

Shoulder season dusting of snow on Niwot Ridge. October 2020. Photo Credit Stephanie Dykema

NWT LTER VII

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

> Year 4 Annual Report 2019-2020

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 interactions across levels of ecological organization as well as connectivity across landscape positions, outlining how responsiveness of one level of ecological organization (Q3) or spatial scale (Q4) 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. In year 3, a lot of effort was put into analyzing our long-term datasets in reference to extended summer and our 4over-arching hypotheses.



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 year 4 we have looked into this assumption by asking whether relationships among these key characteristics are stationary across the 37-year time series, using moving window principal component analysis (PCA) and moving window correlations (Bueno de Mesquita et al, in review). Moving window PCA demonstrated that temperature and the number of growing degree days (GDD) reliably loaded strongly onto axis one. However, the other variables that loaded onto axis one in the all-years PCA did not reliably load on that axis across all moving windows, suggesting non-stationarity in these climate data, particularly between temperature/GDD and the other variables. For instance, while temperature and GDD were strongly positively correlated throughout the study period, the correlation between temperature and growing season length (GSL) changed over time. Breakpoint analysis identified two breaks in the temperature and GSL correlation coefficients occurring in the late 1990s and early 2000s. We are currently exploring alternative ways to adjust how we characterize extended summer given this decoupling.

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, chikadees, pikas, and lakes. Capitalizing on a single metric that describes the phenomena of early snow melt and longer and warmer growing season across years, we have been able to examine a broad range of ecological responses to extended summer conditions. 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 4, we examined if the mechanisms underlying the biodiversity-production relationship (mass-ratio effects or niche complementarity) varies in extended summer years or in years with reduced snow. Using Structural Equation Modeling (SEM) that examine functional trait patterns on the saddle grid, we found that massratio effects are the dominant mechanism that maintain production across all years, and that their strength increases in extended summer years. Concurrently, mass-ratio effects weaken in years with increased snowfall while abiotic drivers increase in strength (Fig. 2; Huxley et al, in prep).



Figure 2. Path coefficients from SEMs for snow depth, multi-trait community weight means (CWM) and functional dispersion (FDis) regressed against extended summer and winter and spring precipitation.

We also began analyzing vegetation responses in long-term experiments where we have manipulated resources and environmental conditions to provide a starting point 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).

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 six Niwot 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) 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 was derailed by the start of the pandemic. We expect to finish this synthesis effort by Fall 2021.

Tundra plant populations. In the previous reporting year, we initiated studies that track species survival and recruitment to better understand population-level responses as well as 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 in moist meadow in 2020 but were unable to do so due to COVID-19 travel restrictions. We plan to complete the 20 moist meadow plots and resample the dry meadow plots in 2021. In the existing 20 dry meadow plots we have tagged and mapped 4907 individuals across 32 species (**Fig. 3**). In the short term, we are currently exploring 2 questions: 1) how to soil resources and spatial structure interact to structure communities; and 2) what is the role of the foundational species *Silene acualis* 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.



Figure 3. Spatial locations of 4907 individual plants across 37 species. Plots will be resampled in 2021 and an additional 20 plots will be established in moist meadow tundra.

Pika. We focus on the American pika (*Ochotona princeps*) as a model species for studying climate sensitivity in small, herbivorous mammals and (especially) sub-surface habitat specialists. We expect that 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. This past year we have continued mark-resight study of pika demography, as well as the pika habitat occupancy survey established in 2016. A new graduate student, funded with an NSF Graduate Research Fellowship, joined NWT in the fall of 2020 and is analyzing the pika survey data using dynamic occupancy models. This student will use NWT LTER data to test a model of pika response to climate that we developed for a nearby landscape in Rocky Mountain National Park.

Recently published work, coauthored by six former NWT LTER undergraduate researchers, reported that pika surface activity during the summer (critical for winter food caching, reproduction, dispersal and territory establishment/defense) depends on the differential between near-surface and deep temperatures in their talus habitats (Benedict et al. 2020). Work currently in revision also supports the importance of climatic or physiological drivers of stress in pika (Whipple et al, in revision) and recent range-wide contractions in populations sizes (Klingler et al, in revision). Lastly, pika stressors might include spillover of pathogens from rodents, based on our newly published study of flea-vectored diseases (Brinkerhoff et al. 2020).

Chickadee. We have monitored the population dynamics of a small bird, the Mountain Chickadee (*Poecile gambeli*), for two years in collaboration with Dr. Scott Taylor. We are now monitoring 150 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 sometimes hybridize 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 had found previously 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 plot in Year 4 and recent analyses have shown that extended summer conditions also increased rates of tree mortality (Andrus et al, in revision). While we observed detrimental effects of warmer climate conditions on seedling establishment and tree mortality, aboveground live tree biomass has increased from 1982-2016 in NWT permanent plots (Chai et al. 2018), a trend we suspect is primarily driven by slow stand development following stand-initiating fires over a century ago.

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 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 4, we addressed these hypotheses through analyses of planktonic phenology and responses to earlier ice-out in a high alpine lake (GL4) (Loria et al. 2020a), and also compare among-lake data to model variation in physical, geochemical, and biotic relationships with the assumption that differences across an elevation gradient might reveal temporal shifts that are likely to occur

under extended summer conditions (e.g., high-elevation lakes will exhibit lower-elevation characteristics) (Loria et al. 2020b; Olesky et al. 2020). We also continued long-term measurements on two lower-elevation lakes (GL1, Albion), 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.

Comparative Lake Surveys. We find that the strongest drivers of primary production in Southern Rocky Mountain lakes are summer meteorological conditions, particularly precipitation and summer air temperatures, yet dynamics depend on spatial and temporal scale, which highlights the importance of seasonal, interannual, and spatial studies (Oleksy et al. 2020). We find that as elevation decreases, lakes exhibit higher DOC, warmer surface waters, stronger thermal stratification, and higher conductivity; trends that we expect may be parallel to expectations for temporal trends in alpine lakes as summers lengthen.

Biotic associations showed similar parallels to the temporal trends we predict will occur in high elevation lakes under extended summer conditions. While maximum values of chlorophyll-a increased in years with extended summer conditions in GL4, we did not find a consistent trend with elevation. However, lakes below tree line displayed higher plankton diversity and densities, with 60% and 77% higher densities of phytoplankton and zooplankton, respectively. In lakes above tree line, average zooplankton body size was 18% higher for cladocerans and 41% higher for copepods (Loria et al. 2020b). We expect that as summers lengthen, alpine lakes might shift away from communities dominated by large-bodied, longerlived zooplankton that are adapted to intense UVR, and towards smaller, denser plankton communities that are typical of lower elevation lakes. We continue our investigation of these shifts through continued long-term monitoring, experimentation, and use of a sensor array.

Long Term Lake Surveys. In Year 4, we evaluated long-term data from GL4 between 2009 and 2019 to better understand the within-season and interannual dynamics of physical, geochemical, and biological factors. 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. Interannually, we find that earlier ice-out dates are associated with warmer water temperatures and higher chl-a concentrations (Fig. 4). Similarly, years with earlier ice-out dates exhibit higher biomass of *Daphnia pulicaria*, likely driven by a longer growing season and resulting warmer water temperatures, but other zooplankton measures, including *Hesperodiaptomus shoshone* biomass, are not responsive to earlier ice-out (Fig. 4).



Figure 4. 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 log10(D. pulicaria+1), log10(neonate+1),log10(H. shoshone+1), and log10(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., 2020a.

Seasonal zooplankton dynamics indicate that the two dominant taxa in GL4, *Daphnia pulicaria*, a large-bodied cladoceran species, and *Hesperodiaptomus shoshone*, a large calanoid copepod, have significantly different life-history strategies which may explain why they appear to respond differently to extended summer conditions. *D. pulicaria* biomass was lowest immediately following ice-out and increased linearly over the course of the growing season, while fecundity was highest following ice-out and declined with time. These patterns indicate that *D. pulicaria* likely reproduces once after ice-off. In contrast, patterns in *H. shoshone* were less linear, with peaks in biomass and fecundity 30-40 days following ice-off; these patterns suggest that *H. shoshone* reproduction occurs repeatedly throughout the season (Loria, et al., 2020a). GL4 only intermittently stratified throughout the ice-free season, and extremely low concentrations of TDP (max=0.70 μ M L-1), TDN, and chl-a emphasize that biological limitations in alpine lakes are likely dictated by the harsh physicochemical conditions. *D.*

pulicaria and *H. shoshone,* zooplankton species typical of high alpine lakes, are well adapted to these extreme conditions. Furthermore, 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.

In-situ Sensor Measurements. In 2018 we deployed a sensor array in GL4 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. Preliminary analysis of sensor data done in Year 4 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. Implications of a novel thermal regime include stronger and longer stratification which influences the availability and distribution of nutrients and oxygen and subsequently the behavior of biota. Following this upcoming winter, we will have four full years of data from this sensor array that 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.

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

Modeling Terrestrial Processes. In Year 3 we had implemented a new set of modeling studies that directly explore limitation across space and time on Niwot Ridge using both the Niwot Biogeochemistry Model, NBM) to look at limitations over a growing season, and a well-tested land-atmosphere model (the NCAR Community Land Model version 4.5, CLM). In Year 4 we have expanded our work with the CLM primarily. First, we developed a scripted workflow to download and manipulate Niwot datasets so they can be used as input, parameterization, and validation for single point simulations of the CLM. This data pipeline uses Niwot data as the foundation for modeling studies that can provide data for additional analyses and forecasts to support NWT hypotheses (e.g. changes in soil moisture in different landscape positions with extended summer). Major accomplishments related to this work include scripts that will facilitate publication of Tvan flux tower data (<u>https://github.com/NWTlter/tvan_L1</u>) to the AmeriFlux data portal (<u>https://ameriflux.lbl.gov/sites/siteinfo/US-NR3</u>), as well as scripts that augment, filter, and gap fill the atmospheric forcing data that are needed to run CLM (<u>https://github.com/hhollandmoritz/NWT_CLM</u>).

In Year 4, we have updated Niwot-specific simulations that now use the latest version of CLM5 (Lawrence et al. 2019) and are evaluating results with flux data from Tvan, snow depth measurements from the Saddle grid, and soil measurements from the sensor network. Relative to our previous work with CLM at Niwot (Wieder et la. 2017) the integration of the soil moisture data from the sensor network provides critical insights into the representation of changes in the soil moisture state across and limitations across different alpine vegetation communities (**Fig. 5**). These efforts will continue in Year 5 of the project to inform our interpretations of results from the black sand experiment (H1) and hindcast the historical temporal variability in soil moisture stress across different landscape positions (H3).



Fig 5. Seasonal changes in soil moisture observed and simulated by CLM5 (black and red lines, respectively) from different vegetation communities at two different depths (top and bottom rows, corresponding to measurements at two depths 5-10 cm and 30). Soil moisture observations at the Tvan towers (fell field) and across the Saddle sensor network (black lines +/- 1 sigma from different measurements. Simulations with CLM5 forced with atmospheric inputs collected from the Tvan towers and Saddle meteorological station.

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.

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 onedimensional mechanistic lake model, the General Lake Model (version 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 already 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. Our lake modeling effort has provided a platform of collaborative research among the varying fields of NWT LTER. NWT lake specialists provided a modeling efforts and promote collaborative research among terrestrial and hydrologic researchers.

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 third year of our "black sand" experiment where we manipulate growing season length. By using a thin layer of black sand to reduce snow albedo and enhance

melt rates without concurrently affecting snowpack depth, we can manipulate the length of the growing season (after Blankinship et al. 2014). Measurements of snow depth continue to confirm that the black sand treatment increases the albedo and speeds snowmelt (with the exception of the lowest elevation site, Soddie), with variable effects on soil moisture (**Fig. 6**).



Figure 6. Effects of black sand on at the Audubon site during the 2019 growing season. Panels show data from soil sensors arrayed at 4 positions from the top to bottom of the plot; points show daily data; lines show the 5-day running mean in each treatment. Diurnal soil temperature range (left) indicates snowmelt occurred several weeks earlier in the Early Snowmelt treatment (days where soil is snow-covered exhibit no diurnal temperature variation due to snow insulation), although the treatment was less strong at the top of the plot. Early snowmelt treatment generally led to an earlier and more concentrated (higher and narrower peak) pulse of soil moisture as compared to the control treatment.

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 the extended growing season and control plots, enabling us to look at the interactive effects of early snowmelt and warming. We have also continued monitoring pollinator visitation in both control and extended growing season plots. We have found that pollinators respond to early snow melt, but that the impact is mediated by landscape position (**Fig. 7**). We are expanding this line of research by recruiting Warren Sconiers (an entomologist from the University of the Ozarks) to collaborate on examining the impact of extended summer on arthropod communities. Warren received a ROA/REU supplement for summer 2020, but due to travel restrictions deferred to next summer. With the completion of the third year of data collection on plant community composition, we will begin analyses this winter and spring focusing on taxonomic and functional responses to extended summer at both the species and community level.



Figure 7. Variation in pollinator visitations among control and early snowmelt plots from Summer 2020. Some sites (Audubon) exhibited strong shifts in the timing of pollinator visitation, while other sites (Leftie) did not.

Manipulation of aquatic growing season length and DOM. Summer 2020 marked the first full growing season 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 a full summer season of experimentation and sampling in the summer of Year 4.

Our original proposal described plans to conduct factorial manipulations of water residence time and terrestrially derived DOM within 12 limnocorrals deployed in Green Lake 4 (GL4) and 12 in Green Lake 1 (GL1). However, our partners at the City of Boulder Watershed (where the lakes are located) were reluctant to allow us to perform manipulations at this scale and the remote setting of the lakes make transporting supplies logistically challenging. Thus, we concluded that the use large-volume mesocosms (2600 L, 2.5 meter diameter, 0.66 meter depth) - which can be deployed inside watershed property and manipulated more directly with higher replication – was a tractable alternative to the original design. 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 biota 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 first full season in Year 4.

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. 8**). 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.



Figure 8. 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.

All tanks were seeded with sediment as well as zooplankton from both GL1 and GL4, providing a mixed community from both alpine and montane lake systems. 8 clay tiles were installed in the megacosms to collect periphyton biomass. Megacosm are instrumented with two thermistors (HOBO Pendant® Temperature/Light 64K Data Logger) that record surface and bottom temperature every 2 hours throughout the entire year. These provide us with finely resolved record of ice-thaw patterns and water temperature.

Spring ice thaw in the megacosms occurred in May 2020; however, due to COVID-19 restrictions, we were not able to access the site until mid-May. After access was granted, we collected observations at the megacosms 1-2 times per week, recording depth, photosynthetically active radiation (PAR), dissolved oxygen (DO), pH, and ion concentrations at each visit. We completed 5 sampling events throughout the summer where we collected water samples for chlorophyll-a and DOC analysis, zooplankton samples, and clay tiles for periphyton biomass analysis. 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. 2020a).

Summer 2020 provided us with an abundance of data and, though some samples have yet to be processed (including DOC and most zooplankton), initial analyses illustrate tractable 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 illustrate that leaf pack significantly increases DOM concentration in treated tanks. A complete evaluation of biotic responses also requires completion of sample processing, but 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*.

Looking forward, the megacosms are prepared for a long, alpine winter. We will monitor the megacosms once per month throughout the winter to make snow and ice observations.

HOBO thermistors are installed with fresh batteries and this data, along with game camera photographs of the tanks will provide us with precise ice-off data. We will re-seed the megacosms with zooplankton from GL4 and GL1 in the spring, if necessary, and continue collecting data and tracking changes in the tanks. We are optimistic that a second full growing season of data from this experiment will 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 that are 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 in (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 upperelevation 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 found a marginally significant effect of shrub that varies across fine-scale topography. The presence of shrubs reduced absolute maximum daytime temperatures on the S-facing aspect and increased absolute minimum daytime temperatures across both aspect (**Fig. 9a**). These changes in microclimate were associated with changes in plant functional traits where species near shrubs were on average taller with larger and thinner leaves, suggesting that shrub microenvironments favor a resource-acquisitive strategy (**Fig. 9b**). Moreover, we found that functional diversity in height, leaf area, and leaf dry matter content increases with the presence of shrubs, suggesting that shrub microclimates allow a wider range of functional strategies than open microclimates (**Fig. 9c**) (Brigham et al. in preparation).



Figure 9. (a) There was a marginally significant interaction such that absolute maximum daytime temperatures were lower with shrubs on the S-facing aspect. Shrubs led to higher absolute minimum daytime temperatures. (b) Plants were taller, had greater leaf area, lower leaf dry matter content, and higher specific leaf area with shrub presence. (c) Functional dispersion was increased with shrub presence for three of the four studied traits (height, leaf area, and leaf dry matter content). The triangle represents the mean for all panels.

Species associations. With ten continuous years of species composition data in the saddle grid (prior to 2008 the measurements were sporadic), we are preparing to conduct analyses that will allow us to infer interaction strengths using our long-term data. Next spring we plan to analyze population change (as annual cover changes) in our long-term vegetation dataset at the Saddle site. We will use Bayesian methods (JAGS in R) to fit a simple population model (Levine and HilleRisLambers 2009, Farrer et al. 2014) and estimate interaction coefficients quantifying the per capita effect of cushion plants (and perhaps other species) on each focal species. We will incorporate melt-out date data into the models to allow interaction coefficients to depend on growing season length. We expect that drier community types (e.g., dry meadow, fellfield) and years with longer growing seasons will be associated with more facilitative effects of cushion

plants. We note that observational approaches do not definitively assess the relative importance of interactions but have value in being able to confirm patterns in species groups that we expect to have large biotic influences, and assess patterns more broadly for a wide range of taxa that cover a range of habitat characteristics.

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 artificial shrubs within each of three subplots, which are paired with 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). These structures act as a small snowfence, accumulating snow at their leeward side (Brigham et al, in preperation). In Year 4, we collected data on the composition and growth of vegetation with and without these artificial shrub structures. Our expectation is that the con-mods will modulate effects of the black sand manipulations on soil moisture and growing season length. These small climate refugia will lead to plot-wide increases in environmental heterogeneity and overall diversity.

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 simulate the increase of terrestrial DOM input to lakes by adding DOM as an additional factorial treatment to the megacosm experiment (discussed above). Treatment consists of leaf-packs composed of locally collected willow leaves enclosed within standardized nylon mesh bundles. We intend to increase dissolved organic carbon concentrations of manipulated mesocosms 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 mesocosms illustrated that this treatment method successfully increases in 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 will quantify 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 mesocosms 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 summer 2020 community and trait data and plan to complete another season of experimentation to increase our statistical power and understand inter-annual variation in the observed patterns. Importantly, this experiment will help to 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 4 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 link the empirical results from both the terrestrial and aquatic fields experiments with the predicted outcomes from of the CLM, GCM. 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.

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 using vegetation and environmental data collected in the Sensor Network Array to characterize temporal variability and uncertainty in soil moisture, soil temperature, and growing season length. We are testing if and when these measures predict the distribution and abundance of individual species across the saddle catchment. Beginning in 2019, we doubled the number of plots in which we collect vegetation data to increase our statistical power to test Hypothesis 3. We also initiated pilot studies to prepare for manipulative transplant experiments that will decouple the effects of the mean, variance, and autocorrelation (predictability) of environmental variables on the performance of plants from different alpine habitats (wet meadow, moist meadow, dry meadow, and snowbed). In Year 4, we collected another year of data from the Sensor Network Array, extended our analysis of those data, and monitored naturally-occurring and transplanted individuals of focal species. Ultimately, we aim to integrate the results of this work with ecosystem measures of hydrological connectivity, snow cover dynamics, and productivity to understand how organism and population-scale responses to temporal variability drive community and ecosystem processes.

A. Characterizing temporal variability and predictability. We have evaluated sensor and phenocam data collected in the Sensor Network Array during the 2017, 2018, and 2019 field seasons to characterize environmental variability and predictability. We are characterizing *variability* in soil moisture and temperature as the number of times the environmental variable crosses a biological threshold and *predictability* using autocorrelation analysis (**Fig. 10**). We

estimated within-year variability and predictability in soil moisture for every plot in the Sensor Network Array (N=16 in 2017, N=32 in 2018 and 2019).



Fig. 10. Illustration of the methods we are using to characterize variability and predictability in soil moisture. The line graph shows hypothetical time series data for soil moisture (volumetric water content, VWC) in two different plots (green and blue). Variability in soil moisture is calculated as the number of times VWC crosses 13% (Billings & Bliss 1959, Winkler et al. 2016); in this example, this value is 7 for the green time series and 1 for the blue series (open circles). Predictability is measured as the autocorrelation (Burgess and Marshall 2014) at a time step of 10 davs (closed circles). Here, the autocorrelation is much higher in the blue series than the green (see inset scatterplot).

In Year 4, we had accumulated enough data (3 consecutive growing seasons) to begin evaluating if plots are consistent in their degree of variability and predictability in soil moisture across growing seasons. We calculated the pairwise correlations between the variability and predictability measures in 2017-2018, 2018-2019, and 2017-2019 (**Fig. 11**). Initial results indicate that the extent of variability in soil moisture is somewhat correlated across growing seasons (r = 0.3-0.6); plots with high temporal variability in one year tended to have high variability in other years (**Fig. 11**, top row). However, we found no support for year-to-year correlations in the predictability of changes in soil moisture through the growing season: plots with relatively predictable changes in soil moisture in one growing season did not show predictable changes in other growing seasons (**Fig. 11**, bottom row).

We are using digital images collected by phenocams in the Sensor Network Array to quantify spatial and temporal variation in growing season length across the saddle catchment. With four consecutive growing seasons of data (2017-2020), we have gained additional insights into the drivers of growing season variation in this landscape (**Fig. 12**). The timing of snowmelt appears to be the dominant trigger for the onset of the growing season each year, and the extent to which the growing season shifts in response to snowmelt timing is highly consistent across the



Fig. 11. Year-to-year variation in within-season variability (top row) and predictability (bottom row) in soil moisture using data from the Sensor Network Array in 2017, 2018, and 2019. Each panel shows the correlation coefficient; asterisks indicate that the correlation is significant at P < 0.05. We calculated the average daily soil moisture at 30 cm soil depth at each plot in the Sensor Network Array prior to estimating the variability and predictability in soil moisture across each growing season (see Fig. 10). Since variability is an integer with a distribution skewed towards zero, we jittered the points the variability plots (top row) to show clusters of points near zero.

landscape (Fig. 12a-c). That is, in a year with late snowmelt, all plots delay green-up, peak greenness, and senescence by similar lengths of time. But despite the strong signature of snowmelt timing across growing seasons, variation in snowmelt timing explains little spatial variation in phenology across the saddle catchment (Fig. 12d-e), particularly as the growing season progresses. Areas with earliest snow-off do tend to green up first (Fig. 12d), but they are not necessarily the first locations to reach peak productivity (Fig. 12e), nor are they the first to senesce (Fig. 12f). Thus, the phenocam data collected through 2020 suggest that the timing of snowmelt is a major driver of year-to-year variation in phenological timing within any given plot, but a relatively poor predictor of differences among plots in late-season phenology. These patterns suggest that snowmelt timing likely provides a reliable cue that predicts the onset of the growing season across the landscape; however, the rate at which plant communities initiate growth in response to snowmelt varies with landscape position, and differences among plots in the timing of peak productivity and senescence is likely driven by factors other than snowmelt timing. We are exploring these patterns in the context of Hypothesis 3 because we predict that the extent of variability and predictability in later-season conditions, especially soil moisture and temperature, favor different adaptive strategies in the plant communities across the landscape, and therefore may explain patterns in phenology.



Fig. 12. Plant community phenology over 4 consecutive growing seasons (2017-2020) measured using phenocams at each node in the Sensor Network Array (N=16 plots/year). The top row illustrates that the timing of snowmelt is a strong predictor for when each plot begins growing (a), reaches peak productivity (b), and senesces (c). The bottom row shows that within a single year, variation in the timing of snowmelt across the saddle catchment can explain which areas green-up earlier vs. later (d), but it does not consistently predict when areas reach peak productivity (e) or senesce (f). Thus, the timing of snowmelt

Moving forward into Year 5, we plan to conduct the same analyses of soil moisture variability and predictability on the 2020 Sensor Network Data to continue to build a robust characterization of each plot that is based on data from multiple growing seasons. We are analyzing soil temperature data using the same approaches as used for soil moisture, and exploring methods for characterizing predictability and variability in growing season length using the phenology data.

B. Ecological responses to variability and predictability. One of the main goals of Hypothesis 3 is to test if patterns of environmental variability and predictability can explain the life history strategies, functional trait variation, and distribution patterns of alpine plant species. In Year 4, we have extended our prior analyses of plant community composition data (summarized in the Year 3 report) from the Sensor Network Array to characterize the distribution and abundance of different taxa with respect to within-season temporal variation in soil moisture (Fig. 13). This year we have been able to leverage a larger data set that includes two consecutive years of data (2018 and 2019) and a doubled sample size for 2019. Our analyses indicate that our measures of variability and predictability in soil moisture can partially explain the distribution of several relatively common species in the Sensor Network Array. Notably, many species are most common in areas that exhibit high variation in soil moisture (i.e., soil volumetric content crosses the 13% threshold multiple times throughout the growing season; see Fig. 10), but they diverge in their association with the extent to which those fluctuations are predictable or stochastic (Fig. 13).

Moving forward, we are preparing to incorporate the 2020 data into this analysis and continue to evaluate alternative modeling techniques for analyzing these data. Beginning next year, we aim to incorporate individual-level performance data using data collected from focal taxa that we have tagged and/or transplanted into the Sensor Network Array. Sampling constraints due to COVID-19 limited the amount of data we could collect from these individuals, but we anticipate collecting more comprehensive individual-level trait and performance data in the 2021 growing season. We also delayed transplant and greenhouse experiments that will manipulate the patterns of variability and predictability in soil moisture experienced by focal taxa to summer 2021.



Fig. 13. The distribution of 4 common species in the Sensor Network Array with respect to soil moisture variability (x-axis) and predictability (y-axis). Soil moisture measures were calculated from daily mean volumetric water content at 30 cm depth. Species' abundances were calculated as the projected plant area of each species as estimated from multi-hit point-intercept sampling in 32 Im x Im plots each year. The intensity of green corresponds to the predicted relative abundance of each species. Data were analyzed using a negative binomial model with the abundance of each species as the response variable, variability, predictability, and their interaction as explanatory variables, and plot as a random effect.

4. CATCHMENT INTEGRATION: How does hydrological connectivity affect catchmentscale 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 much of our 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 between 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 points in time (e.g., early snowmelt vs. late in the growing season) and in some years but not others (e.g., after high but not low snowfall years). 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. We added to these long-term records with the installation of an additional stream gauge that began measuring discharge in the summer 2020. This additional gauge will track missing or losing flows previously observed, more clearly constrain model estimates of the water balance, and therefore 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 contribute "meaningfully" in space and time. We adopted the framework described by Bernhardt and colleagues (2017) of assessing the function of **ecosystem control points**—how they are hydrologically connected across catchment-to-landscape scales and how they will change over time. Ecosystem control points are those areas within a landscape that have high rates of biogeochemical processes, and, thus, a disproportionately large effect on biogeochemical and ecological processes at the catchment scale. At NWT, hydrology, temperature, and substrate availability are first-order control points and their distribution in space. We are leveraging the strengths of our team that cuts across hydrology, biogeochemistry, and ecology to investigate how hydrologic connectivity now, and changes in the future, will affect the function and distribution of ecosystem control points, in particular the wet meadow and wetland communities across the study area that exhibit the highest rates of primary productivity (Seastedt, 2019). Ultimately, we expect that this within-catchment behavior effects the expression of aggregated, catchment-scale behaviors of interest, like stream C and nutrient export.

Since the relative importance of different parts of the catchment should vary with climate variables (e.g., snow distribution, snow melt, and air temperature), 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, couple to our **within-catchment studies** (e.g., H1-H3). Ultimately, we want to integrate hydroclimatological, biogeochemical, and ecological processes to understand the drivers of C, nutrient, and water export at larger scales.

A. Integrative efforts at the Saddle Catchment

Energy and water availability are important drivers of biogeochemical rates in the alpine. Following studies that determine the environmental controls on plant productivity at NWT, recent research evaluated the roles of both energy and water on the timing and magnitude of soil biogeochemical processes during the spring (snowmelt) and summer (growing) seasons.



Figure 14. Net rates of nitrogen transformations across six plant community types in the North Boulder Creek Catchment of Niwot Ridge LTER. **a**) Net mineralization and **b**) net nitrification rates during the spring and summer seasons. **c**) Net mineralization and **d**) net nitrification rates at distinct sampling periods during the spring and summer seasons. Letters indicate statistically significant results among groups (p < 0.05).

Motivated by the modeling study of Fan et al. (2016) and early efforts by Litaor et al. (2008) to understand the distribution of physical controls on herbaceous species diversity, Chen and colleagues (2020) examined net N cycling rates within six plant community types that map across macro- and micro-topographical features within the Saddle Catchment at NWT. They found that the highest rates of net N mineralization and nitrification were observed early in the growing season within the dry and moist meadow communities (Fig, 14a, b) - locally higher, warmer, and drier patches with low plant biomass. In contrast, net N cycling rates were overall lower in the comparatively cool, wet plant communities, including the wet meadow and shrub (near-stream). As summer progressed, wetter areas warmed and dried, and an increase in net N cycling rates was observed (Fig. 14c, d). The findings of Chen and colleagues demonstrate that patches across an alpine catchment have

different temporal trajectories and magnitudes of net N cycling rates. This study pointed to interesting differences in spatio-temporal patterning dependent on soil moisture; the next step is to integrate these findings with hydrological modeling to explore connectivity, and how it influences the movement of N species across the catchment.

A new statistical framework to map soil moisture and determine hydrologic connectivity across the alpine catchment. In Year 4, we made progress toward identifying and connecting patch-scale behavior to catchment-scale soil moisture patterns and hydrological processes. One effort, led by PhD student Anna Hermes and Dr. Eve-Lyn Hinckley, 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, in press). 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 so during the spring and summer (see **Fig. 15a** for the breakdown among dry and wet clusters). 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 (**Fig. 15b**). This effort indicated that ~50% of the catchment is hydrologically connected to the channel; other patches remain hydrologically disconnected throughout the year. These insights will guide follow-up field- and numerical modeling efforts to test both moisture patterns affect a broad suite of biogeochemical processes and explore how the patterns may change in the future as snow dynamics shift.



Figure 15. Results of a statistical analysis to identify within-catchment patches of hydrological functions and the catchment-scale pattern of mapped hydrologic functions. *A*) Time series of soil moisture median (solid lines) and range (shaded area) for each of the six hydrologic functions. Dashed line shows the overall median for each survey (black dots). Two clusters, dry (D) and wet (W), each had three sub-groups: dry (D-D), moist-to-dry (D-MD), wet-to-moist (D-WM), rapid dry-down (W-RD), persistently wet (W-W), and persistently very wet (W-VW). *B*) Random forest predictions for 6-subgroup hydrologic functions. Colors reflect pixel-by-pixel hydrologic function classifications compared to observed classifications (dots). From Hermes et al. (in press).

B. Spatially-explicit hydrological 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 tree-line, will alter the location of snow drifts.

Modeling spatio-temporal distribution of snowmelt and hydrologic response in alpine *landscapes.* In alpine landscapes the interactions among snow, topography, and wind strongly dictate the magnitude of water fluxes into soils and therefore the hydrologic connectivity across the landscape. In the last year, we have continued our work in the higher-elevation GL4 catchment with a focus on evaluating how future changes in climate may alter these snow-wind interactions (Badger et al, in review). A reasonable hypothesis is that a warmer climate will cause snowfall to become more dense (i.e., wetter and heavier), possibly leading to less wind redistribution and thus produce a more uniform snowpack. Using the Distributed Hydrology Soil Vegetation Model (DHSVM; Wigmosta, et al. 1994) we investigated the role of increasingly uniform spatial snowpack distributions on streamflow generation. A set of idealized hydrologic simulation experiments driven by reconstructed snowpack spanning 2001-2014 show that more uniform snow distribution leads to an earlier melt-out of 31 days on average and tends to produce less total runoff, with maximum decreases as large as 13.2% (Fig. 16a,b). Reductions in runoff are largely explained by greater exposure to solar radiation in the uniform case relative to a more heterogeneous snowpack, with this exposure driving shifts towards earlier snowmelt and changes in soil water storage. Overall, we find that the runoff efficiency from shallower snowpack is more sensitive to the effects of uniformity than deeper snowpack, which has further implications for a warming climate where shallower snowpack and enhanced sensitivities may be present. These changes in snowpack spatial heterogeneity have the potential to alter the distribution of ecosystem control points, as well as patterns of plant productivity across the alpine landscape.



Figure 16. Results from the control and snowredistribution simulations with May through September precipitation forcing excluded. (A) Multi-annual mean of DHSVM simulated cumulative runoff (red) and basin averaged SWE (blue) from the control simulation are shown with solid lines. Uncertainty bands show the 95% confidence interval for daily mean runoff and SWE for all years in the period of analysis (2001-2014). (B) Multi-annual mean SWE anomalies compared to the control simulations for each of the redistributed SWE simulations (colored lines) with uncertainty bands derived using the method described above. Vertical dashed lines, consistently colored by simulation, indicate the mean date of snowpack melt out for all years. (C) Multiannual mean cumulative runoff anomalies compared to the control simulations for each of the redistributed SWE simulations (colored lines) with uncertainty bands derived using the method described above. Horizontal lines along the right-hand vertical axis, consistently simulation, colored by indicate mean cumulative runoff for all years of analysis.

Vegetation and snowpack change in sub-alpine forests. Understanding how land-cover change will impact soil moisture and hydrologic connectivity is of critical importance as tree-line potentially moves to higher elevations with climate warming. On one hand, encroachment of forests into alpine landscapes may decrease runoff by increasing evapotranspiration. On the other hand, the interactions among forests, wind, and snow accumulation may lead to decreases in wind-scour and increased snow depth in areas with moderate forest density. To explore these interactions, we coupled the Landscape Disturbance and Succession model (LANDIS-II; Scheller et al., 2007) with a spatially explicit, physics-based, watershed process model, the Regional Hydro-Ecologic Simulation System (RHESSys; Tague and Band, 2004), to simulate land-cover change and its impact on the water budget in the 5.0 km² Como Creek catchment that spans the alpine-subalpine transition (Barnhart et al, in review). We simulated two potential futures, both with greater air temperature (+4 °C/century) and either more precipitation (+15%/century, MP) or less precipitation (-15%/century, LP) from 2000-2100. Forest cover in the catchment increased from 72% in 2000 to 84% and 83% in 2050 and to 95% and 92% in 2100 for MP and LP, respectively. Surprisingly, increases in forest cover led to increases in evapotranspiration and soil moisture. In the year 2100 simulations, mean annual runoff production increased by 91 and 61 mm for MP and LP simulations, respectively, with an annual control runoff of 208 mm. On a seasonal basis, increases in spring runoff and evapotranspiration occurred with the future increases in forest cover while summer ET and runoff decreased (Fig. 17). This result counters previous work as runoff production increased with forested area, highlighting the need to better understand the impacts of forest expansion on the spatial pattern of snow scour and catchment effective precipitation. Identifying the hydrologic response to these forest cover changes is of critical importance for understanding potential changes to biogeochemical cycling in the alpine meadow and wetland systems-the subject of ongoing research this year-described below.



Figure 17: Monthly change in streamflow (a) and evapotranspiration (b) under future climate with more precipitation (MP) and less precipitation (LP) and future land cover conditions (FLC) compared to year 2000 land cover and climate.

C. Integrative efforts across the alpine landscape.

Long-term analyses of sulfur and nitrogen inputs and outputs—motivation for process-based studies. NWT researchers, led by Postdoctoral Scientist Dr. John Crawford, analyzed the long-term record in sulfate export at the Green Lakes Valley catchment of NWT, as well as multiple sites in the Rocky Mountains (US), Western Canada, the European Alps, the Icelandic Shield, and the Himalayas (Asia) (Crawford et al., 2019). They determined that even as atmospheric S deposition has declined, sulfate export in surface waters is increasing, along with export of magnesium, calcium, and silica ions (Fig. 18). This pattern is consistent with increases in air temperature measured at nearby climate stations, leading Crawford and colleagues to suggest that climate-induced weathering is accelerating at NWT and other high elevation sites globally. Their analysis points to the increasing vulnerability of permafrost and glacial features that store high concentrations of these elements. The question now is what is the fate of elevated sulfate export at NWT and other high elevation catchments? Does it interact with and affect the cycling of other elements, such as metals? In our ongoing work to assess biogeochemical and ecological processes in ecosystem control points, we will be investigating this unknown in depth.

A second effort led by Dr. Crawford examined the trends in long-term acid deposition with a focus on atmospheric N deposition and export—at NWT (Crawford et al. in press). This analysis demonstrated that while sulfate and nitrate deposition has declined from 1984 to 2017, ammonium deposition has increased, likely due to increases in agricultural sources. Water quality modeling using WRTDS illuminated some interesting and unexpected trends: sulfate export has increased (consistent with findings reported in Crawford et al. 2019), nitrate export has remained constant, and ammonium export has increased slightly from 1984 to 2017. Their analysis demonstrated that while atmospheric deposition is approaching pre-Industrial conditions, there is a strong need to conduct process-based studies to understand the mechanisms controlling export patterns. This work provides further motivation for our investigation into important biogeochemical processes within the alpine landscape.



Figure 18: Monthly change in streamflow (a) and evapotranspiration (b) under future climate with more precipitation (MP) and less precipitation (LP) and future land cover conditions (FLC) compared to year 2000 land cover and climate.

Investigating ecosystem controls points: their roles and connectivity across the landscape. While much work over the last few decades at NWT has focused on point-based (e.g., plot) studies of environmental controls on alpine ecology and biogeochemistry, there have been few investigations that examine the functional role of what may be important ecosystem controls points within the alpine landscape. Past work demonstrates that the wetter portions of the landscape from the alpine tundra to the sub-alpine zone have higher plant biomass and rates of primary productivity (Seastedt, 2019), accumulation of organic matter (Kinnard and Lewkowicz 2006) and sediment, as well as stored water (as liquid and ice; Leopold et al. 2008). In a series of studies that evaluated relationships among soil moisture, temperature, respiration, and eddy covariance data, Knowles and colleagues previously described the potential importance of these wetland areas to net ecosystem C losses (Knowles et al. 2019, 2015a, 2015b). In particular, they identified high respiration fluxes of older C from solifluction lobes characterized by wet meadow vegetation communities and a subsurface permafrost layer (Knowles et al. 2019). Permafrost is discontinuous across the NWT landscape (Leopold et al., 2008), and its occurrence as a component of solifluction lobes (Fig. 19) may indicate an important ecosystem control point, activated in response to temperature seasonally and a warming climate over longer time scales, resulting in high C efflux (and possibly other elements).

In 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 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). To start, we collected



Figure 19. Photograph of a wet meadow control point/solifluction lobe at NWT (Photo credit: E.S. Hinckley).

organic matter). To start, we collected sediment depth profiles to measure these constituents and to compare the patterns to 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 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 PhD project and undergraduate honors thesis. These field efforts will inform laboratory

incubation studies to determine the effects of warming temperatures and altered wettingdrying cycles on biogeochemical processes of interest, as well as continued sampling efforts

to assess the degree to which wetland features are hydrologically connected to streams and lakes across the landscape (to begin Summer 2021). We anticipate that these studies will yield important results that help to explain catchment-to-landscape scale patterns, including those described in recent long-term data analyses (e.g., Crawford et al. in press; Heindel et al. 2020).

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. Co-PI Suding is active on the LTER Executive Committee. NWT Researcher Dr. Marko Spasojovic is active on the LTER DEI Committee.

B. Synthesis Groups. Niwot investigators are PIs for two of the NCO-sponsored synthesis groups. Suding co-leads the "Synthesizing population and community synchrony to understand drivers of ecological stability across LTER sites" group. Wieder co-leads the "Advancing soil organic matter research: Synthesizing multi-scale observations, manipulations & models" group. Niwot data have also been contributed to 4 cross-site tundra synthesis projects. Three of these are part of a special issue in Arctic Science (Prevey et al. In Review, Rixen et al. In Prep Bjorkman et al. In Prep). A fourth cross-site project, let by postdoctoral scientist Courtney Collins, evaluated tundra plant phenological sensitivity to experimental warming (Collins et al. in review)

In Year 4, NWT leadership solicited proposals for within-site synthesis projects that would facilitate collaboration across research teams and integrative analyses of NWT long-term data. Two proposals were funded. One project, led by Dr. Marko Spasojovic, is evaluating changes in functional traits across all Niwot vegetation datasets; the second, led by Dr. Chris Ray, plans to synthesize datasets on subsurface temperature data across the ridge. Both projects expect to have in-person retreats to facilitate collaboration and synthesis, and therefore each has been delayed due to COVID-19 travel and safety restrictions.

6. OUTREACH and EDUCATION LTER VII.

A. Diversity Equity and Inclusion (DEI) Committee. Niwot Ridge LTER formed a DEI committee in summer 2020. The first step of the committee this Fall 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. We plan to repeat this survey every three years 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 the survey showed that people felt that they could be their authentic selves while at Niwot Ridge. Moreover, people generally felt valued as a member of the Niwot Team and that their contributions were valued. While the overall trends were generally positive and most comments highlighted that people feel welcome and respected at Niwot, several issues were raised in regard to behavior, safety, and feeling valued. Based on this feedback, the NWT DEI committee is developing a plan for next steps that focus on three main issues areas:

Next Steps to Prevent Unacceptable Behaviors:

• A community-wide NWT meeting has been scheduled that is focused on the Indigenous history of Niwot Ridge and incorporating Indigenous knowledge into mountain research (scheduled for December 2020). All members of the community will be expected to attend.

- NWT will hold a stand-alone active bystander training for all NWT researchers (scheduled for February 2021). All members will be required to attend or complete an equivalent training.
- The DEI committee will reduce barriers to reporting concerns. This will involve training 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. In addition, the DEI committee will set up an anonymous online comment "box" for people to anonymously submit issues.

Next steps for field safety:

- In conjunction with the Mountain Research Station, NWT will provide 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.
- All personnel should be trained in wilderness first aid and CPR; The DEI committee is exploring ways to partially or fully fund this.
- All personnel in leadership positions should participate in outdoor leadership training; The DEI committee is exploring ways to partially or fully fund this.

Next steps to improve recognition for contributions:

- NWT leadership will lead a renewed effort to better acknowledge the contributions of all participants in presentations and manuscripts.
- NWT leadership, in collaboration with the DEI committee and the NWT community at large, will develop explicit guidelines for authorship for Niwot Ridge (initiated in November 2020).

Two members of the DEI committee (Co-PI Emery and one graduate student attended the virtual annual meeting of the Society for the Advancement of Chicano and Native Americans to represent NWT, listen and learn about barrier to underrepresented groups in STEM, and recruit students from historically excluded groups to participate in the NWT LTER.

B. Outreach Program. In Year 4, 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. In addition to offering professional development around outreach for our graduate students, we have also been responsive to requests for tours and educational events, continued to grow the impact of our Schoolyard Book, and developed new partnerships for outreach and education in our community. We detail these efforts below.

K-12 Outreach and Education. We introduced hundreds of K-12 students to NWT VII research in the academic year 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/snowschool/) grew 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. Participating schools are high proportion free/reduced lunch from regional urban/rural communities, and we support them and their students by waiving gear rental costs and providing them with mittens, hats and gloves when necessary. We were excited to develop new curricula and activities for the Snow School program, engaging students in the field as citizen scientists participating in data collection for the NASA SnowEx and Community Snow Observations projects. We had children in the field digging snow pits, calculating snow-water equivalents, and taking snow depth measures at the same time the NASA SnowEx project flew sampling flight transects and Niwot researchers dug pits and took snow depth measures higher up in the alpine.

In previous years many of the NWT graduate students who took the outreach and communication seminar put their skills into practice via another productive collaboration with Wild Bear Ecology Center--Summer Science Camp--and they also participate as instructors in the Mountain Research Experience week-long residential field ecology course for high school students led by NWT Education and Outreach Coordinator Alex Rose. Both the collaboration with the Wild Bear Ecology center and the Mountain Research Experience could not be held this summer due to the pandemic, but we plan to continue these outreach events again starting in summer 2021.

In Fall 2019, Dr. Rose and NWT LTER colleagues applied for a large grant through the CU Office of Outreach and Engagement to develop a museum exhibit for the Museum of



Figure 20. NWT LTER graduate researcher shares her research on seed dispersal with 5th graders at the Living Landscapes museum exhibit (Photo credit: Alex Rose).

Boulder called "Our Living Landscape: Exploring Boulder's Watershed". The project was a collaboration between NWT LTER, the Center for Water, Earth Science, and Technology (CWEST), and Boulder Creek Critical Zone Observatory (BcCZO). The exhibit was installed at the Museum of Boulder in February 2019, and before the pandemic closures we hosted field trips for 165 5th graders from Title 1 schools across the region. 10 NWT LTER staff and graduate students were involved in the project (Fig. 20). We hope the exhibit will be available

to the public again soon and the watershed model and panels we created will continue to be on display in new sites in the future, with opportunities for further programming and engagement when safe.

Undergraduate Students. We are strongly committed to engaging and training undergraduate students as part of NWT LTER. LTER directly supports 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.

The Niwot LTER Snow Internship allows undergraduates to engage in the synthesis of field science, outdoor science education, backcountry winter travel and safety, and leadership skills for course credit. Snow Interns are trained to collect snowpack data through skiing to remote locations at two sites in the alpine and sub-alpine on Niwot Ridge. Here they dig weekly snow pits to record temperature, stratigraphy, density, and snow water equivalent (SWE). The data they collect contributes to a long-term data set of seasonal alpine snowpack, which is continuous from 1995 through the present, and unique to Niwot Ridge. Snow interns also present their findings at a scientific conference and conduct outreach with K-12 students. In the summer of 2020, 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. Due to the pandemic, we moved the REU program online. Only two of the accepted students opted to take the two-week professional development and science communication course we offered them, choosing to defer the REU support for summer 2021. One of the three students, a first-generation community college student, completed the REU program virtually, and is currently working on a manuscript on her project.

D. Graduate and Post-doc Training

Graduate Students. In year 4 of NWT VII we have provided GRA and/or supplies funding to approximately 14 grad students. 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. 20 students affiliated with NWT have taken the course so far. In 2019-20, 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.

We have also worked increased training opportunities graduate students in using Niwot data. Specifically, several Niwot personnel served as co-instructors in a graduate course in Ecological Forecasting, where about half the student groups pursued a modeling exercise using data from Niwot Ridge. As well, we hosted a zoom tutorial on how to the General Lake Model (https://aed.see.uwa.edu.au/research/models/GLM/ to improve graduate student modeling skills.

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 Oliver Wigmore (who tackled the UAV multispectral measurements for H4), John Crawford (who tackled data integration, particularly in our water chemistry long-term records) and most recently Kyle Christianson (who brings expertise in limnology and biophysical aquatic work). In addition, Courtney Collins joined the project as a postdoc on LTER-related funding September 2019.

Courtney is working with Sarah Elmendorf on biodiversity and trait synthesis across the alpine and arctic biomes.

E. Public and Stakeholder Audiences. We make it a priority to share our work with. Faculty are regularly interviewed on print and other media; 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 manger, Dr. Rose has been working to develop a series of interpretive trails at the Mountain Research Station. Interpretive signage and self-guided field trip materials are being finalized currently, trails were cleared in Summer 2020 and signposts are installed with the goal of having the trails ready for visitors Spring 2021. Signs orient visitors to the ecology of the subalpine and alpine environments, and they share 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.

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. To do so, a major effort of NWT TER VII has been the migration of all existing NWT datasets from our local catalog to Environmental Data Initiative, to include both creating EML metadata for datasets that had not previously been submitted to EDI, updating datasets on EDI where the two systems had become unsynchronized, and, moving forward, using EDI as the sole repository for NWT data. That migration was completed in 2020 (Year 4) when we added and/or updated 44 datasets (**Table 1**).

Title	Dataset ID
Streamflow data for Albion camp, 1981 - ongoing.	knb-lter-nwt.102.15
Streamflow for Green Lake 4, 1981 - ongoing.	knb-lter-nwt.105.13
Lake ice clearance and formation data for Green Lakes Valley from 1968 - ongoing.	knb-lter-nwt.106.3
Streamflow for Martinelli basin, 1982 - ongoing.	knb-lter-nwt.111.12
Warming and snow experiment plant species composition data for Saddle snowfence, 1993 - 2000.	knb-lter-nwt.159.3
Aboveground net primary productivity data for Saddle grid, 1992 - ongoing.	knb-lter-nwt.16.5
Zooplankton community composition and trait data for Green Lake 4, 2012 to ongoing	knb-lter-nwt.161.3
Soil lysimeter chemistry data from various locations on Niwot Ridge and in the Green Lakes Valley 1994 - 2013.	knb-lter-nwt.167.1
Pika habitat occupancy survey data for Niwot Ridge and Green Lakes Valley, 2016 - ongoing	knb-lter-nwt.17.2
Snowbed experiment species composition data for Niwot Ridge from 2012 to ongoing, yearly	knb-lter-nwt.172.4

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

Jissolved oxygen data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.175.1
A and P addition experiment colonization data for Niwot Ridge from 2015 to 2019, yearly	knb-lter-nwt.176.1
Cemperature data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.188.1
PAR data for the Green Lake 4 buoy, 2018 - ongoing	knb-lter-nwt.189.1
Plot vegetation surveys at the Sensor Network, 2017 to ongoing	knb-lter-nwt.191.2
Fime-lapse camera (phenocam) imagery of Sensor Network plots from 2017 to ongoing	knb-lter-nwt.192.1
ce thickness at Green Lake 4 from 1984 to ongoing, monthly	knb-lter-nwt.199.2
Water chemistry data for Green Lakes Valley, 2018	knb-lter-nwt.209.1
Saddle catchment sensor network data, 2017- ongoing.	knb-lter-nwt.210.2
Free cone presence and abundance from Niwot Ridge, Rollins Pass, and Rocky Mountain National Park, 2015-2018.	knb-lter-nwt.221.1
Black sand extended growing season experiment plant species composition, from 2018 to ongoing, yearly	knb-lter-nwt.225.2
Responses of dry meadow Kobresia myosuroides and Carex rupestris to Nitrogen Pertilization for East of Tvan, 2013 - 2015	knb-lter-nwt.235.1
Soil moisture, temperature, and electrical conductivity data from the black sand extended growing season length experiment, hourly, 2018 - ongoing	knb-lter-nwt.238.1
Genetic survey of bacterioplankton communities of aquatic habitats in Green Lakes Valley, 2014 - 2017	knb-lter-nwt.241.1
Genetic survey of eukaryotic plankton communities of aquatic habitats in Green Lakes Valley, 2014 - 2017	knb-lter-nwt.242.1
Senthos data from the Green Lakes Valley Flowage System, 1981 - 1982	knb-lter-nwt.243.1
Con-mod soil moisture data in the Black Sand experiment plots for East Knoll, Audubon, Lefty, Soddie and Trough in 2019	knb-lter-nwt.245.1
Con-mod species composition in the Black Sand experiment for East Knoll, Audubon, Lefty, Soddie and Trough in 2019	knb-lter-nwt.246.1
Con-mod soil temperature data in the Black Sand experiment control plots for East Knoll, Audubon, Lefty, Soddie and Trough in 2019	knb-lter-nwt.248.1
Deschampsia biomass, soil microbes and endophyte root colonization for snowmelt and nicrobial innoculation transplant experiment in the Green Lakes Valley, 2015-2018	knb-lter-nwt.250.1
Aspirated air temperature and relative humidity data for C1, 2018- ongoing	knb-lter-nwt.252.1
Alnine species transplant experiment within the sensor network for 2010, weekly	knh-lter-nwt 260 1
Black sand extended growing season experiment ITEX warming chamber plant species	Imb Iton mwt 261 1
Supplemental soil moisture data from plant community composition plats within the sensor	MIU-1101-11W1.201.1
network for 2019, weekly	knb-lter-nwt.262.1
Pollinator visitation and floral resource production in Black Sand plots for 2019	knb-lter-nwt.264.2
Black sand extended growing season experiment aboveground net primary productivity,	lash Itan 1 265 1
rom 2019 to ongoing, yearly	knb-lter-nwt.265.1
Commator visitation in Moving Upnill plots for 2019	knb-lter-nWt.266.1
Inforphyn-a data for die Oreen Lake 4 buby, 2018 - Ongoing	KIIU-IICI-IIWL.207.1
Physiological stress of American pika (Ochotona princeps) and associated habitat Pharacteristics for Niwot Ridge 2018 - 2019	knh-lter-nwt 268 1
Physiological stress of American pika (Ochotona princeps) and associated habitat pharacteristics for Niwot Ridge, 2018 - 2019 Time lapse camera photos for Green Lakes Valley, 2011 to ongoing subdaily	knb-lter-nwt.268.1 knb-lter-nwt 270 1

Climate data for saddle data loggers (CR23X and CR1000), 2009 - ongoing, hourly.	knb-lter-nwt.57.4
Streamflow data for Saddle stream, 1999 - ongoing.	knb-lter-nwt.74.5
Snow horizon chemistry data for Niwot Ridge and Green Lakes Valley, 1993 - ongoing.	knb-lter-nwt.94.2

In 2020, we expanded our webpage to include a visualization of real-time meteorological data <u>https://nwt.lternet.edu/real-time-met</u>. This work, and the accompanying workflow for providing more rapid access to these data via ftp, was completed in part at the request of forecasters at the National Weather Service, which harvests them in real time into the MADIS (<u>https://madis.ncep.noaa.gov/</u>) and MesoWest. (<u>https://mesowest.utah.edu/</u>) databases. Partners at the NWS are currently using Niwot data via this workflow in (1) hourly weather forecasts along the Front Range; (2) Colorado Avalanche Information Center; in hourly gridded analyses (RTMA/URMA <u>https://www.nco.ncep.noaa.gov/pmb/products/rtma/</u>) as well as large-scale statistical models (e.g., the National Blend of Models

(<u>https://www.weather.gov/mdl/nbm_home</u>). We continue to archive a static, quality-controlled version of these data with a doi on the EDI data portal on an annual basis.

A second recent website upgrade included an interactive visual map as well as downloadable information on the geolocations of current and past Niwot research projects https://nwt.lternet.edu/research-plots. This information was formerly housed on our old data portal but had not been updated in several years and was identified as a gap in our mid-term site review. We are now coordinating efforts with the Mountain Research Station to identify any new research projects on Niwot Ridge (including non-LTER research, such as NEON and independently funded scientists) and add locations to the map.

Together with Niwot researcher John Knowles, we are working to submit flux data from Niwot's Tvan towers to Ameriflux. While these data have been used in a number of publications by individual PI's and corresponding subsets had been archived on EDI, we previously lacked a formal mechanism for post-processing and data archiving on a regular basis. Scripts were developed in 2020, with just a few more tweaks to the QA/QC routine necessary before completing data submission. Metadata for these two new Ameriflux sites <u>US-NR3</u> and <u>US-NR4</u> can currently be viewed on Ameriflux; we plan to update the Niwot website with pointers to these data when the data submission is complete.

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.

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

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.

Bunnell, D. B., Barbiero, R. P., Ludsin, 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

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

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.

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.

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.LS., and Neff, J.C. (2020). Long-term trends in acid precipitation and watershed elemental export from an alpine catchment of the Colorado Rocky Mountains, USA. *JGR-Biogeosciences*. In Press

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

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 nonsteady-state carbon emissions from snow-scoured alpine tundra. *Nature Communications*, 10(1): 1-9.

Klingler, KB, Jahner JP, Parchman TL, Ray C, Peacock MM. (2020). Genomic variation in the American pika: signatures of geographic isolation and implications for conservation. BMC Evolutionary Ecology. In Press

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. <u>https://doi.org/10.1029/2018MS001583</u>

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 apline zooplankton populations and the importance or lake ice-out. *Journal Of Plankton Research*, 1–15. https://doi.org/10.1093/plankt/fbaa050

Loria, K. A., McKnight, D., Ragar, D. M., & Johnson, P. T. J. (2020b). The life aquatic in high relief: shifts in the physical and biological characteristics of alpine lakes along an elevation gradient in the Rocky Mountains, USA. *Aquatic Sciences*, *82*(1), 1–16. https://doi.org/10.1007/s00027-019-0684-6

Oleksy, I. A., Beck, W. S., Lammers, R. W., Steger, C. E., Wilson, C., Christianson, K., Vincent, K., Johnson, G., Johnson, P. T. J., & Baron, J. S. (2020). The role of warm, dry summers and variation in snowpack on phytoplankton dynamics in mountain lakes. *Ecology*, *101*(10). https://doi.org/10.1002/ecy.3132

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

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.

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.

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.