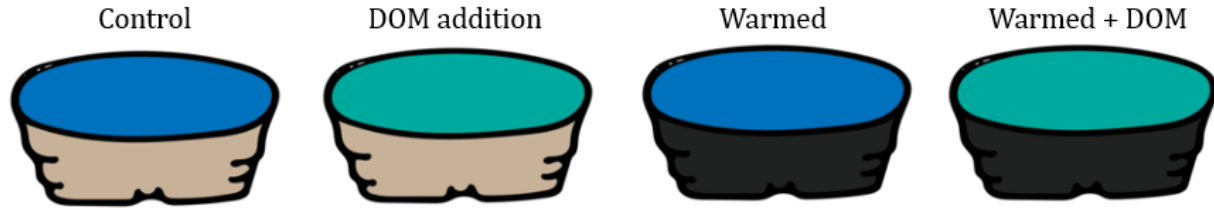


Figure 10. Megacosm experiment involving a 2 x 2 factorial manipulation with a control, a warmed treatment, a DOM subsidy treatment and a combination of warmed and DOM.

In year 5, we improved some aspects of the megacosm experiment from insight we gained in year 4. Tanks were seeded with zooplankton, DOM leaf packs, and tiles as soon as tank ice-out occurred. To accomplish this, zooplankton were collected from under the ice at GL4 and from Red Rock Lake (a montane lake located in neighboring Brainard Lake drainage), providing a mixed community from both alpine and montane lake systems. Our Ash Free Dry Method (AFDM) was improved by replacing the clay tiles placed at the bottom of the tanks for Fiber Reinforced plastic (FRP) tiles; FRP tiles have been shown to be a superior substrate for growing periphyton (attached algae) (Mohapatra et al. 2016). The location of the temperature loggers (HOBO Pendant® Temperature/Light 64K Data Logger) was adjusted from a surface and bottom configuration to a duplicate bottom configuration due to decreasing water levels throughout the summer season causing the surface temperature loggers to become exposed out of the water. Temperature was still recorded every 2 hours throughout the entire year and the duplicate logger configuration provided redundancy in case of sensor failure. These loggers provided us with a finely resolved record of ice-thaw patterns and water temperature that can be linked to DOM and albedo treatments.

Starting with spring ice thaw in May of 2021, megacosms were visited weekly for a total of 20 visits. Each weekly visit included water quality observations for water depth, Photosynthetically Active Radiation (PAR), Dissolved Oxygen (DO), Specific Conductivity (SPC), Total Dissolved Solids (TDS), turbidity, nitrate, and pH. Turbidity was a new measurement added in year 5 to better assess the effect of DOM treatments on water clarity. Along with our weekly water quality measurements we completed five large sampling events throughout the summer (triweekly, once every three weeks). At each sampling event we collected water samples for chlorophyll-a and DOC analysis, and FRP tiles for periphyton biomass analysis. Water samples for nutrient analysis were collected on the 3rd and 5th visits to best capture the entire summer growing season. Zooplankton were collected on the 2nd and 4th visit; our zooplankton collection method was improved from year 4 by using a Van Dorn water sampler to collect 4 liters of water from each megacosm after a 1-minute soak on the bottom of the tank. The zooplankton sample was then concentrated by filtering the 4 liters of water through 80-micron mesh.

We hypothesize that increases in the ice-free season length induced by the warming manipulation will lead to increases in chl-a and phytoplankton biomass and will result in shifts in zooplankton community structure (Preston et al. 2016; Dokulil et al 2009; Loria et al. 2020). Year 5 provided us with an abundance of data and, while some samples have yet to be processed (including DOC and most zooplankton), initial analyses have identified clear differences among treatments. Dark tank albedo effectively induced significantly earlier ice-out, with black tanks losing ice an average of 7 days earlier than beige tanks. Additionally, summer water temperatures in black megacosms were 0.5°C warmer on average. We are waiting for our DOC samples to be processed, and therefore we do not yet have metrics to model the effectiveness of

the DOM treatments; however, data from our pilot studies suggested that leaf pack significantly increases DOM concentration in treated tanks. Furthermore, initial exploration of zooplankton samples indicates that taxa typical of alpine lakes such as *Daphnia pulicaria* and *Chydoridae* spp. persisted in tanks as well as individuals from the montane community including *Bosmina* spp. and *Daphnia rosea*. Furthermore, preliminary analysis of zooplankton density shows a positive correlation with DOM treatment, lending insight into biotic responses to increased DOM inputs from encroachment of terrestrial plants in alpine environments. While a complete evaluation of biotic responses to the experimental treatments will follow the completion of sample processing, these preliminary analyses suggest that several interesting results will emerge from this experiment. We are optimistic that with two full growing seasons of data from this experiment we now have enough data to provide us with unique and valuable insights into the implications that a warmer, extended growing season and increases in terrestrial DOM have for abiotic limitations and subsequent biotic reactions in lake ecosystems.

2. BIOTIC INFLUENCE: How Do Biotic Effects Influence Climate Exposure and Ecological Responsiveness? Our second hypothesis focuses on how biota can influence climate exposure through effects on the physical environment at smaller spatial scales than those examined in Hypothesis 1. We propose fine-scale biotic effects can attenuate exposure to climate changes, influencing environmental heterogeneity and response at a patch-scale. Our approach involves testing for associations across space in conjunction with experimental manipulations that are linked with the climate exposure experiments described in Hypothesis 1. We focus on two well-documented patterns at high elevation: (A) in the alpine, the physical presence of particular life forms (cushion plants, shrubs, krumholz) can affect wind redistribution of snow, increase soil moisture, and modify the temperature and nutrients of the underlying soil, and (B) in aquatic environments, terrestrial subsidies of dissolved organic matter (DOM) can protect phyto- and zooplankton from harmful UV radiation and help offset nutrient limitations related to high flushing rates.

A. Biotic influence of snow accumulation in terrestrial areas. In both tundra and upper-elevation forests, we expected that the presence of individuals that provide physical shelter from wind, causing accumulation of snow and organic matter (e.g., cushion plants, shrubs, trees), will attenuate climate exposure and be associated with shifts in population growth rates, species composition, and ecosystem processes.

Observational studies. To better inform our predictions of our experimental studies below, we first quantified how shrubs (*Salix spp.*) influence microclimate and the functional traits of species associated with those shrubs in 108 plots arrayed across north and south facing aspects. We have found that shrubs buffered temperatures and facilitated resource acquisitive alpine plants (**Fig. 11**), driven by effects on abundance (Brigham et al., in prep). These findings suggest that shrubs offer a protected microclimate that could buffer alpine communities from the very global change drivers that contribute to shrub expansion. Additionally, shrubs enhanced the establishment of a seeded subalpine plant, suggesting that shrubs may act as “stepping-stones” for subalpine plants to move uphill to track their climatic niche (**Fig. 11**).

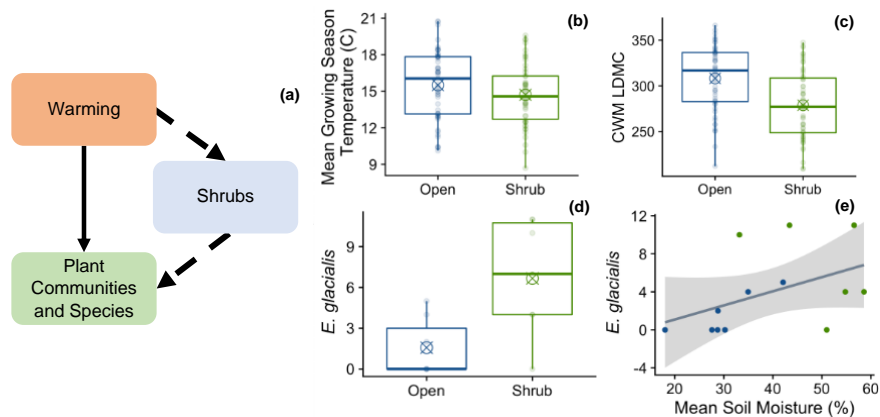


Figure 11. Shrub presence, enhanced by warming temperatures, may shield plant species and communities from the negative effects of warming (a). Shrubs buffered mean soil temperatures in the rooting zone (c) and resulted in lower leaf dry matter content of the plant community (d), indicating a higher abundance of more acquisitive plant species. An experimentally seeded subalpine species (*Erigeron glacialis*) showed greater survival in the presence of shrubs (e), likely due to their positive effects on soil moisture (f).

Species associations. We measured nematodes, plants, and soil microbes, snow cover, pH, soil water holding capacity, and different forms of soil C and N in 98 plots across the vegetated-unvegetated ecotone at the upper reaches of NWT (Porazinska et al. 2021). We found that nematode communities exhibited extensive shifts from a few individuals of a single species in unvegetated soils to hundreds of individuals and tens of species within every feeding group under complex plant communities (Porazinska et al. 2021, **Fig. 12**). Representatives of omnivorous and bacterivorous K-strategists preceded plants and plant parasites and root associates depended on plants most. Nematode densities were a strong contributor to C and N storage and together with plants and water holding capacity explained up to 84 % of the total and microbial C and N variability. Because nematode communities at the uppermost sub-nival zone of Niwot Ridge are largely at their early phases of assembly, with continuing climate warming we predict their increasing abundance and diversity will likely continue, as will their impact on soil C and N processes.

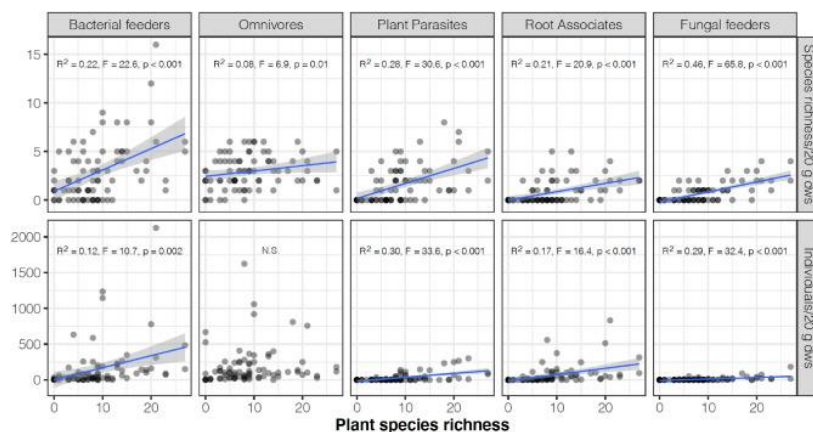


Figure 12. Relationship between plant species richness (x-axis) and richness (number of nematode species) and density (number of nematode individuals) (y-axis, top and bottom panels, respectively) within trophic groups of bacterial feeders, omnivores, plant parasites, root associates, and fungal feeders. Plant species richness is increasing in these high elevation sites as vegetation moves uphill due to warming. dws = dry weight of soil.

Utilizing an 18-year simulated N deposition and species removal experiment, a separate NWT study found that the soil microbial community responded directly to N rather than indirectly through changes in the plant community (**Fig. 13**) despite N also affecting plant composition (Brigham et al. in press).

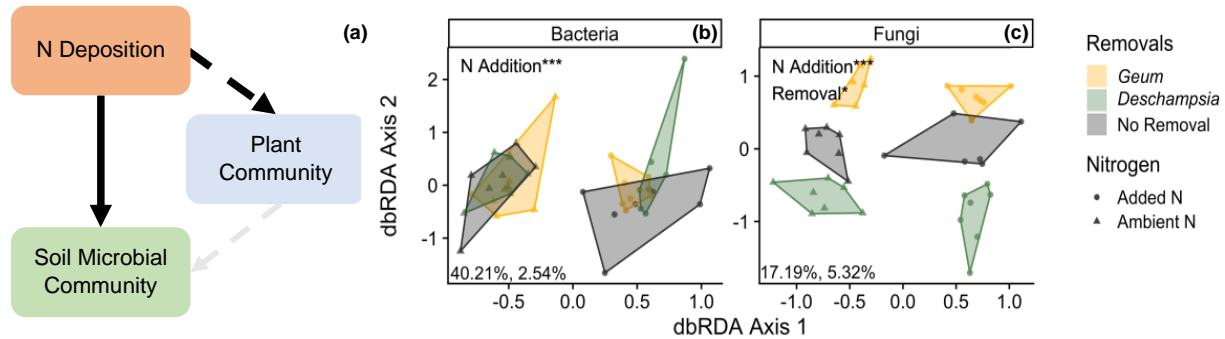


Figure 13. Although N influenced the plant community, this did not cascade to the microbial community (a). Both the bacterial (b) and fungal (c) soil communities responded to N addition directly rather than an experiencing an interaction between N and our plant removal treatment, which would have suggested an influence of the plant community on microbial response to N.

Experimental manipulations. In combination with the extended summer “black sand” manipulations (described above), we are manipulating biotic interactions to elucidate how physical protection from wind can facilitate plant performance. In the fall of 2018, within each of the large plots in the terrestrial growing season length experiment (5 control, 5 early melt-out), we established three pairs of artificial shrub and control subplots. We adapted “con-mods” (Rachal et al 2015) to function as artificial shrub structures. Each con-mod consists of an “X”-shaped structure (30.5 cm tall with each of four winged panels 40 cm long, constructed using rebar and hardware cloth). In Year 5 we explored the abiotic and biotic impacts of these artificial shrubs. We found that our ‘con-mods’ buffer both mean and maximum temperatures in a manner similar to real shrubs. However, unlike real shrubs, the ‘con-mods’ do not accumulate snow and hence have no effect on early season soil moisture or the number of freezing degree days. Additionally, the ‘con-mods’ were not found to impact species composition or beta diversity, in contrast to natural real shrubs (which act as microclimate refugia and impact both of these metrics).

B. Biotic influence of UV protection in lakes. In alpine lakes, Hypothesis 2 revolves around changes in land cover due to uphill vegetation advances that will increase terrestrial subsidies of DOM into lakes. Higher DOM is expected to function as both a carbon subsidy and help to attenuate UV radiation, reducing the investment by zooplankton and phytoplankton in mitigating the deleterious effects of UV and collectively enhancing planktonic production.

Experimental manipulations. We have simulated the increase of terrestrial DOM input to lakes by adding DOM as an additional factorial treatment to the megacosm experiment (discussed above). The DOM treatment consists of leaf-packs composed of locally collected willow leaves enclosed within standardized nylon mesh bundles. We intended to increase dissolved organic carbon concentrations of manipulated megacosms to be comparable to averaged open water DOC concentrations of previously surveyed subalpine lakes located north and south of the Green

Lakes Valley ~1.49 mg/L (range: 0.590 to 2.78 mg/L) and about 0.637 mg/L lower than local alpine lakes (range: 0.486 to 1.743). Pilot studies in which we deployed leaf packs in a set of megacosms illustrated that this treatment method successfully increases DOC and reduces PAR.

We predict that the addition of DOM will increase light attenuation in DOM treated tanks and provide protection for zooplankton from damaging UV radiation (Kelly et al., 2014). We will assess UV radiation stress in zooplankton assemblages by (1) examining *Daphnia* spp. for photo protective pigments and (2) assessing the prominence of taxonomic groups with high UV tolerance (e.g., calanoid copepods and *Holopedium*) (Kessler et al. 2008). Increases in DOM are also expected to amplify the degree of top-down regulation of phytoplankton and chl-a by zooplankton (Leach et al., 2019), which we quantified based on the correlation between variation standing biomass in adjacent trophic levels (e.g., zooplankton and phytoplankton) (Frank et al. 2008; Bunnell et al. 2014). We further hypothesize that the relative importance of DOM will be most influential in megacosms with an extended ice-free season, which will provide time for this added UV protection to take effect. We further anticipate additive or interactive effects between growing season length and enhanced DOM treatments, such that planktonic biomass and community composition shifts will be most pronounced in the presence of both manipulations because plankton will have a longer growing period under less abiotically stressful conditions.

We are currently analyzing the second and final year of the community and trait data, which was collected during the 2021 growing season. Preliminary analyses of zooplankton density show a positive correlation with DOM treatment, lending insight into biotic responses to increased DOM inputs from encroachment of terrestrial plants in alpine environments. Importantly, this experiment will help decouple the relative influence of growing season length, UV-stress, and DOM availability, which typically covary with elevation.

C. Observational, Experimental and Model Integration. In Year 5 we focused on improving the link to long-term climate datasets and accessibility of the terrestrial Community Land Model (CLM) and the aquatic General Lake Model (GLM). In the upcoming year we plan to integrate the empirical results from the terrestrial and aquatic growing season manipulation field experiments with the predicted outcomes from of the CLM and GLM. This modeling and experimental iterative approach broadens our capability to quantify the mechanism of the observed responses and improve our models of the impacts of changing conditions. More broadly, we are working to articulate ways that empirical work and modeling can be better integrated in models like CLM (Kyker-Snowman et al. 2021).

Q3) ADAPTATION STRATEGIES. How do different strategies for managing temporal variability and uncertainty at the organism and population levels aggregate to influence community and ecosystem processes? We expect that terrain- and biota-related differences in exposure, in addition to modulating average conditions (Q1 and Q2), will influence environmental variability and predictability. Species' sensitivities reflect evolutionarily constrained responses to past climate, and constraints at the organism and population levels should be reflected in community and ecosystem responses.

3. Adaptation Strategies. How do different strategies for managing temporal variability and uncertainty at the organism and population levels aggregate to influence community and ecosystem processes? Our third hypothesis is that population, community, and ultimately ecosystem responses to climate change will be shaped by the life history strategies that species

have evolved in response to historical patterns of environmental variation and uncertainty. At Niwot Ridge, we expect that terrain- and biota-related differences in exposure cause spatial variation in the temporal variability and predictability of key environmental variables. For this hypothesis we are currently focusing on strategies and responses of plant species in the alpine tundra.

We are primarily addressing this hypothesis using data that is being collected in the terrestrial Sensor Network Array. Specifically, we are characterizing the magnitude and patterns of within-year variation in soil moisture, soil temperature, and air temperature, and among-year variation in soil moisture, soil temperature (growing degree days and freezing degree days), snow-off date, and growing season length. We are testing if and when these measures predict plant community composition and individual species distribution patterns across the heterogeneous terrain in the saddle catchment. In Year 5, we collected the third year of an expanded sampling design that we initiated in 2019 and have updated our analyses to include data from 2020 (summarized below). We also completed a third year of monitoring a pilot transplant experiment that we installed in 2019 to inform a large, multi-species transplant experiment that we will be proposing as part of the Niwot LTER VIII renewal proposal in March 2022. The transplant experiment will complement our observational analyses in the Sensor Network Array by empirically disentangling the correlated effects of landscape position and microclimate in determining the mean, variance, and autocorrelation (predictability) of environmental variables on plants from different community types and with different climate tolerances.

A. Characterizing spatial and temporal variation in tundra plant communities. Our updated analyses of the vegetation and environmental data collected in the Sensor Network over four consecutive years data (2017-2020, with extended sampling in 2019 and 2020) are beginning to reveal the spatial and temporal distribution of key environmental drivers of tundra plant community composition and phenology. Our analysis of environmental variables alone identifies a primary environmental gradient spanning locations with relatively long, hot, dry growing seasons and cold winters (due to low snow cover) to those with short, cool, wet growing seasons and buffered soil temperatures (due to a high amount of snow cover) (**Fig. 14A**). In 2020, we had developed methods for characterizing *variability* in soil moisture and temperature as the number of times the environmental variable crosses a biological threshold and *predictability* using autocorrelation analysis (see Year 4 report for summary of these methods). This year we have started exploring alternative methods for quantifying predictability and stochasticity, e.g. wavelets, quantmod, and fourier transformations, including resources that have been organized by Jennifer Rudgers (Sevilleta LTER) and John Kominoski (Florida Coastal Everglades LTER). After more carefully investigating these different metrics, we plan to include them in our analysis of environmental variation to fully characterize spatial and temporal conditions experienced by the tundra plant communities in the Sensor Network Array.

We are also evaluating the relative importance of soil temperature, soil moisture, snowmelt date, and air temperature in driving patterns of community composition and fine-scale species distribution patterns. So far, we have found that variation in plant community composition among plots far exceeds variation *within* plots across years, though there are some potentially interesting differences in community stability among plots (**Fig. 14B**). Our next step is to test which of the measured environmental variables (including mean values and measures of

variability and predictability) best predict patterns of community composition (e.g., graminoid vs. forb cover) and the fine-scale distribution patterns of individual plant species.

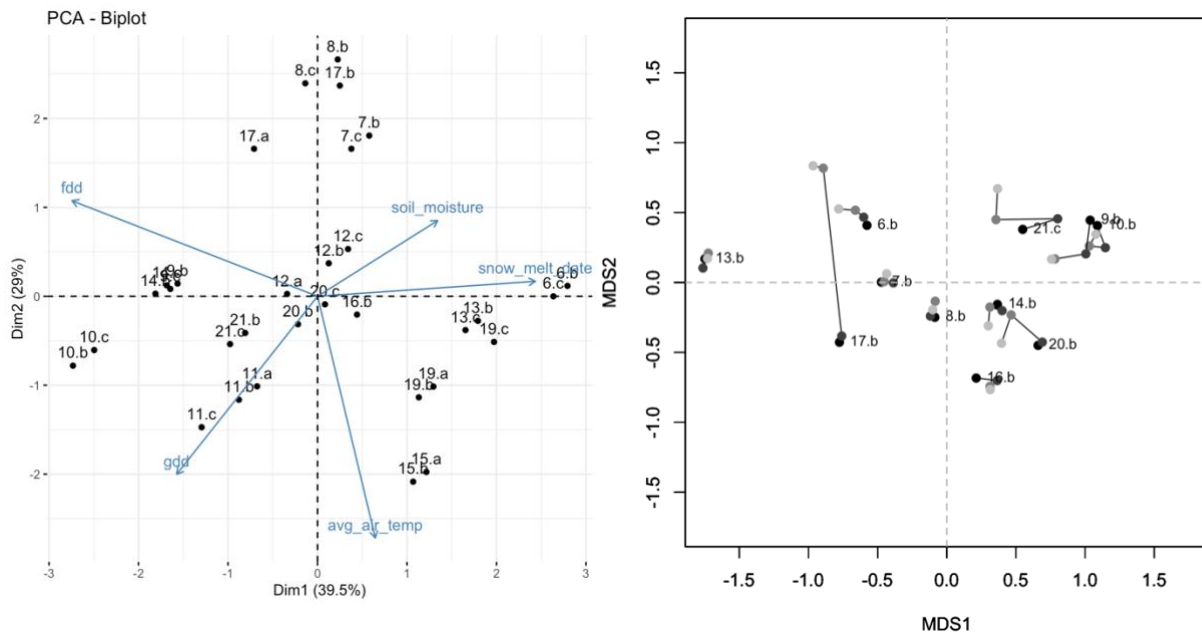


Figure 14. Analyses of environmental and plant community composition from the terrestrial Sensor Network Array. **A)** Spatial variation in environmental variables, illustrated as a biplot from a principal components analysis. Arrows identify the eigenvectors for *fdd* = freezing degree days, *gdd* = growing degree days, *snow_melt_date* = mean day of year when snow melted off of the plot, *soil_moisture* = average soil moisture during the growing season (5 cm below soil surface), *avg_air_temp* = mean annual air temperature. Data were averaged across years and standardized (to Z-scores) prior to analysis. Other environmental variables that are measured in these plots (e.g., seasonal soil temperatures, soil moisture at 30 cm depth, and maximum snow depth) were removed from this analysis because they are highly correlated with the variables shown here. The Sensor Network plots are identified by their node number and the plot replicate (e.g., “10b” is plot *b* at Node #10). **B)** Multidimensional scaling plot showing variation in plant community composition of the sensor network plots over four years (2017-2020). Consecutive years are identified by dots of increasing darkness (lightest gray = 2017, black = 2020). The multiple years of data from the same plot are connected with lines.

B. Environmental drivers of tundra phenology

We have continued to analyze digital images from phenocams in the Sensor Network using fine-scale temperature and moisture data from the Sensor Network Array to understand the environmental triggers of start, peak and end of growing seasons across this heterogeneous area. While phenological transitions are often assumed to occur after a particular threshold of cumulative degree days, or triggered directly by snowmelt, we find that instead time-to-event models (Templ et al. 2017), which consider multiple constraints, better predict the timing of phenological transitions (Fig. 15).

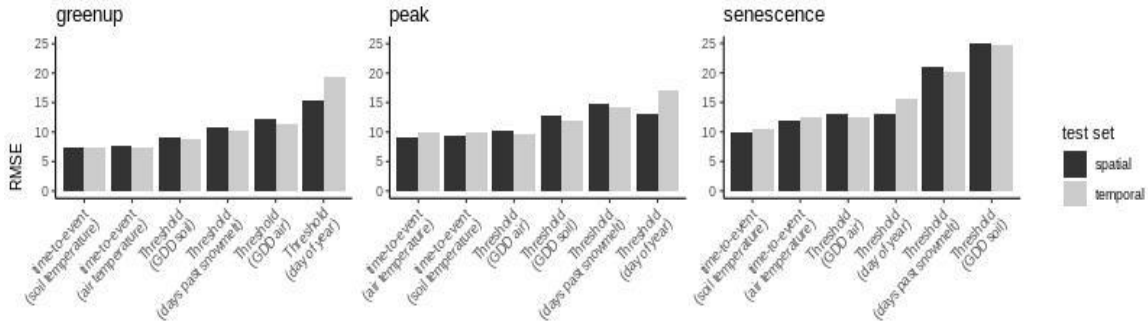


Figure 15 Comparison of time-to-event models (which incorporate temperature, moisture, time since snowmelt, and calendar date) vs. threshold models in predicting the timing of greenup, peak season and senescence timing. We performed leave-one-out cross-validation over space (by removing single nodes) and time (by removing single years) to assess the predictive capacity of the model (RMSE in days).

An example of the constraints on senescence is provided in **Fig. 16**, where the daily probability of senescence increases with days past snowmelt as well as calendar date, but decreases when there is abundant soil moisture or warm soil temperatures. These results have important implications for improving carbon cycling models such as CLM 5.0, which use algorithms calibrated for temperature environments but show consistent biases in the timing of greenup and senescence against empirical data in the Arctic/Boreal zone (Birch et al 2021).

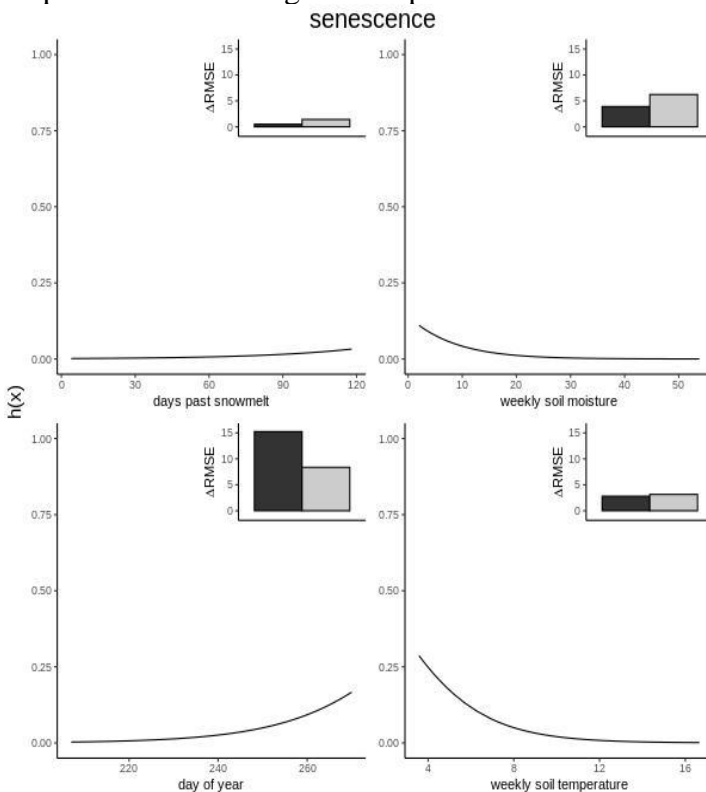


Figure 16. Daily probability of senescence as a function of environmental drivers. Insets show the improvement in model fit for predicting a test subset of the data spatially (node) or temporally (year) when each variable is dropped from the model. While senescence timing shows some canalization (strong predictive importance of day of year), it can be delayed by late snowmelt, high soil moisture,

4. CATCHMENT INTEGRATION: How does hydrological connectivity affect catchment-scale processes? In our fourth hypothesis, we focus on how variability in hydrologic fluxes (e.g. snowmelt) can (1) provide a strong spatial and temporal context for the fine-scale foci of H1-H3 and (2) affect biogeochemical and ecological processes at catchment-to-landscape scales. Flow paths, water sources, and residence times will dictate connectivity between high and low elevation ecosystems (e.g., alpine to montane) as well as terrestrial and aquatic ecosystems (e.g., hillslopes to streams and lakes) (Webb et al. 2018). We expect that at the catchment scale, some areas within the terrestrial ecosystem may only meaningfully contribute water and solutes to aquatic ecosystems during particular periods of time, such as early snowmelt. Identifying how these patterns and the driving mechanisms change interannually, as well as how they will change under future forcings, requires the long-term observational record that NWT collects. In the summer of 2020, we began supplementing the long-term records of stream discharge with the installation of an additional stream gauge that began measuring discharge. This additional gauge will track missing or losing flows that we have previously observed, providing data that can more clearly constrain model estimates of the water balance to provide a clearer sense of the distribution of snow water and precipitation throughout the basin.

During the last year, we have dug deeper into thinking about how portions of the landscape may contribute disproportionately to catchment- or ecosystem-scale processes. We adopted the framework described by Bernhardt and colleagues (2017) of assessing the function of **ecosystem control points** and how they will change over time. Ecosystem control points are those areas within a landscape that have high rates of biogeochemical processes and therefore a disproportionately large effect on biogeochemical and ecological processes at the catchment scale. At NWT, hydrology, temperature, and substrate availability are first-order controls on biogeochemical processes (Chen et al., 2020) and, as a result, the occurrence of ecosystem control points and their distribution in space.

We expect the relative importance of different parts of the catchment to vary with climate variables (e.g., snow distribution, snow melt, and air temperature), and so we take several parallel **catchment-to-landscape scale studies** to integrate processes and temporal dynamics in response to climate conditions. We focus on two catchments that differ in their biophysical setting: the Saddle Catchment, which extends from established tundra through krummholz to subalpine forest, and the Green Lakes Valley 4 (GL4) catchment, which extends from the Continental Divide through talus slopes to Green Lake 5 and 4. At an even broader scale, we have focused our studies on the alpine landscapes of the Green Lakes Valley and on the sub-alpine forests of the Como Creek Catchment. These efforts, detailed below, are coupled with our **within-catchment studies** (e.g., H1-H3). Ultimately, we want to integrate hydroclimatological, biogeochemical, and ecological processes to understand the drivers of carbon, nutrient, and water export at larger scales.

A. Integrative efforts at the Saddle Catchment

A new statistical framework to map soil moisture and determine hydrologic connectivity across the alpine catchment. In Year 5, we published a study that connects patch-scale behavior to catchment-scale soil moisture patterns and hydrological processes. Ph.D. student Anna Hermes, Dr. Hinckley, and colleagues used an unsupervised hierarchical clustering approach coupled with a large soil moisture dataset to determine unique hydrologic functions across the Saddle Catchment (Hermes et al., 2020). This work identified six hydrologic groups within the

catchment, including four relatively dry clusters that had a dramatic decline in soil moisture earlier in the season, and two relatively wet clusters that remained wet during the spring and summer. A random forest model and datasets of underlying soil moisture drivers (e.g., snow, plant productivity, macro- and micro-topography, and flow accumulation patterns) were used to map these functions across the catchment and gain insight into broader patterns of soil moisture and hydrologic connectivity. This effort indicated that > 55% of the catchment is hydrologically connected to the channel; other patches remain hydrologically disconnected throughout the year. These insights are now guiding field- and numerical modeling efforts to test both how moisture patterns affect a broad suite of biogeochemical processes and explore how the patterns may change in the future as snow dynamics shift.

B. Spatially-explicit modeling to assess hydrologic connectivity at multiple scales. In alpine ecosystems, snowmelt is a primary driver of soil moisture and hydrologic connectivity. Future changes in the spatio-temporal distribution of snowmelt associated with climate warming and vegetation change have potentially profound implications for biogeochemical processes, patterns of plant productivity, and the distribution and types of ecosystem control points. To evaluate the potential impacts of snowpack changes on soil moisture and runoff, we used distributed hydrologic and eco-hydrologic models representing different scenarios of future snowpack and vegetation characteristics. In both alpine and sub-alpine landscapes, we hypothesize that climate warming will impact the density of snowfall and therefore may reduce wind-redistribution of snow. In addition, we hypothesize that changes in the distribution of vegetation, in particular an increase in the elevation of tree-line, will alter the location of snow drifts.

Evaluating snow water storage and hydrologic partitioning at the sub-catchment scale and into the future. The Distributed Hydrology Soil Vegetation Model (DHSVM) has been run using the historical dataset (WY2000-WY2018), and **Fig. 17** shows the average annual Water Tower Index (WTI) map of the Saddle Catchment. The WTI represents the time and quantity of water that is stored in the snowpack relative to the timing of precipitation. During the reporting period, significant effort has been placed on improving the representation of vegetation in model calculations of WTI, which are evident in the spatial patterns shown in Fig. 17. This analysis required us to make substantial updates to the Saddle vegetation file that served as an input file to DHSVM. These data have been submitted and it currently being processed for proper storage by the NWT data manager. All DHSVM model input files and output files (e.g., hourly, spatially distributed precipitation, SWE, soil moisture, etc.) have also been filed with NWT, in collaboration with Ph.D. student Nels Bjarke and Dr. Ben Livneh.

The DHSVM model using future climate (years 2070-2100) has been completed, and we are currently conducting preliminary analyses with the output files to evaluate the spatial patterns of future snow water storage (as WTI). To generate updated input files for the future climate simulation, we needed to obtain data from the Weather Research Forecasting (WRF) model 2-dimensional retrospective simulation, including precipitation, specific humidity, air temperature, shortwave radiation, and long-wave radiation. Using both control and pseudo-global warming WRF output, delta values (warming value – control value) were generated for each variable at the 9 WRF pixels containing and surrounding the Saddle Catchment. An average delta value per variable per day was then implemented within the DHSVM meteorology input file. We predict that areas with a high WTI in the Saddle Catchment (**Fig. 17**, areas in blue) will show the greatest sensitivity in WTI with warming and greatest change in hydrologic partitioning. This is expected

because there is more potential for change where precipitation and surface water inputs are out-of-phase. Areas with a lower WTI (**Fig. 17**, areas in red), are expected to remain somewhat the same in WTI value and partitioning behavior through time due to continued water limitation.

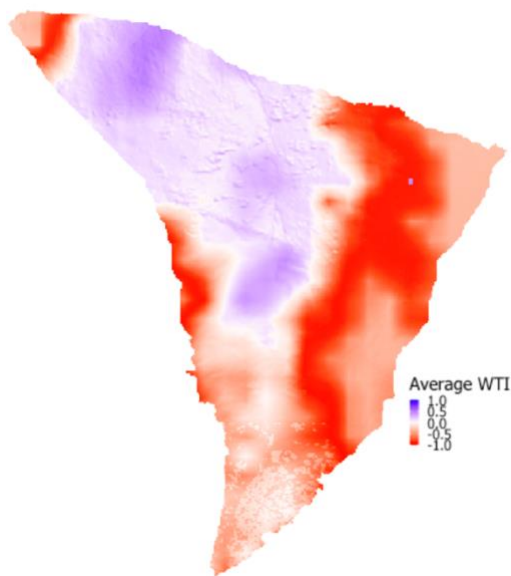


Figure 17: Average annual WTI (a metric quantifying magnitude and timing of snow water storage) across the Saddle Catchment.

Climate and topographic controls on the variability of snow water equivalent and snowmelt in a continental alpine watershed. Seasonal snowpack is an essential component in the Earth's surface hydrological cycle and energy balance. Recent climate warming has caused decreased peak snow accumulation, altered snowmelt rates, and earlier snow disappearance in many mountain ecosystems. Understanding and characterizing the spatial and temporal distribution of snow, often reported as snow water equivalent (SWE), is of crucial importance for assessing water availability to surrounding environments. During the reporting period, we conducted a comprehensive assessment of the long-term interannual variability of SWE distributions and snowmelt in the alpine Green Lakes Valley (GLV) located in the Colorado Front Range. We leverage physically-based energy and mass balance models, satellite observations of Fractional Snow Covered Area (FSCA), and long-term quality controlled daily meteorological data to estimate SWE distribution. Using a 23-year record of SWE distribution (i.e. 1997-2019), we evaluate the impacts of topographic and climate variables on interannual variability of SWE and snowmelt. Specifically, we use a linear regression model to compare metrics of elevation, aspect, slope, wind exposure, vegetation fractional coverage, and air temperature against metrics of SWE variability, including the temporal coefficient of variation in annual maximum SWE, the standard deviation of annual maximum SWE, the range in maximum SWE, maximum and average snowmelt rate, and snow disappearance date.

We find that the magnitude and interannual variability of maximum SWE in GLV shows high variabilities, with a 23-yr average of 70 ± 17 cm, and the coefficient of variation (C_v) of 0.88 ± 0.18 . Wind shelter index overall has the greatest impacts on the interannual variability in maximum SWE, while the C_v is mostly controlled by the elevation (**Fig. 18**). The snowmelt also shows high spatial variability. Net radiation provides the dominant energy for snowmelt in the GLV, which is about 2.4 times the total turbulent flux. Wind shelter index controls snowmelt rate and snow disappearance, while snowmelt onset is controlled by air temperature. The historical relationships between SWE distribution and topography have the potential to elucidate potential

ecosystem response to future changes in snowpack and associated impacts on eco-hydrologic processes.

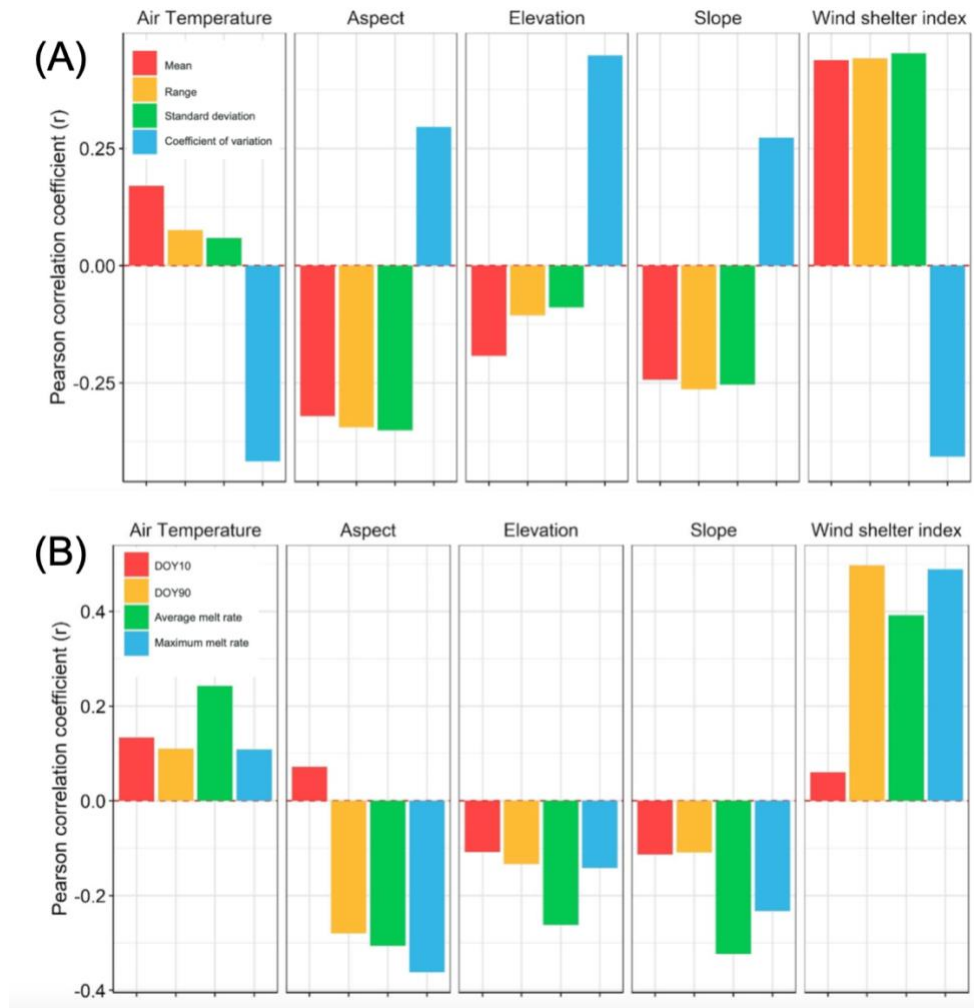


Figure 18. The relationships between topographic and climate variables with maximum SWE (A) and snowmelt (B). The topographic variables include aspect, elevation, slope and wind shelter index, while the air temperature is used as the climate variable. The mean, range, standard deviation and coefficient of variation values are used to characterize maximum SWE in the GLV. The day of year with 10% snowmelt (DOY10), day of year with 90% snowmelt (DOY90), average snowmelt and maximum snowmelt rate between DOY10 and DOY90 are used to characterize snowmelt in the GLV.

C. Integrative efforts across the alpine landscape.

Investigating ecosystem controls points: their roles and connectivity across the landscape.

In the summer 2020, we began investigating the function and potential changes to wetland features with global change across the alpine-to-sub-alpine landscape. Specifically, we hypothesize that wetlands—including alpine wet meadows and periglacial solifluction lobes—may have optimal conditions to support high rates of biogeochemical processes (particularly related to C, N, S, Fe, and Hg cycling) due to favorable conditions for microbial activity (e.g., temperature, water content, organic matter). During the summers of 2020 and 2021, we collected sediment depth profiles to measure these constituents in both wetlands and drier portions of the landscape. We also included an effort to investigate the coupling of biogeochemical cycles,

particularly C, S, and Hg, to determine whether Hg may be transformed to toxic methylmercury (MeHg) in the presence of sulfate reducing bacteria and enter the terrestrial and aquatic food webs where it could negatively affect pika, weasel, and fish populations. The latter food web study is the subject of both a new Ph.D. project and two undergraduate honors theses. These studies aim to explain catchment-to-landscape scale patterns, including those described in recent long-term data analyses (e.g., Crawford et al. 2020; Heindel et al. 2020).

Wetter portions of the NWT landscape have disproportionately high storage of reactive elements. Recent research by master's student Molly Huber demonstrated that alpine wetland areas—particularly alpine wet meadows and periglacial solifluction lobes—have significantly higher organic matter content as well as storage of sulfate and carbon compared with dry meadow locations ($p < 0.05$; Huber et al., in prep). Huber's findings are important, as they provide evidence that wetland areas, which constitute $< 10\%$ of the landscape, function differently than surrounding dry meadow areas, which are $> 55\%$ of the landscape (Hermes et al., 2020). They support the potential for disproportionately high biogeochemical activity that will affect ecosystem- or catchment-scale responses; we will begin exploring these differences in biogeochemical rates in NWT VIII.

Motivated by evidence for increased storage and transport of C and S in wetland areas at NWT, Ph.D. student Hannah Miller and undergraduate honors thesis student Clifford Adamchak began to evaluate the potential for MeHg movement into the terrestrial and aquatic food webs, a type of landscape connectivity. Methylmercury is a potent neurotoxin that is stimulated by sulfate reduction and bioaccumulates and biomagnifies in the food chain; it is a concern in many environments, including those at high elevations. Miller and Adamchak measured accumulation of total mercury (THg) in plant functional groups (including some of the first measurements of Hg in alpine herbaceous plants). In addition, they found accumulation of MeHg in weasel (*Mustela* spp.) tissues. Weasels feed both in terrestrial and aquatic ecosystems. Measurement of MeHg in pika (*O. princeps*, a food source for weasels) was minimal, pointing to the potential for aquatic animals to be sources of MeHg for weasels. In Summer 2021, undergraduate honors thesis Phillip Thornton and Dr. Hinckley measured THg and MeHg in fish species within the Green Lakes Valley. These data are forthcoming and will be integrated into a larger manuscript examining the sources and flows of Hg across the alpine landscape.

5. CROSS-SITE SYNTHESIS.

A. Network-level Participation. Researchers are active participants in synthesis efforts coming from the past science council meetings and are active in the IM and Outreach Network Committees, and social media communication efforts. PI Suding and co-PI Emery are active on the LTER Executive Committee. NWT Researcher Dr. Meagan Oldfather is active on the LTER DEI Committee.

B. Synthesis Groups. Niwot investigators are PIs for two of the NCO-sponsored synthesis groups. Dr. Suding co-leads the “Synthesizing population and community synchrony to understand drivers of ecological stability across LTER sites” group. Dr. Wieder co-leads the “Advancing soil organic matter research: Synthesizing multi-scale observations, manipulations & models” group that has resulted in two recent publications (Wieder et al 2021; Billings et al 2021). Niwot data have also been contributed to multiple cross-site tundra synthesis projects including one recently published in a special issue in Arctic Science (Prevey et al. 2021).

Another cross-site project, led by postdoctoral scientist Dr. Courtney Collins, evaluated tundra plant phenological sensitivity to experimental warming (Collins et al. 2021)

6. OUTREACH and EDUCATION LTER VII.

A. Diversity Equity and Inclusion (DEI) Committee. Niwot Ridge LTER formed a DEI committee in the summer of 2020. The first step of the committee in the Fall of 2020 was to perform a climate survey of our community. The goal of this survey was to assess the current climate of diversity, equity, and inclusion at the Niwot Ridge LTER to identify key areas to prioritize in our efforts to create a more diverse, equitable, and inclusive workplace where all members of the community feel they are valued, respected, and free to be their authentic selves. In Year 5, the DEI committee analyzed the results of this survey and produced a summary report for the NWT leadership team. The leadership team distributed a letter to the NWT community to propose priority activities based on the results of the survey (see below). This past year, the NWT DEI committee also developed and implemented a shorter post-field season survey to assess the community climate specifically during field season. We plan to repeat the larger survey every three years, and the post-field season survey every fall, to closely monitor the social climate of our community and assess the success of our efforts to improve diversity, equity, and inclusion in the Niwot LTER.

In general, the result of both surveys indicated that people feel that they could be their authentic selves while at Niwot Ridge. Moreover, people feel valued as a member of the Niwot Team and that their contributions are recognized and appreciated. While the overall trends were generally positive and most comments highlighted that people feel welcome and respected at Niwot, several issues were raised regarding behavior, safety, and authorship. Based on this feedback, the NWT DEI committee has taken or is planning to take the following steps that focus on three main issues areas:

Prevent Unacceptable Behaviors:

- NWT held a stand-alone active bystander training for all NWT researchers lead by Dr. Blair Schneider (ADVANCEGeo, KU) in February 2021.
- The DEI committee will reduce barriers to reporting concerns. First, the DEI committee set up an anonymous online comment “box” for people to anonymously submit issues. We still plan to train several personnel from all career stages so that an individual has multiple different people that they can approach with concerns, rather than a single supervisor.

Field safety:

- In conjunction with the Mountain Research Station, NWT provided a map to all field personnel that includes locations of all safety and emergency equipment and develop a general safety communication system for all researchers on the ridge.
- NWT LTER fully funded all associates to be trained in wilderness first aid and CPR.
- All personnel in leadership positions are being encouraged participate in outdoor leadership training; the DEI committee is exploring ways to partially or fully fund this.

Improve recognition for contributions:

- NWT leadership, in collaboration with the DEI committee and the NWT community at large, developed explicit guidelines for authorship for Niwot Ridge.

- NWT leadership has committed to lead a renewed effort to better acknowledge the contributions of all participants in presentations and manuscripts.
- NWT LTER held a community-wide NWT meeting focused on the Indigenous history of Niwot Ridge and incorporating Indigenous knowledge into mountain research in December 2020.

One member of the DEI committee, Dr. Meagan Oldfather, attended the virtual annual meeting of the Society for the Advancement of Chicano and Native Americans to represent NWT, listen and learn about barriers to underrepresented groups in STEM, and recruit students from historically excluded groups to participate in the NWT LTER.

B. Outreach Program. In Year 5, the NWT LTER VII outreach program has maintained its focus on training graduate students in science communication and outreach and providing them with opportunities to practice their skills with K-12 and public audiences. This strategy supports our graduate students in becoming scholars who can communicate the results of their research in creative and impactful ways, prepares them for careers as engaged scholars, and makes NWT research accessible and relevant to public audiences of all ages.

K-12 Outreach and Education. We have introduced hundreds of K-12 students to NWT VII research in the academic years prior to the pandemic closures. Using graduate students trained in science communication, we hosted field trips to the Mountain Research Station and lab tours on campus. Our partnership with Wild Bear Ecology Center (a non-profit, all-ages nature center located near NWT) and the Winter Wildlands Alliance and their Snow School program (<https://winterwildlands.org/snowschoo/>) has grown significantly as we connected LTER scientists and CU undergraduates (via our snow science internship) with ~300 children in 1st through 6th grade, and got them out on snowshoes, exploring snow science at the Mountain Research Station and sub alpine sites nearby. During the pandemic, when regular K-12 Snow School programming was impossible, Niwot researchers and graduate students conducted snowshoe tours for family groups representing over 40 people, incorporating Snow School activities and discussing ongoing Niwot LTER research. The Science Communication and Outreach seminar was taught virtually in 2021, and students created virtual outreach demonstrations in the form of short videos, which they presented to over 90 regional high school students and teachers via a series of “reverse science fairs”.

In the summer of 2021, we were able to creatively and safely conduct the Mountain Research Experience for high school students by collaborating with Cal-Wood Environmental Education center. This collaboration and a small grant from the CU Office of Outreach and Engagement allowed us to recruit 14 participants from low income, Latinx, and first generation college student backgrounds. Students camped near the site of the Cal-Wood fire, and we spent the week discussing sub-alpine forest ecology, forest management, and wildfire impacts and restoration. In future summers we plan to continue this partnership with Cal-Wood but return to Niwot Ridge via daytrips.

Undergraduate Students. We are strongly committed to engaging and training undergraduate students as part of NWT LTER. We directly support undergraduate workers as field assistants and many undergraduates obtain funding from their schools (CU and beyond) to do research at NWT; faculty and graduate students place high priority of mentoring these students. We also

support a Snow Internship as well as REUs. In the summer of 2021, we again partnered with the Research Experience for Community College Students (RECCS) program through the Cooperative Institute for Research in Environmental Sciences (CIRES) to host 3 REU students from regional community colleges worked on projects in Pika occupancy, the lake megacosm experiment, and the biogeochemical heterogeneity.

C. Graduate and Post-doc Training

Graduate Students. We provided GRA and/or supplies funding to approximately 11 grad students this year. The cornerstone of our Education and Outreach work in the proposal was the initiation of a semester-long practicum on science communication and “engaged scholarship” for graduate students receiving LTER support. A total of 22 students affiliated with NWT have taken the course so far. In 2020-2021, the course focused on the design and presentation of hands-on demonstrations, games, and info-graphics to explain NWT research. These demonstrations were presented to public audiences on campus, at a Meet a Scientist event at the Boulder Public Library, at the Museum of Boulder, and they will be used in future outreach events and teaching. Students participating in the course currently are producing virtual outreach videos and infographics to be promoted via our website and social media.

Rotating Synthesis Postdoc. In addition to encouraging integration through our research planning process, we support a rotating 2-year postdoctoral fellow. We have found allocating a scientist with a proven track record of productivity to in-depth analysis and synthesis of NWT LTER projects exploits and amplifies a proven strength of the LTER program. This has proven a very successful approach for us, allowing us to bring in talented individuals such as Dr. Oliver Wigmore (who tackled the UAV multispectral measurements for H4), Dr. John Crawford (who tackled data integration, particularly in our water chemistry long-term records) and most recently Dr. Kyle Christianson (who brings expertise in limnology and biophysical aquatic work) and Dr. Courtney Collins (who focused on synthesizing observation and empirical plant phenology data).

E. Public and Stakeholder Audiences. We make it a priority to share our work with the broader community. Faculty are regularly interviewed on print and other media; Dr. Ray’s work on American pika was recently featured in an episode of *National Geographic Photo Ark*. In collaboration with the CU Mountain Research Station director and manager, Dr. Rose has been developing a series of interpretive trails at the Mountain Research Station. Interpretive signage and self-guided field trip materials are being finalized, trails were cleared in Summer 2020, and signposts are being installed with the goal of having the trails ready for visitors Spring 2022. Signs orient visitors to the ecology of the subalpine and alpine environments while sharing the research of CU and NWT LTER scientists.

Ongoing collaborations with Rocky Mountain National Park and the City of Boulder allow us to translate our results to important management questions. Niwot faculty and graduate students participate each year in a day long workshop with scientists and volunteers from Rocky Mountain National Park to share research findings and strategies. In Year 5, we will again hold a symposium specifically focused on the City of Boulder Watershed to share results related to Boulders water supply and downstream citizens. We have also started new collaborations with the Colorado Forest Restoration Institute, the Denver Botanic Gardens, and the Protect Our Winters organization to build a more cohesive consortium of stakeholders with shared goals and cross-communication in the coming year.

7. INFORMATION MANAGEMENT. The primary goals of the Information Management (IM) program are to ensure the quality, security, integrity, and timely availability of data collected at NWT LTER in order to facilitate scientific discovery. All current IM procedures are consistent with LTER network data access policy (<https://lternet.edu/data-access-policy/>); and generally follow guidance as laid out by DataOne's data management best practices hub (<https://dataoneorg.github.io/Education/>). Niwot Ridge LTER continues to use the Environmental Data Initiative as its primary repository (hosting >99% of NWT datasets). Exceptions are made for select datasets (i.e. Ameriflux, NADP) that are part of a larger, coordinated network devoted to specific focal data types.

During the current reporting period, we added and/or updated to extended the time series in 87 datasets (Table 1).

Table 1. Datasets published in the Y4 reporting period with associated EDI ID.

Title	Package ID
25cm NDVI data from UAV campaign at Niwot Ridge Saddle Catchment, 2017	knb-lter-nwt.283.1
5cm multispectral imagery from UAV campaign at Niwot Ridge, 2017	knb-lter-nwt.67.1
Aboveground net primary productivity data for Saddle grid, 1992 - ongoing.	knb-lter-nwt.16.5
Air temperature and relative humidity data for B1 HOBO logger, 2012 - ongoing.	knb-lter-nwt.5.4
Air temperature data for C1 chart recorder, 1952 - ongoing.	knb-lter-nwt.411.13
Air temperature data for D1 chart recorder, 1952 - ongoing.	knb-lter-nwt.412.11
Air temperature data for Saddle chart recorder, 1981 - 2017.	knb-lter-nwt.413.11
Black sand extended growing season experiment plant species composition, from 2018 to ongoing, yearly	knb-lter-nwt.225.3
Chlorophyll-a data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.267.2
Climate data for C1 data loggers (CR23X and CR1000), 2000 - ongoing, daily.	knb-lter-nwt.401.5
Climate data for D1 data loggers (CR23X and CR1000), 2000 - ongoing, daily.	knb-lter-nwt.402.4
Climate data for saddle data loggers (CR23X and CR1000), 2000 - ongoing, daily.	knb-lter-nwt.405.5
Climate data for saddle data loggers (CR23X and CR1000), 2009 - ongoing, hourly.	knb-lter-nwt.57.5
Co-dominant removal and N and C fertilization experiment for moist meadow tundra from 2002 to 2018	knb-lter-nwt.6.3
Co-dominant removal and N and C fertilization experiment for moist meadow tundra from 2002 to 2018	knb-lter-nwt.6.4
Con-mod soil moisture data in the Black Sand experiment plots for East Knoll, Audubon, Lefty, Soddie and Trough, 2019 - ongoing.	knb-lter-nwt.245.2
Con-mod soil temperature data in the Black Sand experiment control plots for East Knoll, Audubon, Lefty, Soddie and Trough, 2019 - ongoing.	knb-lter-nwt.248.2
Con-mod species composition in the Black Sand experiment for East Knoll, Audubon, Lefty, Soddie and Trough, 2019 - ongoing.	knb-lter-nwt.246.2
Dissolved oxygen data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.175.2
Federal sampler data for NWT saddle and C1 2016- ongoing	knb-lter-nwt.205.3
Geodetic snow depth from UAV campaign at Niwot Ridge, 2017	knb-lter-nwt.288.1
Hobo temperature data from the black sand extended growing season length and ITEX chamber experiment, hourly, 2018 - 2020	knb-lter-nwt.232.1

Ice thickness at Green Lake 4 from 1984 to ongoing, monthly	knb-lter-nwt.199.2
Increased temperature, N and snowpack experiment for north of saddle from 2006 to ongoing, yearly	knb-lter-nwt.13.4
Infilled climate data for C1, Saddle, and D1, 1990 - 2019, hourly.	knb-lter-nwt.168.2
Infilled precipitation data for C1 chart recorder, 1952 - ongoing, daily	knb-lter-nwt.184.3
Infilled precipitation data for C1 chart recorder, 1952 - ongoing, daily	knb-lter-nwt.184.4
Infilled precipitation data for C1 chart recorder, 1952 - ongoing, daily	knb-lter-nwt.184.5
Infilled precipitation data for D1 chart recorder, 1952 - ongoing, daily	knb-lter-nwt.186.3
Lake ice clearance and formation data for Green Lakes Valley from 1968 - ongoing.	knb-lter-nwt.106.3 https://nadp.slh.wisc.edu/sites/ntn-CO02/
National Atmospheric Deposition Program (NADP) SITE CO02	
PAR data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.189.2
Permanent forest plot data from 1982-2016 at Niwot Ridge, Colorado	knb-lter-nwt.207.4
Permanent forest plot data from 1982-2019 at Niwot Ridge, Colorado	knb-lter-nwt.207.5
Pika demography data for west knoll and Indian Peaks wilderness, 2008 - ongoing	knb-lter-nwt.8.4
Plant species composition data for Saddle grid, 1989 - ongoing.	knb-lter-nwt.93.5
Plot vegetation surveys at the Sensor Network, 2017 to ongoing	knb-lter-nwt.191.3
Precipitation data for C1 chart recorder, 1952 - ongoing.	knb-lter-nwt.414.13
Precipitation data for D1 chart recorder, 1964 - ongoing.	knb-lter-nwt.415.14
Precipitation data for Saddle chart recorder, 1981 - ongoing.	knb-lter-nwt.416.11
Saddle catchment sensor network data, 2017- ongoing.	knb-lter-nwt.210.3
Saddle catchment vegetation cover for Distributed Hydrology Soil Vegetation Model (DHSVM), 2 meter, 2019	knb-lter-nwt.285.1
Snow cover profile data for Niwot Ridge and Green Lakes Valley, 1993 - ongoing.	knb-lter-nwt.98.16
Snow depth data for Saddle grid, 1992 - ongoing	knb-lter-nwt.31.18
Snow grain data for Niwot Ridge and Green Lakes Valley, 1995 - ongoing.	knb-lter-nwt.97.15
Snow pit chemistry data for Niwot Ridge and Green Lakes Valley, 1993 - 2000.	knb-lter-nwt.95.1
Snow water equivalent data for Niwot Ridge and Green Lakes Valley, 1993 - ongoing.	knb-lter-nwt.96.17
Snowbed experiment species composition data for Niwot Ridge from 2012 to ongoing, yearly	knb-lter-nwt.172.4
Soil moisture and snowdepth measurements in the Black Sand experiment for East Knoll, Audubon, Lefty, Soddie and Trough, 2018 - ongoing.	knb-lter-nwt.181.3
Soil moisture and snowdepth measurements in the Black Sand experiment for East Knoll, Audubon, Lefty, Soddie and Trough, 2018 - ongoing.	knb-lter-nwt.181.4
Soil moisture, temperature, and electrical conductivity data from the black sand extended growing season length experiment, hourly, 2018 - ongoing	knb-lter-nwt.238.2
Spatial distribution of snow depth for the Green Lakes Valley, 1997 - 2019	knb-lter-nwt.284.1
Stream and lake water chemistry data for Green Lakes Valley, 1998 - ongoing.	knb-lter-nwt.10.3
Stream water chemistry data for Albion site, 1982 - ongoing.	knb-lter-nwt.103.13
Stream water chemistry data for Albion site, 1982 - ongoing.	knb-lter-nwt.103.14
Stream water chemistry data for Arikaree cirque, 1984 - ongoing.	knb-lter-nwt.104.12
Stream water chemistry data for Arikaree cirque, 1984 - ongoing.	knb-lter-nwt.104.13

Stream water chemistry data for Como creek, 1998-2013	knb-lter-nwt.278.1
Stream water chemistry data for Green Lake 4, 1982 - ongoing.	knb-lter-nwt.108.11
Stream water chemistry data for Green Lake 4, 1982 - ongoing.	knb-lter-nwt.108.12
Stream water chemistry data for Green Lake 5 outlet, 1984 - ongoing.	knb-lter-nwt.109.11
Stream water chemistry data for Green Lake 5 outlet, 1984 - ongoing.	knb-lter-nwt.109.12
Stream water chemistry data for Green Lake 5 Rock Glacier, 1998 - ongoing.	knb-lter-nwt.163.2
Stream water chemistry data for Green Lake 5 Rock Glacier, 1998 - ongoing.	knb-lter-nwt.163.3
Stream water chemistry data for Martinelli basin, 1984 - ongoing.	knb-lter-nwt.112.3
Stream water chemistry data for Martinelli basin, 1984 - ongoing.	knb-lter-nwt.112.4
Stream water chemistry data for Navajo meadow, 1984 - ongoing.	knb-lter-nwt.113.10
Stream water chemistry data for Saddle stream (007), 1994 - ongoing.	knb-lter-nwt.9.3
Stream water chemistry data for Saddle stream (007), 1994 - ongoing.	knb-lter-nwt.9.4
Stream water chemistry data for Saddle Stream site, 1994 - ongoing.	knb-lter-nwt.160.2
Stream water chemistry data for Saddle Stream site, 1994 - ongoing.	knb-lter-nwt.160.3
Streamflow data for Albion camp, 1981 - ongoing.	knb-lter-nwt.102.16
Streamflow data for Como creek, 2006 - 2014	knb-lter-nwt.236.1
Streamflow data for Green Lake 5 outlet, 2006 - 2017	knb-lter-nwt.170.1
Streamflow data for outlet from Navajo meadow, 1994 - 2014	knb-lter-nwt.169.1
Streamflow data for Saddle stream, 1999 - ongoing.	knb-lter-nwt.74.5
Streamflow data for Saddle stream, 1999 - ongoing.	knb-lter-nwt.74.6
Streamflow for Green Lake 4, 1981 - ongoing.	knb-lter-nwt.105.14
Streamflow for Martinelli basin, 1982 - ongoing.	knb-lter-nwt.111.13
Surface temperature mapped from thermal infrared survey from UAV campaign at Niwot Ridge, 2017	knb-lter-nwt.287.1
Temperature data for Green Lake 4 inlet and outlet, 2019 - ongoing	knb-lter-nwt.259.1
Temperature data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.188.2
Time lapse camera photos for Green Lakes Valley, 2011 to ongoing, subdaily	knb-lter-nwt.270.2
Time-lapse camera (phenocam) imagery of Sensor Network plots from 2017 to ongoing	knb-lter-nwt.192.2 https://ameriflux.lbl.gov/sites/siteinfo/US-NR3
US-NR3: Niwot Ridge Alpine (T-Van West)	https://ameriflux.lbl.gov/sites/siteinfo/US-NR4
US-NR4: Niwot Ridge Alpine (T-Van East)	
Water quality data for Green Lakes Valley, 2000 - ongoing.	knb-lter-nwt.157.6

We also invested substantial effort into quality control and development of a reusable code pipeline to update data from 2 eddy covariance towers located on Niwot Ridge into the correct format for Ameriflux submission. At 3494m asl, the Niwot Ridge eddy covariance towers are the highest in North America ([Knowles et al 2019](#)). Previously, the data from the paired towers had been combined into a single time series and processed periodically for graduate student-led projects, but the code base developed proved difficult to maintain. Flux experts affiliated with the NWT Ridge LTER (John Knowles & Peter Blanken) provided sample code, advice, and subject matter expertise into the reprocessing over 13 years of EC data from the two

towers. The resulting datasets have been downloaded on average ~20x/ month for use in synthesis projects.

Last, we have been working closely with IT experts from INSTAAR and CU's Office of Information Technology to migrate our hardware and backup workflow for data collected by NWT LTER. While data are archived in publicly available archives (as described above) after QA/QC, NWT retains raw data (e.g. read directly off sensors, scans of datasheets, original transcriptions) for all records. We currently use a Dell server as our primary server, with automated nightly backups to a ReadyNAS located in a separate location, which in turn syncs nightly to an external hard drive. However, the warranty has expired for the ~8-year-old Dell server and its hardware is likely not compatible with a required a Red Hat upgrade. Consequently, we are in the process of migrating to use the ReadyNAS running a Debian linux distribution as our primary server and using CU's petalibrary (<https://www.colorado.edu/rc/resources/petalibrary>) as a third (offsite) backup, at which point we will deprecate and decommission the Dell server. The new setup will adhere to best practices for data management, with automated backups to 2 locations (including one off-site), and is the most cost-effective solution because annual fees for use of the petalibrary are less than that of replacing and maintaining a separate server.

REFERENCES

Andrus, R. A., B. J. Harvey, K. C. Rodman, S. J. Hart, and T. T. Veblen. (2018) Moisture availability limits subalpine tree establishment. *Ecology* 99:567-575.

Andrus, RA, RK Chai, BJ Harvey, KC Rodman, TT Veblen. Increasing rates of subalpine tree mortality linked to warmer and drier summers. *Journal of Ecology* 109:2203–2218. <https://doi.org/10.1111/1365-2745.1365-2745.13634>

Benedict, L. M., Wiebe, M. Plichta, M. Batts, H. Johnson, J. Monk, E. and Ray, C. (2020). "Microclimate and Summer Surface Activity in the American Pika (*Ochotona princeps*)," *Western North American Naturalist* 80(3), 316-329. <https://doi.org/10.3398/064.080.0303>

Benson, B., J. Magnuson, and S. Sharma. 2000, Global Lake and River Ice Phenology Database, Version 1. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center. doi:[10.7265/N5W66HP8](https://doi.org/10.7265/N5W66HP8).

Bernhardt, Emily S., et al. "Control points in ecosystems: moving beyond the hot spot hot moment concept." *Ecosystems* 20.4 (2017): 665-682.

Birch, L., Schwalm, C. R., Natali, S., Lombardozzi, D., Keppel-Aleks, G., Watts, J., Lin, X., Zona, D., Oechel, W., Sachs, T., Black, T. A., and Rogers, B. M.: Addressing biases in Arctic–boreal carbon cycling in the Community Land Model Version 5, *Geosci. Model Dev.*, 14, 3361–3382, <https://doi.org/10.5194/gmd-14-3361-2021>, 2021.

Billings, SA, K Lajtha, A Malhotra, AA Berhe, M-A de Graaff, S Earl, J Fraterrigo, K Georgiou, S Grandy, S Hobbie, JAM Moore, K Nadelhoffer, D Pierson*, C Rasmussen, WL Silver, BN

Sulman, S Weintraub, W Wieder (2021). Soil organic carbon is not just for soil scientists: measurement recommendations for diverse practitioners. *Ecological Applications* 31(3), e02290. doi:10.1002/eap.2290.

Blankinship, J. C., M. W. Meadows, R. G. Lucas, and S. C. Hart. 2014. Snowmelt timing alters shallow but not deep soil moisture in the Sierra Nevada. *Water Resources Research* 50:1448-1456.

Brigham, L. M., Bueno de Mesquita, C. P., Smith, J. G., Sartwell, S. A., Schmidt, S. K., & Suding, K. N. (2021). Do plant–soil interactions influence how the microbial community responds to environmental change? *Ecology*, e03554

Bueno de Mesquita, C., Caitlin T. White, Emily C. Farrer, Lauren M. Hallett, Katharine N. Suding. 2020. Taking climate change into account: Non-stationarity in climate drivers of ecological response. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13572>

Bunnell, D. B., Barbiero, R. P., Ludsins, S. A., Madenjian, C. P., Warren, G. J., Dolan, D. M., Brenden, T. O., Briland, R., Gorman, O. T., He, J. X., Johengen, T. H., Lantry, B. F., Lesht, B. M., Nalepa, T. F., Riley, S. C., Riseng, C. M., Treska, T. J., Tsehaye, I., Walsh, M. G., ... Weidel, B. C. (2014). Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *BioScience*, 64(1), 26–39. <https://doi.org/10.1093/biosci/bit001>

Caine, T. 2018. Lake ice clearance and formation data for Green Lakes Valley from 1968 - ongoing. Environmental Data Initiative. doi:10.6073/pasta/84e39dccd8439f0f3e320f60f4c42759.

Chen, Y., Wieder, W.R., Hermes, A.L. and Hinckley, E.L.S., (2020). The role of physical properties in controlling soil nitrogen cycling across a tundra-forest ecotone of the Colorado Rocky Mountains, USA. *CATENA*, 186, p.104369.

Christianson, K. R., Loria, K. A., Blanken, P. D., Caine, N., & Johnson, P. T. (2021). On thin ice: Linking elevation and long-term losses of lake ice cover. *Limnology and Oceanography Letters*, 6(2), 77-84.

Clow, D. W. (2010). Changes in the Timing of Snowmelt and Streamflow in Colorado: A Response to Recent Warming. *Journal of Climate* 23:2293-2306.

Collins, C.G., Elmendorf, S.C., Hollister, R.D. *et al.* Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nature Communications* 12, 3442 (2021). <https://doi.org/10.1038/s41467-021-23841-2>

Crawford, J.T., Hinckley, E.L.S., Litaor, M.I., Brahney, J. and Neff, J.C. (2019) Evidence for accelerated weathering and sulfate export in high alpine environments. *Environmental Research Letters*, 14(12), 124092.

Crawford, J. T., Hinckley, E.-L. S., & Neff, J. C. (2020). Long-term trends in acid precipitation and watershed elemental export from an alpine catchment of the Colorado Rocky Mountains, USA. *Journal of Geophysical Research: Biogeosciences*, 125, e2020JG005683. <https://doi.org/10.1029/2020JG005683>

Dawson, T. P., S. T. Jackson, J. I. Housepres, I. C. Prentice, and G. M. Mace. (2011). Beyond Predictions: Biodiversity Conservation in a Changing Climate. *Science* 332:53-58.

Dickinson, M. G., C. D. L. Orme, K. B. Suttle, and G. M. Mace. (2014). Separating sensitivity from exposure in assessing extinction risk from climate change. *Scientific Reports* 4.

Dokulil, M. T., & Herzig, A. (2009). An analysis of long-term winter data on phytoplankton and zooplankton in Neusiedler See, a shallow temperate lake, Austria. *Aquatic Ecology*, 43(3), 715–725. <https://doi.org/10.1007/s10452-009-9282-3>

Fan, Z., Neff, J.C. and Wieder, W.R. (2016) Model-based analysis of environmental controls over ecosystem primary production in an alpine tundra dry meadow. *Biogeochemistry*, 128(1-2), 35-49.

Farrer, E. C., and K. N. Suding. (2016). Teasing apart plant community responses to N enrichment: the roles of resource limitation, competition and soil microbes. *Ecology Letters* 19:1287-1296.

Heindel, R.C., Putman, A.L., Murphy, S.F., Repert, D.A. and Hinckley, E.L.S. (2020) Atmospheric dust deposition varies by season and elevation in the Colorado Front Range, USA. *Journal of Geophysical Research: Earth Surface*, 125(5), p.e2019JF005436.

Hermes, A.L., Wainwright, H.M., Wigmore, O., Falco, N., Molotch, N.P., and Hinckley, E.L.S. (2020) From patch to catchment: A statistical framework to identify and map soil moisture patterns across complex alpine terrain. *Frontiers in Water* (Special Issue: Water in the Critical Zone), 2, doi:10.3389/frwa.2020.578602.

Kelly, P. T., Solomon, C. T., Weidel, B. C., & Jones, S. E. (2014). Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. *Ecology*, 95(5), 1236–1242. <https://doi.org/10.1890/13-1586.1>

Kessler, K., Lockwood, R. S., Williamson, C. E., & Saros, J. E. (2008). Vertical distribution of zooplankton in subalpine and alpine lakes: Ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. *Limnology and Oceanography*, 53(6), 2374–2382. <https://doi.org/10.4319/lo.2008.53.6.2374>

Kimoto, C., DeBano, S.J., Thorp, R.W., Rao, S., & Stephen, W.P. (2012) Investigating temporal patterns of a native bee community in a remnant North American bunchgrass prairie using blue vane traps. *Journal of Insect Science*, 12, 108.

- Kinnard, C. and Lewkowicz, A.G. (2006) Frontal advance of turf-banked solifluction lobes, Kluane Range, Yukon Territory, Canada. *Geomorphology*, 73(3-4), 261-276.
- Knowles, J.F., Blanken, P.D. and Williams, M.W. (2015a) Soil respiration variability across a soil moisture and vegetation community gradient within a snow-scoured alpine meadow. *Biogeochemistry*, 125(2): 185-202.
- Knowles, J.F., Burns, S.P., Blanken, P.D. and Monson, R.K. (2015b) Fluxes of energy, water, and carbon dioxide from mountain ecosystems at Niwot Ridge, Colorado. *Plant Ecology & Diversity*, 8(5-6): 663-676.
- Knowles, J.F., Blanken, P.D., Lawrence, C.R. and Williams, M.W. (2019) Evidence for non-steady-state carbon emissions from snow-scoured alpine tundra. *Nature Communications*, 10(1): 1-9.
- Klingler, K.B., Jahner, J.P., Parchman, T.L. *et al.* Genomic variation in the American pika: signatures of geographic isolation and implications for conservation. *BMC Ecol Evo* 21, 2 (2021). <https://doi.org/10.1186/s12862-020-01739-9>
- Kyker-Snowman E*, DL Lombardozzi, GB Bonan, SJ Cheng, JS Dukes, SD Frey, EM Jacobs, JM Rady*, NG Smith, RQ Thomas, WR Wieder, AS Grandy (2021). Increasing the spatial and temporal impact of ecological research: A roadmap for integrating a novel terrestrial process into an Earth system model. *Global Change Biology*. doi: 10.1111/gcb.15894.
- Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., et al. (2019). The Community Land Model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems*, 11, 4245– 4287. <https://doi.org/10.1029/2018MS001583>
- Leach, T. H., Winslow, L. A., Hayes, N. M., & Rose, K. C. (2019). Decoupled trophic responses to long - term recovery from acidification and associated browning in lakes. *Global Change Biology*, 25(January), 1779–1792. <https://doi.org/10.1111/gcb.14580>
- Leopold, M., Dethier, D., Völkel, J., Raab, T., Rikert, T.C. and Caine, N. (2008) Using geophysical methods to study the shallow subsurface of a sensitive alpine environment, Niwot Ridge, Colorado Front Range, USA. *Arctic, Antarctic, and Alpine Research*, 40(3): 519-530.
- Levine, J. M., and J. HilleRisLambers. (2009). The importance of niches for the maintenance of species diversity. *Nature* 461:254-U130.
- Litaor, M.I., Williams, M. and Seastedt, T.R. (2008) Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *Journal of Geophysical Research: Biogeosciences*, 113(G2).

Loria, K. A., Christianson, K. R., & Johnson, P. T. J. (2020a). Phenology of alpine zooplankton populations and the importance of lake ice-out. *Journal Of Plankton Research*, 1–15. <https://doi.org/10.1093/plankt/fbaa050>

Janet S. Prevéy, Sarah Claire Elmendorf, Anne Björkman, Juha M. Alatalo, Isabel Ashton, Jakob J. Assmann, Robert G. Björk, Mats P. Björkman, Nicoletta Cannone, Michele Carbognani, Chelsea Chisholm, Karin Clark, Courtney G. Collins, Elisabeth J. Cooper, Bo Elberling, Esther R. Frei, Gregory R. H. Henry, Robert D. Hollister, Toke Thomas Høye, Ingibjörg Svala Jónsdóttir, Jeffrey T. Kerby, Kari Klanderud, Christopher Kopp, Esther Levesque, Marguerite Mauritz, Ulf Molau, Isla H. Myers-Smith, Susan M. Natali, Steven F. Oberbauer, Zoe Panchen, Alessandro Petraglia, Eric Post, Christian Rixen, Heidi Rodenhizer, Sabine B. Rumpf, Niels Martin Schmidt, Ted Schuur, Philipp Semenchuk, Jane Griffin Smith, Katharine Suding, Ørjan Totland, Tiffany Troxler, Henrik Wahren, Jeffrey M. Welker, Sonja Wipf, and Yue Yang. The tundra phenology database: more than two decades of tundra phenology responses to climate change. *Arctic Science*. e-First <https://doi.org/10.1139/as-2020-0041>

Mohapatra, B. C., Sahu, H., Mahanta, S. K., Lenka, S., Anantharaja, K., & Jayasankar, P. (2016). Growth of periphyton on different plastic materials in freshwater medium. *Advances in Applied Science Research*, 7, 228-234.

Dorota L. Porazinska, Clifton P. Bueno de Mesquita, Emily C. Farrer, Marko J. Spasojevic, Katharine N. Suding, Steven K. Schmidt, 2021. Nematode community diversity and function across an alpine landscape undergoing plant colonization of previously unvegetated soils, *Soil Biology and Biochemistry* 161, 108380, <https://doi.org/10.1016/j.soilbio.2021.108380>.

Preston, D. L., Caine, N., McKnight, D. M., Williams, M. W., Hell, K., Miller, M. P., Hart, S. J., & Johnson, P. T. J. (2016). Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. *Geophysical Research Letters*, 43(10), 5353–5360. <https://doi.org/10.1002/2016GL069036>

Rachal, D. M., G. S. Okin, C. Alexander, J. E. Herrick, and D. P. C. Peters. (2015). Modifying landscape connectivity by reducing wind driven sediment redistribution, Northern Chihuahuan Desert, USA. *Aeolian Research* 17:129-137.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J. (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution, *Ecological Modelling*, Volume 201, Issues 3–4, 10.1016/j.ecolmodel.2006.10.009

Seastedt, T.R. (2019) Patterns and controls on the productivity and plant diversity of alpine ecosystems. *Earth Syst. Environ. Sci.* doi: 10.1016/B978-0-12-409548-9.11787-7

Shapiro, L.H., Tepedino, V.J., & Minckley, R.L. (2014) Bowling for bees: optimal sample number for “bee bowl” sampling transects. *Journal of Insect Conservation*, 18, 1105-1113.

Tague, C.L., and Band, L.E. (2004) RHESSys: Regional Hydro-Ecologic Simulation System—An object-oriented approach to spatially distributed modeling of carbon, water, and nutrient Cycling. *Earth Interact.*, doi:10.1175/1087-3562, 2004.

Templ, B., Fleck, S. & Templ, M. Change of plant phenophases explained by survival modeling. *Int J Biometeorol* **61**, 881–889 (2017). <https://doi.org/10.1007/s00484-016-1267-z>

Vaughan, D., J. C. Comiso, I. Allison, J. Carrasco, G. Kaser, R. Kwok, and P. Mote. (2013). Observations: Cryosphere. In T. Stocker, editor. *Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Webb, R.W., Williams, M.W. and Erickson, T.A. (2018) The spatial and temporal variability of meltwater flow paths: Insights from a grid of over 100 snow lysimeters. *Water Resources Research*, *54*(2), 1146-1160.

Wieder, W. R., J. F. Knowles, P. D. Blanken, S. C. Swenson, and K. N. Suding. (2017). Ecosystem function in complex mountain terrain: Combining models and long-term observations to advance process-based understanding. *Journal of Geophysical Research-Biogeosciences* *122*:825-845.

Wieder, WR, D Pierson, S Earl, K Lajtha, GS Baer, F Ballantyne, AA Berhe, SA Billings, LM Brigham, SS Chacon, J Fraterrigo, SD Frey, K Georgiou, MA de Graaff, AS Grandy, MD Hartman, SE Hobbie, C Johnson, J Kaye, E Kyker-Snowman, ME Litvak, M Mack, A Malhotra, JAM Moore, K Nadelhoffer, C Rasmussen, WL Silver, BN Sulman, X Walker, & S Weintraub (2021). SoDaH: the SOils DAta Harmonization database, an open-source synthesis of soil data from research networks, version 1.0. *Earth Syst. Sci. Data*, *13*(5), 1843-1854. doi:10.5194/essd-13-1843-2021.

Wigmosta, M. S., Vail, L. W., & Lettenmaier, D. P. (1994). A distributed hydrology-vegetation model for complex terrain. *Water Resources Research*, *30*(6), 1665-1679.

Whipple, A., Ray, C., Wasser, M., Kitchens, J. N., Hove, A. A., Varner, J. V., Wilkening, J. L., Temporal vs. spatial variation in stress-associated metabolites within a population of climate-sensitive small mammals, *Conservation Physiology*, Volume 9, Issue 1, 2021, coab024, <https://doi.org/10.1093/conphys/coab024>