NWT LTER VII

Long-term research on the dynamics of high-elevation ecosystems: a framework to understand ecological responsiveness to climate change

Year 2 Annual Report
2017-2018

Photo: Looking towards the Tundra Lab on Niwot Ridge in May (Grace Hood, Colorado Public Radio)
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 structure our research in LTER VII using a framework of climate exposure and sensitivity, where multiple levels of variability (plasticity and genetic variation within populations, species abundance within a community, and patches within a landscape) integrate over space and time to influence ecological response to climate change. We take an integrative approach, attempting to identify underlying principles across levels of ecological organization (e.g., ecosystem production, community diversity, population growth rate, individual development), across taxonomic groups (e.g., microbes, plants, small mammals) and across habitat types (e.g., talus, tundra, lake, subalpine forest). We explicitly incorporate spatial scale, testing fine-scale processes where local interactions predominate (which we consider up to a few meters in terrestrial or single-center lake measures), patch-scale variation that incorporates the influence of biota (e.g., tundra areas with and without wind protection from shrubs, different depths within a lake), and consequences at the landscape- and catchment-scale that integrate hydrology and topography (from tens of hectares to many km$^2$).

Our research is broken into four main questions:

**Q1: Shifting Limitations.** How do terrain-related differences on climate exposure affect ecological response? *We hypothesize that ecological responsiveness to climate will be strongest in locations where climate exposure results in a shift in limiting factors.*

**Q2: Biotic Influence.** How do biotic effects influence climate exposure and ecological responsiveness? *We hypothesize that biophysical effects of biota can modify exposure to climate change, and that heterogeneity in these effects influence population persistence and coexistence dynamics.*

**Q3: Adaptation Strategies.** How do different responses to temporal variation at the organism and population levels aggregate to influence community and ecosystem processes? *We hypothesize that taxon-specific responses to temporal environmental variability and uncertainty play deciding roles in landscape distributional patterns as well as the degree of responsiveness to climate change.*

**Q4: Catchment Integration.** How do synchronous and asynchronous responses across a landscape aggregate to affect catchment hydrology? *We hypothesize that climate-related changes in hydrological connectivity will alter the relative contribution of water and nutrients from various portions of the catchment and limit the degree to which landscape asynchronies stabilize catchment hydrological responses.*

In the following sections, we detail our accomplishments, rationale for changes to our plans, and our next steps towards meeting or stated objectives for each 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 this first hypothesis, we focus on resource and abiotic control of responsiveness as driven by climate exposure. Heterogeneity in climate exposure at the landscape scale has only recently begun to be considered and linkages to physiological limitations remain largely unexplored (e.g., Webb et al 2018). We expect terrain-related differences in climate exposure will interact with abiotic and resource variability to cause differential shifts in limiting factors across a landscape. Because a shift in limiting factors will select for different traits leading to a turnover in populations and species with concomitant impacts on ecosystem function, we expect that ecological process rates will be more responsive in areas where limitations shift rather than in areas where limitations intensify without shifting. Based on experimental work, we also expect strong legacy effects of some resources, particularly nitrogen, that might buffer responsiveness (Bowman et al 2018).

To test predictions related to H1, we proposed a series of approaches, including a) continued monitoring, with expansion of select ecological observations; b) modeling limitation of plant growth and expanding modelling to lakes; c) adding consideration of physiological trait mechanisms and d) experimental manipulations of extended summer conditions in tundra, forest, and lakes.

1A. Continued monitoring of tundra, forests, lakes, and pikas. Pikas. In August of 2018 we completed the 3rd year of pika occupancy surveys across 72 plots on Niwot Ridge and at lower elevations in the Green Lakes Valley and Brainard Lake Recreation Area and installed sensors to record sub-surface temperature year-round in each plot. Pika occupancy data from 2016 and 2017 was modeled as a function of previous estimates of average May 1 snow water equivalent (SWE) for each plot as part of a distinguished (Summa Cum Laude) honors thesis by a NWT REU student. Contrary to recently published hypotheses, this metric of SWE did not explain pika occupancy within our plots. Alternative explanations are under investigation by a NWT Master's student who is measuring stress hormone levels in pikas occupying active versus fossil rock glaciers at NWT and in Rocky Mountain National Park. Pikas were sampled non-invasively at each rock glacier during both early and late summer of 2018, and laboratory analyses of stress hormone metabolites are well underway. Results of the stress study will help generalize and provide context for a recent prediction of pika decline in the National Park.

To examine long-term trends in pika demography, we revisited an historical (1981-1990) NWT dataset for comparison with 2004-2018 data from the same location. Pikas on the West Knoll of Niwot Ridge were marked, weighed and identified to sex and stage during both periods, allowing analyses of trends in sex and stage ratios over time. Sex ratios remained stable but juvenile:adult ratios declined significantly from 1981 to 2018 (Figure 1a), suggesting a decline in recruitment. Recruitment is likely affected by the phenology of dispersal, because dispersing pikas are exposed to surface temperatures that can be lethal for this species during summer. The timing of dispersal is related to parturition (birth) date, because maturing juveniles are forced to disperse by territorial adults. Using a pika growth curve based on West Knoll data
(Golian and Whitworth 1985), we determined parturion date for each juvenile in each dataset. Using parturion date (rather than weight) as a phenological metric avoided error introduced by variation in capture dates between years and datasets. We found a striking and robustly significant relationship between parturion date and our multivariate metric of extended summer at Niwot (Figure 1b). This relationship suggests that pikas were born much earlier in years with more extended summers—64 days earlier based on the full dataset or 33 days earlier after conservatively omitting data from the 2 years with the highest and lowest mean parturion dates. This apparent effect of extended summer on parturion date in the current year suggests two new hypotheses: 1) West Knoll females produce fewer late-season litters in years with more extended summer; 2) fewer dispersing juveniles are successful in reaching the West Knoll from other locations during extended summers. A manuscript summarizing these trends in pika demography is in preparation, with an REU student as coauthor.

Subalpine forests. Analysis of the 2016 census in 10 large (> 0.19 ha) and 30 smaller long-term permanent plots indicate that aboveground live tree biomass has increased since plot installation in the early 1980s despite increases in tree mortality (Chai, masters thesis). These results are consistent with the flux tower results showing the forest is still a sink for carbon.

Dendroclimatic analyses of tree cores collected from Engelmann spruce and subalpine fir were performed to examine sensitivity of tree radial growth to climatic variability over the period 1950-2014 at abrupt, diffuse and krummholz treelines. Tree radial growth at krummholz sites was limited by the length of the growing season, whereas radial growth at abrupt (forest) treelines is strongly limited by drought (Treml and Veblen 2017). In the treeline zone, trees limited by the length of the growing season or by the growing season temperature were characterized by increasing growth rates since c. 1990. Additional tree coring within the
long-term permanent forest plots representing a range of forest site conditions was performed in 2016 for ongoing dendroclimatic analyses to examine the potential for compensatory radial growth (proxy for forest productivity) responses across forest sites of varying degrees of moisture limitations.

In 2017, we added three new permanent plots close to treeline to our series of permanent plots (Figure 2). We also collected tree seed in 12 permanent plots and re-measured tree seedling plots, which we plan to continue to do on an annual basis, to assess seedling establishment and survival in relation to monitored microclimatic conditions. Analysis of tree-ring aged juvenile trees by doctoral student Andrus (Andrus et al. 2018a) indicates that over the 1940-2010 period seedling establishment events were more frequent in years with high snowpack (SWE) and cool and wet summers. In the recent half of the study period (1975–2010), a decrease in the number of fir and spruce establishment events across the subalpine forest zone coincided with declining snowpack and a multi-decadal trend of rising summer temperature and increasing moisture deficits. Additionally, data from long-term monitoring of permanent plots was used to show higher rates of subalpine fir recruitment into the main tree canopy, whereas Engelmann spruce exhibited higher overall rates of net population increase and longer residence time in the main canopy (Andrus et al. 2018b). Considering these differences in Engelmann spruce and subalpine fir vital rates is essential to modeling of future projected demographic trajectories of these species.

**Expanded sampling of focal lakes.** As proposed, in the summer of 2017 we expanded our lake monitoring to include bi-weekly sampling of two additional lakes within the Green Lakes Valley (GL1 and Albion) during the ice-free period. While sampled opportunistically in the past, these lakes are now monitored for all the same parameters as GL4, which has been our focal system. In addition, in the winter of 2016-2017 we incorporated monthly winter sample collections of zooplankton from GL4, which will offer insights into biological interactions during a time that has historically been unobserved. After seeing more similarity in the zooplankton communities of Lake Albion and Green Lake 1 as compared to Green Lake 4 we were able to opportunistically collect zooplankton samples from the other three lakes within the Green Lakes Valley Green Lake 2, Green Lake 3, Green Lake 5 to compare changes in zooplankton community dynamics along the very hydrologically connected lake chain.
We also piloted some techniques to evaluate the benthic macroinvertebrate communities at the 3 focal lakes (Green Lake 4, Green Lake 1 and Lake Albion). An REU student compared both benthic macroinvertebrate communities within lake in four different regions along the littoral zone of each lake and at the natural inlet and outlets of each lake. Our preliminary data show that the presence of fish had a slight negative effect on macrobenthic invertebrate species richness and that for the duration of our sampling period the communities of Lake Albion and GL1 were dominated by Chronomids and Mayflies.

We also will plan to continue to take monthly winter zooplankton samples from GL4 and accompany these samples with water samples for phytoplankton analysis, a limited suite of water chemistry and YSI lake profiles for temperature, pH, dissolved oxygen, conductivity and nitrate.

Regional comparison of alpine lake ecology. To better understand regional patterns in alpine lake biology and water chemistry, in summer 2016 we sampled 14 lakes ranging from 21 km north to 16 km south of the Green Lakes Valley (Rocky Mountain National Park and Arapahoe Roosevelt National Forests). These lakes ranged in elevation gradient from 2480 m to 3512 m ASL. Lakes were each sampled three times, spanning from immediately after ice-off through the summer months. Samples were collected to measure total N and P, nitrate, ion concentrations, dissolved organic carbon (DOC), chlorophyll-a, and the communities of phytoplankton and zooplankton. We also collected vertical profiles of temperature, dissolved oxygen, PAR, and light. These data substantially expand our understanding of biophysical properties of alpine lakes and how they vary across an elevation gradient, while concurrently offering a powerful comparative framework with the long-term data from Green Lakes Valley. Some of the preliminary data from this manuscript was presented at the ASLO 2018 Summer Meeting: Water Connects in session SS008 Understanding Mountain Lakes in a Changing World by Kelly Loria. Dr. Pieter Johnson is also co-authoring a manuscript using the chlorophyll-a and water clarity data from this analysis with Bella Oleksy et al.

Soil processes. In our proposal, we described targeted long-term monitoring of soil processes in select tundra and forest permanent plots. As our first step in determining an efficacious way to monitor soil processes, we conducted a pilot soil survey of 74 locations within the saddle catchment, allowing co-located comparisons with many abiotic, plant, biogeochemical, and hydrologic characteristics (we describe these measures more in section 4, below) (Hermes, PhD student). This survey, completed during Summer 2017, included measurements of soil physical and chemical properties, as well as repeated measurements of soil water status. Hermes, Hinckley, and Haruko Wainwright (Lawrence Berkeley Laboratory) are analyzing these data using a statistical model to determine “patches” or “zones” across the landscape that describe areas with like subsurface attributes/behavior. In addition, in Summer 2018, Rey (PhD student, Colorado School of Mines) began conducting geophysical surveys (repeated transects) across the Saddle Catchment to characterize subsurface structure and changes in hydrologic storage. Both efforts will assist in choosing where to continue process-based soil biogeochemical measurements to capture spatial and temporal heterogeneity in soil and hydrological properties; we anticipate that two manuscripts will be submitted in 2019 describing these first efforts.
We have also begun efforts to map plant species richness and density, soil bacterial, fungal and
eukaryotic species richness and phylogenetic diversity (using 16S, ITS, and 18S gene
sequencing), and ecosystem function (levels of soil C and N, and rates of microbial enzyme
activities) along a natural gradient in plant richness and density in high-elevation, C-deficient
soils to examine the coupling between above- and belowground systems (Porazinska et al 2018).
We find that microbial communities in early successional systems, such as the high-elevation
talus-tundra systems at Niwot, are dependent on contemporary inputs from plants and
therefore are strongly correlated with plant diversity and density.

**Biome Shifts.** Based on manually classified vegetation from high-resolution repeat aerial
photographs from 1972 and 2008 at Niwot Ridge, Colorado, USA, we found that trees and
shrubs have colonized tundra, while tundra colonized barren soils (Bueno de Mesquita et al
2018). Only shrubs expanded their elevational range. Several fine-scale topographic, soil and
snow characteristics, including elevation, slope, solar radiation, soil bulk density, and
interannual snowpack variability, modulated where plant establishment occurred. These results
build on our predictions that fine-scale heterogeneity may strongly control how plants in
mountainous regions respond to climate change, and different vegetation types may be
sensitive to different aspects of this heterogeneity.

**1B. Modeling limitation of plant growth.** We originally described a new model for Niwot Ridge
presented in a manuscript under review during the proposal submission period. That paper (Fan
et al, 2016) has now been published and the basic hypotheses regarding the shifting seasonal
nature of nutrient limitation on Niwot Ridge now are available to guide observations. These
model predictions and more specifically, the challenges associated with modeling specific sites
on Niwot Ridge without adequate data are one of the main reasons why we have developed the
new sensor network on the Niwot Ridge Saddle.

The sensor network is described elsewhere (see section 4) but is now generating data that will
allow for the use of the NBM 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.

**1C. Addition of physiological/trait mechanisms.** In 2017/2018, we completed a new
model-based analysis of the role of plant traits in overall plant responses to environmental
change. The manuscript, in press at *Ecology and Evolution*, makes some surprising predictions of
how plants may respond to longer and hotter summers and highlights the important role that
quantitative modeling plays in helping delineate future research questions on Niwot Ridge. In
this manuscript, Wentz et al (in press) describe a new model developed specifically to simulate
plant photosynthetic responses to environmental constraints on Niwot Ridge. The new
modeling approach uses assemblages of traits representing acquisitive and conservative species
on Niwot Ridge. In this work, Wentz et al, show that photosynthetic rates are influenced by a
number of factors including leaf N, leaf shape, and plant height. More surprisingly, the
trait-based modeling identified leaf temperature as a critical factor in C assimilation and

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specifically linked lower rates of C assimilation in conservative (dry) communities to high leaf temperatures during the peak growing season. The high leaf temperatures occur in part because of lower plant stature in these communities and the interaction of plant height with leaf temperature during the warmest periods of the year. In these simulations and associated calculations of soil water availability, the mid-season growth limitation in the dry meadow areas appears to be temperature rather than water; a result that is surprising given prior assumptions of water control over community structure on the ridge.

We also continued efforts to build a comprehensive trait database for the project, following efforts across the globe (e.g., Bjorkman et al 2018). Between 2017 and 2018, we measured plant height, specific leaf area, leaf size, chlorophyll content, leaf dry matter content, and leaf chemical composition (nitrogen, carbon, δ13C, δ15N) on 1210 individual plants from 65 species (Figure 3). These measurements were collected to capture intraspecific trait variation among the key habitat types on Niwot Ridge and to examine how species traits respond to global change in the ITEX experiment. Based on traits of 2689 individual plants, we are now moving forward with functional characterization of species, for instance, to characterize axes of variation related to water use (e.g., delta 13C) and nitrogen use (e.g., leaf N concentration, SLA), as well as to assess relationships of these traits to landscape distributional patterns.

1D. New experiments: manipulation of extended summer conditions in terrestrial and aquatic systems. Terrestrial Manipulation of Growing Season Length. Based on long-term field data showing the importance of snowmelt timing on plant composition, phenology, and physiology (Winkler et al 2018), we established experimental manipulations of growing season length at five sites along Niwot Ridge (2 northeast facing, 2 south/southeast facing, and a site at a diffuse treeline location with more woody species present; Figure 4a). Rather than structure our design by habitat type, each of these larger sites encompasses a range of vegetation types (e.g., one might span dry meadow, wet meadow, to tree colonists) along a hillslope gradient. Each habitat type is represented in at least three of these larger treatment plots.
Fall 2017, we established large treatment plots and paired controls approximately 40m x 10m long aligned along the topographic runoff flow lines and starting at the top of the hillslope crest with little water flow from adjacent uphill areas (Figure 4b). We used a thin layer (~500 g/m$^2$) of inert black vitreous sand (Mission Laboratories, Los Angeles, CA, composed primarily of silicon dioxide, iron oxide, and calcium oxide) applied over the snow at peak snowpack. In the first year of the snowmelt manipulation (applied May 2018), black sand increased the snow free date by 0-14 days depending on site and location along the hillslope. We also added the sand to control plots after snowmelt to account for any effects on soil albedo, texture or microbes.

![Figure 4b](image)

Figure 4. In 2018, we initiated an experiment manipulating the timing of snowmelt at five locations across the site (A), by adding a thin layer of black sand in 10 x 40m plots at peak snowpack (B), which increases the albedo (C, also G) and speeds snowmelt (D). We combined these manipulations with a summer warming (ITEX chambers)(E) and artificial shrubs (to simulate smaller-scale influence of biotic-induced heterogeneity, our H2).

Over the 2018 growing season, we established subplots (n=80, dimensions=0.5 x 1m) for long term tracking of plant community composition and abundance using the point intercept method. Plots were set up approximately 5, 15, 25, and 35 m from the top of the plot, encompassing different snowpack and moisture conditions, and different plant communities going from the slope crest to toe. Further, we added open-top passive warming chambers (following the International Tundra Experiment protocol) at four of our sites (paired with their own control subplots), allowing us to track biotic responses to early snowmelt, warming and the combination of the two (Figure 4e). We also tagged woody species at each site to monitor tree and shrub mortality and colonization. Phenology and flower production of a total of ~1200 individual plants was tracked for 8 weeks at four sites, which are currently being analyzed for total anion and cation supply. Soil moisture was recorded using a handheld TDR probe 2-3 times per week at a depth of 12 cm. In September, we installed continuous soil moisture and temperature loggers at 4 locations within each plot, corresponding to the vegetation monitoring plots.

Aquatic manipulation of early ice melt-off. We had originally proposed to conduct factorial manipulations of water residence time and terrestrially derived dissolved organic matter (DOM).
The scientific objectives were to test how reduced flushing rates (associated with earlier ice-off on lakes) and increased DOM (associated with encroachment of terrestrial plants in the alpine watershed) interactively affect phytoplankton and zooplankton biomass. We expected the weakening of physical limitations, such as flushing as UV penetration (which is partially ameliorated through higher DOM concentrations), would enhance biomass of both groups but also allow an opportunity for zooplankton to regulate phytoplankton (i.e., greater top-down control).

In the winter of 2017 we piloted a warming technique by spreading a thin layer of black sand (~400 g/m²) on 8 pilot tanks located at the University of Colorado Boulder Science Discovery building (1600m) and 6 tanks at the University of Colorado's Mountain Research station (2900m). We wanted to see how effectively black sand could increase the mesocosm ice albedo and thus accelerate ice-off. Prior to sand application, snow was scraped off both treatment and control tanks to prevent unwanted insulation or albedo effects of snow on the ice surface. An additional layer of sand was applied in late spring to account for any seasonal snowfall. Once all the tanks thawed we added a thin layer to our control mesocosms after to account for any experimental impacts of sand on the liquid water effects. The black sand warming technique trials showed that the sand application was associated with a very marginal increase in melting, surface water temperature, and a marginal decrease surface ice thickness. Trials with the black sand application in Boulder showed no significant difference surface ice-off date, ice-thickness or tank water temperature. Trials with sand application at the Mountain Research Station did show an effect of sand on increasing tank temperature (GLM: $\beta_{\text{sand}}: 0.212 \pm 0.10, p=0.037$) but this increase in temperature was not strong enough to compel the tanks to fully thaw more than a few days ahead of the control tanks (Figure 5a). Ideally, we want to deploy a warming treatment that causes tanks to become ice-free by a larger window of time to mimic the climate warming trends which have been predicted to be as high as 3-5°C over the next 50 years under a moderate emission scenario (Lukas et al. 2014).

![Graphs](image)

*Figure 5(a). The average temperature of mesocosm tanks treated with black sand at two locations the University of Colorado Boulder Science Discovery building (1600m, 4 treated and 4 control tanks) and the University of Colorado’s Mountain Research station (2900m and 3 treated and 3 control tanks).*

*Figure 5(b). The average photosynthetically active radiation of mesocosm tanks treated with willow packs for 5 week period in the summer of 2018 at the University of Colorado Boulder Science Discovery building (1600m, 7 treated and 3 control tanks).*
**Current Pilot Goals.** This winter we are investigating if we can create a stronger warming effect by deploying tanks of the same make and model in either reflecting and absorbing colors. This fall we deployed 8 tanks (3 black 1100L, 3 beige 1100L, 1 black 2500 and 1 beige 2500L tank) at Soddie (40.047778, -105.570833; 3350m) as well as 4 tanks (1 black 1100L, 1 beige 1100L, 1 black 2500 and 1 beige 2500L tank) University of Colorado Boulder Science Discovery building (1600m). Besides evaluating the effectiveness of using different color tanks as a warming treatment; this round of piloting will help us determine (1) how the tanks withstand the variable snow drifting patterns at this high elevation location, (2) whether this location will be suitable for the full manipulation in future, and (3) the ability of the tanks to fill and retain water during the summer. The tanks are equipped with thermistors (HOBO Pendant® Temperature/Light 64K Data Logger), that record both surface and hypolimnion temperature and light in each mesocosm. These temperature measurements will be supplemented with regular observations and one or more game cameras to provide a more finely resolved record of ice-thaw patterns and identify any sources of potential damage. Weekly following ice-off we will collect water samples following long-term protocols to describe chl-a, water chemistry, DOM, and phytoplankton and zooplankton composition. To estimate benthic chl-a values, clay tiles on the bottom of each mesocosm will be scraped weekly.

We hypothesize that increases in growing season length induced by black sand addition will lead to increases in chl-a, phytoplankton biomass, and zooplankton biomass, with concurrent reductions in DIN. We further expect an interaction between elevation and growing season length, such that the effect size of the black sand manipulation will be most pronounced at intermediate and high elevations. Although mesocosms cannot capture the full complexity of biological and abiotic interactions unfolding within lakes, 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 between phytoplankton and zooplankton.

2. BIOTIC INFLUENCE: How Do Biotic Effects Influence Climate Exposure And Ecological Responsiveness? Biota can influence climate exposure through effects on both the physical and resource environment. In tundra and at treeline, for instance, the physical presence of particular life forms (cushion plants, shrubs, trees) can affect wind redistribution of snow, increase soil moisture, and modify the temperature of the underlying soil. Terrestrial biota can also influence climate exposure in lakes: terrestrial plant and microbe subsidy of dissolved organic matter (DOM) protects plankton from UV radiation, relaxing a major abiotic limitation in high-elevation lakes. Thus, the aim of this second hypothesis is to determine how biotic effects may also create microrefugia in the face of a changing climate.

2A. Long-term observations to describe positive and negative associations. We have begun initial work using repeated measures of population growth rates or abundance over time allow the estimation of population dynamics in a simple competition model that can take into account effects of other species or functional groups, effects of focal species density or frequency, as well as effects of climate or environmental parameters such as snowpack. Currently, we have 10 years of continuous plant composition data from the saddle grid (prior to 2008, we did not take
composition data annually). Because a couple more years of data will best enable this modelling, we will prioritize this effort in yrs 3 and 4 of the project.

2B. Adding biotic manipulations to the terrestrial growing season length experiment. In the terrestrial growing season length experiment described above, we established subplots in the larger treatment (black sand) and control plots where will placed structures developed at the Jornada LTER (which they call connectivity modifiers or con-mods to simulate the snow-capturing effect of shrubs) (Figure 4f). We expect that they will influence snow distribution and create small-scale heterogeneity within the larger black-sand manipulations.

2C. Adding terrestrial DOM subsidy to the mesocosm experiment. In the mesocosm experiment described above, in half of the mesocosms, we will also add enhanced terrestrial DOM as a treatment. Thus, the experimental design will be 2 x 2 x 3 manipulation with black sand added (yes/no) and DOM added (yes/no) performed across the three, elevation-stratified locations (4 replicates per treatment at each elevation with 12 total replicates per treatment and 48 total mesocosms). DOM additions will follow standard willow “leaf-pack”-type additions composed of air-dried tundra vegetation enclosed within Vexar mesh and added to the mesocosms in late-summer prior to filling. Willow leaves can leach up to 40 mg C / g dry leaf mass and will be added in sufficient quantities to raise DOM concentrations in mesocosms to limit UVR penetration to < 1% within the top 10 cm of the tank. In tanks without DOM additions, UVR sufficient to limit primary and secondary productivity should be able to penetrate to the bottom of the mesocosm tanks.

We hypothesize that the relative importance of autochthonously-derived DOM stemming from phytoplankton will be most influential in mesocosms at high elevation and with an extended growing season, which will provide time for this added UV protection to take effect. We predict that this benefit from autochthonously-derived DOM will only be detectable in mesocosms without leaf additions. We will assess UV stress in zooplankton assemblages by (1) examining Daphnia for photoprotective pigments and (2) assessing the prominence of taxonomic groups with high UV tolerance (e.g., Calanoids and Holopedium). Alternatively, we do not expect differences in zooplankton assemblages indicative of differing UV stress among mesocosms with DOM supplements provided by leaf-packs. Increases in DOM are also expected to amplify the degree of top-down regulation of phytoplankton and chl-a by zooplankton, which we will quantify based on the correlation between variation standing biomass in adjacent trophic levels (e.g., zooplankton and phytoplankton). Together with the black sand manipulation, these treatments will help capture major environmental shifts in lakes within the GLV: namely, accelerated ice-off dates and increased inputs of DOM from the upward movement of tundra vegetation and increased phytoplankton production.

In the summer of 2018 we tested the effectiveness of using leaf packs to change the photo-quality and DOC concentrations in 10 black 1000L mesocosm tanks University of Colorado Boulder Science Discovery building (1600m). Willow leaves were collected from areas near the University of Colorado's Mountain Research station (2900m) to simulate natural sources of organic material that could become more abundant with changes in treeline. Willow leaves were air dried for at least 48 hours before weighing and being divided into packs.
devised three size classes of willow packs: small (75.0g), medium (250.0g), and large (500.0g) and wrapped each in mesh. There were two replicates of each willow pack treatment, and three controls. Leaf packs were deployed in mesocosms and allowed to sit for two weeks (until July 23rd) after which half of the willow packs were removed and YSI and LI-COR measurements were collected to assess water quality (Temperature, pH, conductivity, nitrate and PAR) every Monday or Wednesday until September 7th. Water samples were collected for dissolved organic carbon and chlorophyll-a every other week. We are still waiting on chlorophyll-a and DOC analysis from laboratory analysis. Preliminary analysis of our measured parameters for water quality show that PAR was significantly lower (as compared with control tanks) in tanks with leaf packs (GLM: \( \text{willow} : -9.476 \pm 4.11, p= 0.050 \)) (Figure 5b). The 2018 willowpack pilot indicated that there are some differences between leaf pack sizes, and we plan to pilot willow pack treatments again in 2019 to optimize the use of leaf packs given a much stronger ultraviolet radiation regime at present at higher elevations.

3. ADAPTATION STRATEGIES. How do different responses to temporal variation at the organism and population levels aggregate to influence community and ecosystem processes? We have been working to develop these new hypothesis and research direction and have submitted reworked rationale and plan for this work as a separate document.

4. CATCHMENT INTEGRATION: How do asynchronous responses across a landscape affect catchment-scale processes? Water quality and quantity leaving a catchment provides an integrated signal of the biotic and abiotic processes occurring along flow paths that generate stream and lake inputs. These flow paths are largely controlled by characteristics of the “physical template” of the landscape (e.g., soils and subsurface structure). However, it has become increasingly important to consider how spatial variation in climate exposure and sensitivity — our focus on the first three hypotheses — could cause different parts of catchment to respond differently relative to their position in the landscape, which then may affect quantity and quality of water leaving a catchment. Climate also influences hydrologic connectivity: some areas of the catchment may be connected via flow paths in some years but not in others. Because variation in ecological responsiveness has rarely been considered at the catchment scale, our goal in this last section is to investigate interactions between these two processes. We proposed a combination of spatial-explicit measurements, modeling and the implementation of a tracer studies to address this last question.

4A. Continued hydrological and snow measurements, extensions to sensor network and remote sensing. The saddle catchment sensor network. To better describe the spatial variability that characterizes a high-elevation catchment, we established a sensor network to collect real-time spatially-explicit measurements of snow depth, soil moisture/temperature, air temperature, and plant productivity. This sensor network instruments a small drainage, the saddle catchment, where hydrologic discharge measurement has been historically recorded. Sixteen sensor ‘nodes’ were installed during the summer and fall of 2015. Sensor node locations were selected to capture the heterogeneity of the alpine-subalpine transition zone, and provide a platform for integrated observations from patch- to catchment-scales (Figure 6). Each sensor node captures air temperature and relative humidity (CS 215), snow depth (maxbotix), soil
moisture (decagon) from six sensors, soil temperature (decagon) from two sensors, and provides remote data accessibility.

The sensor network began with the installation of Metronome System’s datalogger and radio communications in summer of 2016. It was quickly discovered that this system lacked the reliable networking capacity and rugged dataloggers required for the harsh site conditions. Limited IT support failed to remedy the network. A poor data record from this first year supported a shift of equipment to Campbell Scientific. During summer 2017 a complete overhaul to Campbell Scientific dataloggers (CR1000/1000X), air temperature/relative humidity (CS 215), and radio communications (RF 407) took place. Installation of Campbell Scientific equipment was completed August 1st through mid-October of 2017. Currently, all of the sensor network nodes are recording data with reliable remote accessibility. Roughly half of the snow depth sensors failed after the first winter and were replaced in 2018.

In 2016, we conducted a pilot study to investigate soil inorganic nitrogen (N) pools and net N mineralization and nitrification rates across 24 sampling locations within the Saddle Catchment. Our sampling locations covered six types of plant communities (i.e., dry, moist, and wet meadow, shrubs, krummholz, and subalpine forest), and included most of the sensor nodes. In 2017, we expanded the dataset by evaluating N availability and transformation rates at several timepoints. We increased the number of sampling locations to 26, and included all the sensor nodes. At each location, we conducted in-field incubations for soil N transformation rates (0-15 cm depth) during snowmelt (June to July), peak growing season (July to August), and the seasonal transition (August to September). Our preliminary results showed both interannual and season variation in N cycling, as we expected, as well as stronger seasonal variation in some landscape positions (dry meadows) and more stable cycling rates in other positions. Chen (Visiting PhD student), Wieder, and Hinckley have now drafted a manuscript describing the soil N transformations across the Saddle Catchment, and plan submission in late 2018/early 2019.

**Deployment of lake sensor array:** As an important next step in our study of alpine lake ecology, we deployed a sensor network across a depth transect in GL4 (from a subsurface float to 13-m depth). The sensor array collects depth-specific data on temperature, dissolved oxygen, chlorophyll-\(a\), and photosynthetically active radiation (PAR) at regular time intervals (Figure 7). This project is approved by the Boulder County Watershed, which controls access to Green Lakes Valley. Such high-resolution data will help identify mixing events and provide perspective as to how these events influence nutrient cycling and biotic productivity across multiple trophic

![Figure 6. Map of the location of the sixteen sensor nodes along the saddle catchment on Niwot Ridge.](image)
levels, particularly in combination with our new protocol of collecting zooplankton monthly during the winter. We feel that this is a logical next step prior to attempting to model lake production, a goal we included in the LTER VII proposal.

We were able to successfully deploy the sensor network buoy on July 7th 2018 - August 21st within Green Lake 4 in a summer configuration. This configuration includes temperature sensors (RBR soloT) at 0.4, 1.5, 3, 5.1, 6.5, 7.5, 9, 10, and 11.5 meters; dissolved oxygen sensors (PME miniDOT) with antifouling wipers at 2, 9, and 11.5 meters; a Turner Designs Cyclops-7 submersible spectral fluorometer equipped with optics for chlorophyll-a and an internal data logger manufactured by PME with antifouling wiper at 9 meters; and a photosynthetically active radiation (PAR) sensor (PME miniPAR) with an antifouling wiper also at 9 meters. There were signs of clear thermal stratification and mixing however these events do not appear to be inspired by either wind or precipitation based off of the closest current SNOTEL site at Silver lake, however we will have a better idea of the causes once the DI precipitation and wind speed data are available.

The buoy was then redeployed in a winter configuration August 23rd until July 2019 (Figure 8). The winter configuration consists of temperature sensors meter depth intervals (2.5 to 13m); dissolved oxygen sensors at 2.5, 7 and 11 meters, the Cyclops-7 at 2.5 meters and the PAR sensor also at 2.5 meters. The Cyclops-7, and PAR sensors were moved closer to the

Figure 7. Temperature and Dissolved oxygen collected by the sensor array across a depth transect set up in Green Lake 4 over a 30 minute timestamp.

Figure 8. Configuration of summer and winter buoys deployed in Green Lake 4, consisting of temperature, dissolved oxygen, chlorophyll-a and PAR sensors.
surface as the area closest to the ice has been identified to be the most productive under winter conditions (Hampton et al., 2015; Hampton et al., 2017), and Green Lake 4 tends to have some degree of ice-cove for the majority of the year (~October-June). During our winter data collection, we will take YSI profiles to get comparison data points for temperature and dissolved oxygen probes installed on the buoy.

**Extensions to remote sensing.** Fine-scale heterogeneity and frequent cloud cover has made the use of traditional remote sensing challenging. To address this gap, we have reconfigured and tuned a custom built multispectral - visible (RGB), near infrared (NIR) and thermal infrared (TIR) – UAS for operation in the challenging conditions of Niwot Ridge, where wind speeds regularly exceed 10m/s, and high elevations (>3500m) reduce lift and maximum flight times. Using this platform we have completed weekly surveys through the snow melt season (June-August 2017) of approximately 80ha at the tundra treeline transition, overlapping the saddle catchment sensor network. We have completed 8 individual survey flights to date. An additional suite of surface measurements have also been collected coincident with the UAS surveys; including, >250 surface soil moisture measurements, ~200 snow depths and numerous ground control points, all surveyed to sub-cm accuracy with differential GNSS. In late 2017 we completed processing of the large imagery datasets totaling around 1.5TB of imagery and over 35,000 individual frames using a Structure from Motion workflow. Primary datasets include RGB orthomosaics at 5cm resolution, NIR/Red defined wavelength orthomosaics at 5cm, land surface temperature at 30cm resolution, and repeat DSM’s at 10cm.

Since the last annual report we have continued working with these datasets, and deriving new ones. Using calibration plates we converted NIR/Red imagery to surface reflectance and derived 5cm spatial resolution NDVI maps for each survey date. Through DSM differencing we have estimated snow depth at each date, as well as change in snow depth, and depth change rates. High resolution (30cm) thermal maps have proven extremely effective in improving our understanding of hydrologic flow paths, and connectivity within the survey area (Figure 9). Preliminary results from this unprecedented dataset were presented at AGU 2017. Furthermore these datasets have fostered active
collaboration across the research objectives, including use by Hinkley and Hermes for patch analysis, and Livneh in hydrologic modelling efforts.

In 2018, we began quantitative analysis of these datasets to identify spatiotemporal patterns in, and controls on fine scale snow distribution and vegetation productivity, including the identification of ‘hot spots’ and ‘hot moments’ across the survey time series (Figure 10). We have publications in preparation and findings from this research have been presented at the Western Snow Conference (2018), and Boulder offices of NEON, and the NSIDC.

4B. Spatially-explicit modeling at the catchment scale. The key areas of focus for the hydrologic modeling (DHSVM: Distributed Hydrology Soil Vegetation Model) has been towards accurately estimating the total water balance, spatially distributing station precipitation, as well as QA/QC of model input and outputs. Assumptions were needed to spatially distribute precipitation from the one gauge located within the catchment to all ~75,000 model grid cells (2m horizontal resolution). A transfer approach previously implemented by Livneh et al. (2014) has been applied, where remotely sensed spatial information is used as a scalar to distribute precipitation. We are currently exploring several products that each observe different aspects of precipitation: the Jepsen SWE reconstruction data (1996-2007 at 30m), Landsat snow cover (1984-2018 at 30m), MODIS snow cover (2000-2018 at 500m), as well as more recent snow cover data from a drone flight (2017 at 1 m). DHSVM simulated snow cover fits reasonably well among these (Figure 11a). A combination of these data is currently being evaluated to construct a map of spatial precipitation distribution for each year, 2001-2018.

Preliminary simulations of catchment-wide streamflow have been compared with observations from the Saddle gauge (Figure 11b). Although the un-calibrated results are not expected to capture detailed features of the hydrograph, the overall simulated water balance is within -23 % of the observed. During a catchment visit this summer, we observed a relatively small streamflow in the upper reach, whereas the channel at the gauging location was completely dry, suggesting losses within the system that may skew direct comparison of simulated and observed streamflows. The hydrologic connectivity analysis has been postponed until model calibration and validation issues are resolved.
4C. Integrating spatially explicit hydrology into fine-scale biogeochemical modeling. We originally proposed to iteratively force the biogeochemical model (Fan et al. 2016) used to quantify limitations in H1 using fluxes of water from DHSVM. Although we still intend to examine these issues in conjunction with the hydrologic modeling, we decided prior to our last annual report that we first need a better understanding empirically of the links between terrestrial biogeochemistry, hydrology, and catchment-scale water flow and nutrient export (and to the lake dynamics and ecology). The photosynthetic modeling described above (Wentz et al., in press) is one such approach that we have taken in the prior year and as with the Fan et al., 2016 publication has provided further insight into the core issues underlying both Hypothesis 1 and the integration activities proposed for Hypothesis 4.

In our prior annual report, we proposed recruiting a postdoc carry out a comprehensive analysis of long-term observations to examine the associations between terrestrial, stream, and lake systems. We launched a national search for this postdoctoral associate in July of 2018, received over 60 applications for the position and selected a finalist in October. The new postdoctoral fellow, John Crawford, will start his position January 1, 2019 and will immediately launch a project to examine long-term aquatic and terrestrial records to explore patterns of change and temporal/geographic synchrony or dis-synchrony in existing data. The initial results of this study will be available for the site-review in 2019 and will be used to prioritize the next steps toward a coupled modeling effort the later years of LTER VII.

4D. Integrating hydrological and biogeochemical modeling efforts with new field tracer studies. We plan to take an iterative model-observational approach, first forcing DHSVM using dynamic inputs (meteorology) and static fields (topography, soils, vegetation), and validate model soil moisture, streamflow, and fluxes to local observations. Then, preliminary simulations will be used to identify locations of high and low connectivity where we will then employ tracer studies. We are still in the process of developing the DHSVM to quantify connectivity, and expect to consider tracer studies in years 3 or 4 of the project once we have completed this first step.
5. CROSS-SITE SYNTHESIS. Niwot investigators are PIs for two of the NCO-sponsored synthesis groups. Suding co-leads “Synthesizing population and community synchrony to understand drivers of ecological stability across LTER sites.” Whether populations rise and fall in tandem, independently or alternately can affect ecological stability. Offset fluctuations between species can enhance ecosystem stability. Or alternate fluctuations of the same species in different regions can support species stability. Building on many sources of long-term data, the LTER Synchrony working group aims to understand the drivers and timescales of synchrony and its effect on ecological stability.

Wieder co-leads the “Advancing soil organic matter research: Synthesizing multi-scale observations, manipulations & models” group, which aims to explore the Soil organic matter, a massive storehouse for carbon, as well as a key regulator of nutrient cycling and soil quality in terrestrial ecosystems. Their goal is to use LTER data to increase our understanding of the controls on stabilization and breakdown of soil organic matter. Two sets of competing theories underlie models that adequately predict site-specific dynamics, but result in different sets of predictions about the response of soil organic matter to perturbations.

Niwot also has been active in other synthesis efforts, including one to synthesis plant traits across tundra biomes (Bjorkman et al, 2018a) and comparisons of ambient versus experimental changes in plant species abundances in global change experiments (Langley et al 2018). Of particular note, niwot investigators worked on a global analysis of biome-wide relationships between temperature, moisture and seven key plant functional traits both across space and over three decades of warming at 117 tundra locations which showed the importance of temperature mediated soil moisture effects (Bjorkman et al 2018b)

6. EDUCATION AND OUTREACH LTER VII. **Professional Development for Graduate 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. **9 students affiliated with NWT** and 3 unaffiliated students took the course in Fall 2017. The class was designed to provide professional development for our students in science communication and engaged scholarship. The capstone project for the course was a digital storytelling assignment. Four groups of students developed video storylines about aspects of NWT science. Intended for audiences ranging from middle and high school students to adults who enjoy recreating in the alpine, these digital stories are about: the importance of long term ecological research; what climate change looks like from the perspective of alpine and subalpine organisms; what it’s like to be a field ecologist; and why snowpack matters. The final versions of these projects are still under production—but will soon be disseminated via NWT, INSTAAR, CU, and other affiliated social media feeds and incorporated into K-12 classroom education through ongoing collaborations with teachers across the state.

**Six NWT graduate students** who took the outreach and communication practicum put their skills into practice via a *new collaboration between Wild Bear Ecology Center* (a non-profit, all-ages nature center located near NWT) and NWT. NWT grads, staff and techs took children ages 10-15 into the field with them for four hours on each of 9 Wednesdays during the summer,
demonstrating field techniques and teaching them about topics including pika biology, water chemistry, climate data, limnology, subalpine forest ecology, phenology, and chickadee biology.

**Eight NWT grads**, including several who participated in the outreach and communication practicum, participated 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. For the second year, **8 of the 14 high school students were recruited on scholarship** through the Nature Kids Lafayette/Jovenes de la Naturaleza program—an initiative to increase outdoor stewardship and environmental literacy in children from low-income and Latino families in Lafayette, Colorado.

**K-12 Outreach and Education.** In addition to giving graduate students opportunities to connect with students and practice science communication, our other major outreach goal was to re-think how our Schoolyard Books (My Water Comes from the Rocky/San Juan Mountains) is being used in schools. With colleagues from the CU Museum of Natural History, we received a **CU Boulder Outreach Award** that has allowed us to design an entirely new curriculum kit for 4th grade classrooms called Adaptation and Variation in Colorado Mammals. The kits use the My Water books in the context of teaching early evolution literacy concepts. We are proud to announce that the kit and its **curriculum has been adopted by the Boulder Valley School District**, and was used as part of our formative assessment implementation in 26 classrooms at 9 schools in 2017-18 (~650 students), and will be used in over 80 classrooms around the district in the 2018-19 school year. Additionally, **we distributed the kits to 17 rural, and underserved districts** around the state in conjunction with professional development workshops for teachers in those areas. Ongoing efforts are to translate the My Water books in a digital format into a Spanish language version for use in bilingual and English language learning classrooms.

We also introduced well over **200 middle and high school students** to NWT research this past year through field trips to the Mountain Research Station and lab tours on campus. Our **partnership with the Winter Wildlands Alliance and their Snow School program** (https://winterwildlands.org/snowschool/) connected LTER scientists and CU undergraduates with ~120 children in 1st through 6th grade, and got them out on snowshoes, exploring snow science at the Mountain Research Station and subalpine sites nearby. Additionally, NWT grad students Cliff Bueno de Mesquita and Ashley Whipple helped design new activities about their NWT based graduate research for Snow School sites around the country.  

https://winterwildlands.org/snowschool-snow-science-curriculum-modules
Public and Stakeholder Audiences: NWT pika biologist Dr. Chris Ray continues to be active in the field of public outreach and engagement. She participated alongside other CU Boulder and NOAA researchers in an online lecture series for The Academy for Lifelong Learning on the topic of climate change. Dr. Ray and her lab group are frequent bloggers and social media posters and they help run a successful citizen science project (http://www.pikapartners.org), and teach a field courses on pika ecology and population monitoring techniques for National Park volunteers and the general public.

Five Niwot faculty and graduate students participated in a day long workshop with Rocky Mountain National Park scientists and volunteers to share research findings and strategies with the goal of improving collaboration between CU Boulder and RMNP.

To help RMNP meet its wildlife and habitat monitoring needs, NWT PI Chris Ray has initiated a collaboration between the park and a citizen-science project managed by the Denver Zoo for long-term monitoring of pika occupancy and habitat characteristics in in RMNP using the NWT pika monitoring protocol. This collaborative effort began in 2018 with grants from the National Park Service and CU to develop a volunteer program sufficient to meet park needs and to educate park visitors about wildlife and climate change issues.

7. INFORMATION MANAGEMENT. NWT hired a new information manager this June (Sarah Elmendorf) to replace outgoing IM Hope Humphries. Sarah attended EDI’s workshop: "Creating EML with R and publishing data packages in the EDI repository" in Albuquerque. Since arriving, her major focus has been on updating the website and metadata to take leverage EDI and accelerate data and metadata archiving in EDI.

Updates to local data catalog. In August, we updated our local data catalog (http://niwot.colorado.edu/data) to use EDI rather than a local data source as the back-end. Briefly, the old Niwot catalog was maintained using a local data source (expression engine-based, with a mysql back end). Datasets were independently submitted to EDI. To improve efficiencies and take advantage of the speed and enhanced search capabilities of LTER-wide resources provided by EDI (specifically, PASTA's solr search client), the new data catalog instead uses PASTA's API to query Niwot datasets on EDI. Code (HTML, CSS, and JavaScript) embedded in the Niwot website provide a search interface tailored to Niwot data users to search Niwot data on EDI; clicking on a dataset redirects users to the dataset page on EDI where metadata can be examined in more detail and data can be downloaded. We are developing code to further enhance the search page (filter by experiment, taxon, date & implement query-boosting to promote Niwot's signature datasets (with credit going to initial legwork provided by the IM at BLE: https://github.com/BLE-LTER/PASTA-JavaScript-Search-Client). These advanced search features rely on updating keyword sets in the EML files themselves, work we are doing in concert (see below). When the majority of the datasets have updated EML, we will introduce the advanced search features on our main data search page.

Migrating existing datasets to EDI. We have developed R scripts to migrate the bulk of Niwot's existing datasets (which had much of the required metadata content stored in ASCII text files) into EML, and are in the process of transferring the remainder of Niwot's datasets into EDI. Until
all datasets are available through EDI, we are maintaining links to our 'legacy' data catalog where datasets that have not yet been migrated can still be accessed.

**Delivering new datasets to EDI.** We have also developed a machine-readable metadata template which will greatly speed up the preparation of EML and subsequent archiving of new datasets.

**Data QA/QC and analysis.** We also have initiated a NWT GitHub page, where code used for both data and metadata preparation as well as scientific researchers is shared. While qa/qc of short-term experiments and graduate student research remains the responsibility of the data providers, we are developing standardized qa/qc scripts to systematically quality-control Niwot's signature datasets to improve data quality going forward.

We are continuing to use the GCE Data Toolbox as our primary tool to handle raw NWT sensor data, and working to get the new sensor array datasets integrated into this workflow.

**REFERENCES.**


