NWT LTER VII

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

Year 1 Annual Report
2016-2017

Photo: view from the Continental Divide to the Green Lakes Valley. Niwot Ridge is to the left, the melt pool of the Arikaree glacier is front-center, and Green Lake 5 and then 4 are next in the string of alpine lakes.
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 (demographic rates for a population, species abundance within a community, and patches within a landscape) integrate over space and time to influence ecological response to climate change. We are taking an integrative approach, attempting to identify underlying principles across levels of ecological organization (e.g., ecosystem production, community diversity, population growth rate), 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 km²).

As depicted in our conceptual framework (Fig. 1), 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 influences population persistence and coexistence dynamics.*

**Q3: Compensatory Dynamics.** Can opposing responses to climate variation – among populations, among species, and across geographic locations – lead to increased stability at higher levels of organization and at larger spatial scales? *We hypothesize that climate change will increase synchronous responses as ecosystem components approach shared tolerance and growth constraints.*

**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 the proposal workplan, and next steps towards meeting our stated objectives for each question. Our structure follows the order of the work plan in our proposal, with the first four sections addressing the four research questions (1-4), followed by sections on outreach (section 5) and information management (section 6).

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. 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.

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, pikas and marmots. *Pika and marmots.* We expanded our monitoring of pika populations in yr 1 of LTER VII. American pika dynamics were monitored with a second year of data on habitat characteristics and pika presence/absence within 74 plots on Niwot Ridge and at lower elevations in the Green Lakes Valley and Brainard Lake Recreation Area. With this second year of surveys, we completed the first full cycle in the three-panel study design (Fig. 2), re-visiting 24 plots in the annual panel and conducting the first survey of 24 plots in the odd-year panel. In each odd-year plot, a sensor programmed to record sub-surface temperatures over the next 2 years was positioned under the surface of the talus during the plot survey. Sensors positioned in even-year plots during 2016 are still recording data, and annual plots will receive sensors next year.

Our next steps are to model pika occupancy in 2016 and 2017 as a function of several habitat characteristics, including mean snow water equivalent (SWE). We plan to also measure stress hormone concentrations in pika fecal pellets collected as part of the pika monitoring protocol, to help characterize the range of suitability of currently occupied habitats. Over the next two years, stress hormone patterns and occupancy will be compared between datasets collected at NWT and Rocky Mountain National Park, to help generalize and provide context for an assessment of predicted pika decline in the National Park.

Although we had proposed to continue our initial efforts at monitoring marmots, we decided to discontinue these efforts due to the low numbers and high turnover of individuals on the ridge over the previous 4 years. In addition, our colleague that led the marmot monitoring efforts (Brett Woods) changed institutions and began an administrative position, so was no longer able to continue his work at NWT.

![Figure 2. Three-panel study design to expand our monitoring of pika populations beyond our core area on the West Knoll of Niwot Ridge.](image-url)
Subalpine forests. During the summer of 2016 we assessed tree status, diameter at breast height, and for dead trees, cause of death in 10 long-term permanent plots. Comparisons of biomass between 1982 and 2016 indicate that biomass is increasing 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. In 2017, we added three new permanent plots close to treeline and the closed canopy transition (Figure 3). We also re-measured seedling plots, which we plan to do on an annual basis, to assess seedling establishment and survival. Analyses by doctoral student Andrus indicate that seeding establishment events were more frequent during periods of high snow (SWE) and in cool and wet summers.

Plant demography. We proposed to start demographic observations for tundra focal plants including Silene acaulis and Bistorta vivipara, and trees Abies lasiocarpa and Picea engelmannii. As we describe in section 3, we are revisiting our focal species and demographic work.

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 of 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 period that has historically been unobserved by us. We are working on methods to also include water chemistry and phytoplankton sampling during the winter months.

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 nitrogen (N) and phosphorus (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. As of Fall 2017 we have completed the processing of all samples and their quality checks/assurance, setting the stage for statistical analyses related to the proposal. These data will 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.

**Soil processes.** In our proposal, we also proposed 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 are conducting a pilot biogeochemical survey of 74 plots within the saddle catchment, allowing co-located comparisons with many abiotic, plant, and hydrologic characteristics (we describe these measures more in section 4, below)(Hermes, PhD thesis). Our hope is to identify a suite of measurements that are repeatable and indicative of interannual process-level changes.

**1B. Modeling limitation of plant growth.** We originally described a new model (Niwot Biogeochemistry Model, NBM) 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 filled 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.** We have moved quickly to assess the role of plant traits in overall plant responses to environmental change in a new series of modeling exercises. In a new modeling project completed for a Masters thesis and currently in final revision prior to submission as a manuscript, Katherine Wentz developed and tested a new model for plant photosynthesis on Niwot Ridge. The new modeling approach uses assemblages of traits representing acquisitive and conservative species on Niwot Ridge. These two groupings generally represent the wet meadow and dry meadow plant communities respectively. The model is based on classic approaches to photosynthesis-stomatal conductance modeling and expands on these techniques to incorporate a number of new features. The model produced realistic estimates of photosynthesis, nitrogen-use efficiency, water-use efficiency and other gas-exchange processes in the alpine tundra but generated surprising results that will guide future work on Niwot Ridge.

Photosynthetic rates are influenced by a number of factors including leaf N, leaf shape, and plant height. The modeling in this study reinforced the importance of nitrogen in alpine plant growth rates but also suggested that both acquisitive and conservative plant species are fundamentally
similar in the way that they use nitrogen for C assimilation. Where these communities differ is in the rate of nitrogen supply to plants highlighting the central role of soil processes and plant/soil interactions in nutrient supply. More surprisingly, the trait-based modeling identified leaf temperature as a critical factor in C assimilation and 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, the primarily mid-season growth limitation in the dry meadow areas appears to be temperature rather than water.

The modeling study has also allowed us to explore the implications of a longer and hotter summer (the extended summer scenario in the proposal) through the lens of plant traits and physiological constraints. These results shown in Table 1 below, show that on balance, a longer growing season would lead to higher C assimilation, but if that growing season is combined with warmer mid-summer temperatures, then the net result on growth will be negligible. In effect, the extended summer scenario would lead to lower overall rates of growth but a longer overall period of growth. These results raise interesting questions about how such a response would influence plant dynamics, nutrient cycling, and long-term plant composition.

Table 1. Change in cumulative C assimilation as a result of three different extended summer scenarios. *Extended summer scenario refers to a combination of a longer growing season and hotter temperatures (Wentz et al., in preparation).*

<table>
<thead>
<tr>
<th>Entire Growing Season</th>
<th>Extended Summer Scenario</th>
<th>Longer Growing Season Scenario</th>
<th>Hotter Temperatures Scenario</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conservative Species</td>
<td>Dry Meadow</td>
<td>+0%</td>
<td>+17%</td>
</tr>
<tr>
<td>Δ Assimilation</td>
<td>Wet Meadow</td>
<td>+0%</td>
<td>+9%</td>
</tr>
<tr>
<td>Acquisitive Species</td>
<td>Dry Meadow</td>
<td>+8%</td>
<td>+12%</td>
</tr>
<tr>
<td>Δ Assimilation</td>
<td>Wet Meadow</td>
<td>+6%</td>
<td>+7%</td>
</tr>
</tbody>
</table>

In 2017, we measured plant height, specific leaf area, leaf size, chlorophyll content, and leaf dry matter content on 1101 individual plants from 52 species. 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. To date all leaf samples have been processed for morphological traits and are being prepared to be analyzed for leaf chemical composition (nitrogen, carbon, δ13C, δ15N). This sampling has increased the species coverage of the trait database for Niwot ridge which now includes 2580 individual plants measured. Our aim will be to use this information to build additional realism into our modeling efforts.
Our next step will be to test our model predictions of limitations with empirical work. Some evidence indicates, for instance, that there is stronger moisture limitation than our modelling work would suggest. For instance, Winkler et al (2016) found that positive productivity responses to warming at the community level occur only when warming is combined with supplemental watering; otherwise warming decreased productivity (Fig. 4). Watering also increased community productivity in the absence of warming. Interestingly, Winkler et al (2016) found that forbs drove the contingent community response to warming, while cushions drove the generally positive response to watering and graminoids muted the community response.

**1D. New experiments: manipulation of extended summer conditions in terrestrial and aquatic systems.**

**Terrestrial Manipulation of Growing Season Length.** We originally proposed to conduct early snowmelt manipulations in a spatially distributed design within subalpine forest, open canopy treeline, dry meadow tundra, moist meadow tundra, snowbed tundra, and unvegetated talus sites. Within each habitat type, our plan was to establish 6 replicate blocks (for a total of 36 blocks), and in each block establish an early snowmelt treatment in 3x3m plots. Based on pilot experiments, advice from our external advisory committee, and discussion among our project team, we decided that fewer but larger treatment plots would better encompass the scale of critical hydrological processes.

This summer, we identified five sites: 2 northeast facing, 2 south/southeast facing, and a site at a diffuse treeline location with more woody species present (Figure 5a). 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 by at least one of these larger treatment plots, and our intention is to establish subplots within these manipulations to monitor habitat-specific responses.

Our modified plan is to conduct our snowmelt manipulations in very large treatment plots and paired controls approximately 40m long x 12m wide, aligned along the topographic runoff flow lines and starting at the top of the hillslope crest with little water flow from adjacent uphill areas (Fig. 5b). These plots are established, general vegetation types have been mapped, and tall corner markers have been set to allow identification at peak snowpack.

We still intend to follow our original plan of using a thin layer (~400 g/m²) of inert black vitreous sand (Mission Laboratories, Los Angeles, CA, composed primarily of silicon dioxide, iron oxide, and calcium oxide) over the snow at peak snowpack (first application would be May 2018). We completed pilot studies in 2015 and 2016 that indicated the black sand application extended growing season by 7-10 days (9-13% increase) with no effects on soil temperature. The pilot studies in 2016 demonstrated that we can conduct this manipulation at a larger scale than we originally proposed, with edge effects ~1m. We will also add the sand to control plots after snowmelt to account for any soil albedo or microbial substrate effects.

**Figure 5.** Aerial image of the NWT LTER site, including the tundra lab, indicating the five sites of the early snowmelt experiment (A; top left). The sites encompass different aspects and elevations. Below (B): detailed imagery for each site, showing the paired rectangular plots that run along the major flowpaths. Each of the red rectangles indicates a plot 40m long and 10m wide. At peak snowpack (typically mid-May), we plan to spread a thin layer of black sand to one of each of the pairs. In pilot experiments, we have found this treatment to speed snowmelt by 1-2 weeks, but not affect melt physics or microbial/nutrient dynamics. We plan to initiate these manipulations May 2018 and continue for 5-6 years.
We anticipate that application of black sand to each of these large treatment plots will take 2 people days per plot, or a total of 10 people days in May 2018. We tentatively are planning to recruit people to help in application in conjunction with our annual snow survey. Next summer we will need to purchase and install Campbell loggers to record soil temperature and soil moisture as well as light availability and snowfree date; we have not yet arrived at a consensus protocol about how many and where these sensors should be placed, although we would like them to be comparable to the saddle catchment network. Physical barriers at the top of each plot to reduce overland flow will also need to be established summer 2018.

One critical need for next summer will be to finalize a plot for ecological response measurements related to this experiment. We also have yet to decide where subplots should be established to monitor ecological response measures. We will need salary support to make these measurements next year, following our LTER protocols in our observational long-term plots. One tentative calculation is that these measures might involve 60 1m² subplots (6 subplots at each of 10 plots); if we followed LTER plant composition and ANPP measurement protocols, it might require 20 people days to make these measures at peak season next year. These measurements would be appropriate for the vegetation staff or an interested graduate student as a summer GRA. We also intend to tag woody tree individuals in each site to monitor tree mortality and colonization, and develop a scheme for monitoring soil biogeochemistry processes.

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) within 12 limnocorals deployed in GL4 and 12 in GL1. Solar-powered pumps would be used to alter flushing rate, thereby mimicking a heavy snow year with substantial snowmelt, while concentrated lake water from nearby GL1 – which has higher DOM concentrations – was going to be used to enhance DOM within half of the limnocorals in GL4. 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 and 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).

As of summer 2017, two significant developments have occurred causing us to rethink the design of this manipulation. First, given that the Green Lakes contain the water supply for Boulder County, we have encountered administrative resistance to performing within-lake manipulations at this scale and magnitude (i.e., 12 large limnocorals per lakes and likely over more than one year with pilot studies, etc.). This is in addition to the logistical challenges associated with transporting supplies and large volumes of concentrated DOM water to GL4, which is remotely position within the talus-slope landscape. Second, results of a recent mesocosm study performed at the Mountain Research Station suggest that smaller-scale manipulations may offer a useful intermediate stage in our experiments. Specifically, mesocosms (378 L) seeded with water, sediment, and zooplankton from GL4 and studied over 8 weeks maintained a similar...
composition of flora and fauna, as determined by direct zooplankton counts and the use of FlowCam on phytoplankton samples. These findings suggest that mesocosms – which can be deployed across an elevation gradient outside of watershed property – may provide a tractable next step to test our hypotheses (and one that will parallel our terrestrial manipulations more directly).

Pending the outcome of ongoing discussions with our external advisory committee and other disciplinary experts, our modified plan is to use experimental mesocosms distributed across an elevational gradient to evaluate the effects of changes in growing season length and terrestrial DOM inputs. Across each of three locations distributed from the subalpine forest to the unvegetated talus slopes, we will establish 1000-L mesocosms in late summer. We will allow mesocosms to fill naturally with water from precipitation, after which we will use standard methods to seed tanks with sediment, phytoplankton, and zooplankton collected from a homogenized mixture of material from lakes Albion, GL1 and GL4. Drain holes will be drilled 6 cm from the surface of each tank to allow natural flushing. In early May while ice-cover is still intact, we will spread a thin layer of black sand over half of the mesocosms at each elevation to increase albedo and accelerate ice-off. We will also add a thin layer to our control mesocosms after melt concludes to account for any albedo effects. These manipulations will be replicated eight times per treatment (early ice-off and control) at three elevations for a total of 48 mesocosms. Thermistors will record both surface and bottom temperature and light in each mesocosm, providing a more finely resolved record of ice-thaw patterns. 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. Tests of this hypothesis included analysis of long-
term observations and adding biotic manipulations to both the terrestrial and aquatic experiment described above (in section 1D).

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, allowing 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, and 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 will establish subplots in the larger treatment (black sand) and control plots where we will establish biotic manipulations of snowpack. We are currently piloting structures developed at the Jornada LTER (which they call connectivity modifiers or con-mods) for this purpose (Fig. 6). If they do influence snow distribution and create small-scale heterogeneity as we intend, we plan to establish several “con-mod” structures within subplots in the experimental black sand manipulations. The location and size of these subplots will be determined spring 2018, with the installation of the con-mods prior to snowfall 2018.

We hypothesize that adding these structures will increase small-scale heterogeneity in snow pack and snowmelt timing. We expect that this increased heterogeneity will increase diversity as well as create microrefugia in the early snowmelt treatments, allowing species that would otherwise decline to persist.

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

Figure 6. Pilot “con-mod” structures to simulate the biotic influence of plants on snow distribution and environmental heterogeneity.
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 variations in 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.

3. COMPENSATORY DYNAMICS. Can opposing responses to climate variation – among populations, among species, and across geographic locations – lead to increased stability at higher levels of organization and at larger spatial scales? In this third section, we are interested in how processes integrate across populations, communities, and other ecosystem components. We expect that a positive response in one component of an ecosystem may often be accompanied by a negative response in another; these opposing responses can dampen aggregate responsiveness and lead to stability. For these efforts, we proposed a largely data analysis effort aimed at investigating these dynamics. Unfortunately, one of our investigators and co-lead for this question (Doak) has transitioned off the project. Due to the loss of his expertise, we have decided to drop the demographic measures and assessment of demographic compensation from our research plan.

In 2017, we initiated work on a new line of population level investigation that focuses on adaptation and hybridization of one widespread genus at Niwot, *Potentilla*. We have identified 12 species of Potentilla along the elevation gradient at Niwot, and are currently conducting molecular analyses to confirm identification of species and possible hybrids. Dr. Nancy Emery is leading this work. We feel that this may be an excellent study system to investigate plasticity and local adaptation at the population level, and to tie to analogous measures of species turnover at the community level. A goal for year 2 of LTER VII will be to revision this section of our proposal.
in light of this new direction. This re-visioning will be one focus of our annual external advisory meeting next summer.

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. Spatial variation in climate exposure and sensitivity – our focus on the first three hypotheses – could cause different parts of a catchment to respond differently depending on position, which then may affect quantity and quality of water leaving a catchment. However, 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 spatially-explicit measurements, modeling and the implementation of 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 are establishing 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 (Fig. 7a). Each sensor node captures air temperature and relative humidity (CS 215), snowdepth (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, 15 of 16 sensor network nodes are recording data with reliable remote accessibility. Roughly half of the snow depth sensors have failed after the first winter and are scheduled to be replaced by early winter 2018.
Time-lapse cameras were installed at each sensor node in spring 2017 to track snow and plant seasonality in the sensor network. The cameras are low-cost Cuddeback 1224 trail cameras in modified Pelican cases to protect them from the harsh alpine environment. The cameras recorded images every 30 minutes during daylight hours from June through November 2017. The camera’s frame of view included at least one 1 m² plot co-located with a soil moisture sensor. The plots were assessed for plant species abundance using point-intercept above-ground surveys and dry weight plant biomass harvests. Key phenological dates will be extracted from greenness curves of each plot over the course of the growing season, which are actively being analyzed using the phenopix package in R. Future analysis will evaluate the spatial and temporal heterogeneity of plant community greenness across the sensor network using data from the phenocams and the other sensors in the array. The cameras will continue to be used in 2018 and beyond.

We are also following soil inorganic nitrogen (N) pool and net N mineralization and nitrification rates on this. We have established 26 sampling locations, including 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 seasonal 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. We also have quantified soil texture, total organic matter, saturated and unsaturated hydrologic conductivity, and soil water retention curves and hydrologic properties to aid in parameterizing the hydrologic model (described below).

**Deployment of lake sensor array:** As an important next step in our study of alpine lake ecology, next summer we will deploy a sensor network across a depth transect in GL4 (from a subsurface...
The sensor array will collect depth-specific data on temperature, dissolved oxygen, chlorophyll-\(a\), and photosynthetically active radiation (PAR) at regular time intervals (Fig. 8). This project has already been approved by the Boulder County Watershed, which controls access to Green Lakes Valley. Sensors will be deployed in July 2018 during the ice-free period and, after a period of validation and trouble-shooting, retained in the lake through the winter months. 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 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, and hope to deploy similar sensor arrays in our other focal lakes in the following years.

**Figure 8.** Schematic of the mooring design with reference bathymetric map and marked deployment location. Symbols represent depths where sensors will be tethered to ½ inch polyester rope; (+) temperature, (O) dissolved oxygen, (a) Chlorophyll \(a\), and (Δ) PAR.

**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 of approximately 60ha of the saddle catchment through the snow melt season (June-August). 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.

We have recently completed processing of the large imagery datasets totalling around 1.5TB of imagery and over 35,000 individual frames using a Structure from Motion workflow (Fig. 9). Primary datasets include RGB orthomosaics at 5cm resolution, NIR/Red defined wavelength orthomosaics at 5cm, land surface temperature at 30cm resolution. We are currently processing secondary datasets which include NIR/Red calibrated surface reflectance, NDVI, surface soil moisture (from surface temperature/vegetation index (Ts/VI) approach), and snow depth (from DEM differencing). This will be completed by mid/end of December. We also produce derived datasets which will include object oriented classification of land cover and vegetation classes – ideally at the community level - including identification of key ecosystems e.g. dry meadow, wet meadow, krummholz, etc.; mapping of surface/subsurface hydrologic pathways, e.g. melt channels, springs and streams; and, DEM derived products, e.g. slope, shading, drainage networks etc.

Once all data processing is complete we will have compiled an unprecedented UAS dataset, which exploits both the high spatial (centimetre) and high temporal (weekly) benefits of UAS, and does so over a relatively large (~60ha) highly heterogeneous and extremely challenging environment.

To place the empirical measures in a broader watershed context, we plan to use NDVI derived from the Landsat satellite time series (e.g. Landsat 5 – 8) to identify water versus...
energy limitation based on correlations between NDVI and snowmelt versus correlations between NDVI and PET. We plan to start this work in year 2 of LTER VII.

**4B. Spatially-explicit modeling at the catchment scale.** We have configured the DHSVM (Distributed Hydrology Soil Vegetation Model) for the Saddle catchment, at 2m horizontal resolution. This involved collating and resampling landscape data (soil, vegetation, and topography) together with observational time series of meteorological input data for the Saddle domain. Where possible, locally observed data were used. For example, a digital elevation model (DEM) from a local LiDar scan (1m resolution) was used to define the watershed boundary, a series of solar shading maps, and a stream network. Continuously collected meteorological data, from five different stations located at and around the basin, are used for atmospheric forcing (see Fig. 7b). An initial simulation of hourly hydrology 2011-2014 is underway. The goals of the initial simulations are to validate the model setup and parameters, and to identify important factors influencing the Saddle’s hydrology. This includes exploring different approaches for spatially interpolating precipitation, including using the Jepsen-reconstructed SWE data (Jepsen et al 2011). Interim goals will be to estimate hydrologic connectivity based on temporal correlations between spatially distributed observed meteorology, simulated soil moisture and evapotranspiration (ET) with streamflow. Longer-term goals will involve tracking moisture transport between model grids to quantify connectivity.

**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 have decided 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). Thus, we have prioritized recruiting a postdoc to investigate these connections in our long-term records. Our hope is that a comprehensive analysis of long-term observations will highlight associations between terrestrial, stream, and lake systems, which we can then prioritize in coupled modeling efforts in 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. EDUCATION AND OUTREACH.** 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. The anticipated participation was 4-6 students, but we have 12 students participating currently. The purpose of the class is to provide professional development
for our students in science communication and engaged scholarship. In response to feedback from reviewers on the broader impacts section of the proposal, the capstone project for the course is a digital storytelling assignment. Students in small groups are developing four digital media presentations (e.g. videos, slide streams, narrated cartoons) 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 will 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. Graduate students in this class will also be required to spend 10 hours after the course is over doing some kind of outreach activity with public audiences.

**K-12 Outreach and Education.** Besides developing the graduate course, our other major outreach goal was to re-think how our Schoolyard Books (My Water Comes from the Rocky/San Juan Mountains) are being used in schools. With colleagues from the CU Museum of Natural History, we received a CU Boulder Outreach Awards that has allowed us to design an entirely new curriculum kit for 4th grade classrooms called Adaptation and Variation in Colorado Mammals (Fig. 10). The kits use the My Water books in the context of teaching early evolution literacy concepts. The kit contains skulls, furs, tracks, and scat replicates of animals featured in the drawings of the My Water books and it emphasizes how organisms are adapted to survive, grow and reproduce in their environments and how environments change over space and time.

The curriculum was developed as part of a Master’s thesis by a Museum and Field Studies student, and it features a Phenomenon-Based teaching approach that uses Next Generation Science Standards guidelines. We were invited to participate in a 16-hour professional development opportunity for 17 4th grade teachers in the Boulder Valley School District this Fall.

* Figure 10. Teachers from Boulder Valley School District at a professional development workshop about Adaptation and Variation in Colorado Mammals featuring tracks, skulls, and scat from mammals featured in the My Water Comes from the Rocky Mountains schoolyard book.*
The Master’s student who developed the curriculum and NWT Ed-Out representative, Alex Rose presented the kits, books, and the curriculum to the teachers from 12 different elementary schools in BVSD. Teachers who participated in the professional development course will instruct other 4th grade teachers at their schools how to use the kits and over the course of this school year the kits will be evaluated based on feedback from these teachers. Using their feedback, we will revise the curriculum and kit contents, and give final versions of the kits back to BVSD for permanent use. Additionally, we will be producing an additional 17 kits that will be distributed for free to rural school districts across the state. We are working with two teachers, Marty Downs at the LTER NCO, and Amy Rinehart, the book series publisher, to translate the My Water books in a digital format into a Spanish language version for use in bi-lingual 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 (Fig. 11). Notably, we have initiated a partnership with the Winter Wildlands Alliance and their Snow School program (https://winterwildlands.org/snowschool/) through which LTER scientists and, in the coming year, CU undergraduates, are helping lead snowshoe based field trips for 6th graders on the topics of climate change and snow science.

Public Audiences.
NWT Pika biologist Dr. Chris Ray has helped provide scientific content for several educational video and documentary projects for adult audiences around pikas and their response to climate change. These projects have been collaborations with the Colorado Fourteener Initiative (http://www.14ers.org/) and documentarians Jere Folgert and Mimi Matsuda. Their film "The Adventures of the American Pika", won the Best North American film at the Wildlife Conservation Film Festival in 2017. Dr. Ray and her lab group are frequent bloggers and social media posters and they help run a successful citizen science project.

Figure 11. High school students learn about isotope ecology on Niwot Ridge as part of the Mountain Research Experience 2017.
(http://www.pikapartners.org), and teach a field courses on Pika ecology and population monitoring techniques for National Park volunteers and the general public.

6. INFORMATION MANAGEMENT. Hope Humphries, NWT’s Information Manager, attended the annual meeting of LTER Information Managers in Bloomington, IN, held July 24th, in conjunction with the annual Earth Science Information Partners meeting. New long-term data sets posted to the NWT website include zooplankton community composition; snow lysimeter data for the Soddie site; infilled hourly climate data for C1, Saddle, and D1; stream discharge for the Saddle stream; and Community Land Model (v4.5) simulations of water, energy, and fluxes for the Saddle. We have implemented more comprehensive systems for tracking data sets, including an agreed-upon schedule for core data set delivery and posting.

Progress toward milestones. (1) Integrated system that is synchronized across platforms: Work was conducted to develop R scripts to produce EML (ecological metadata language) from existing ASCII metadata files. The new scripts are modifications of scripts developed by the Environmental Data Initiative. Training by Colin Smith (EDI) in the use of these scripts was acquired during the EDI “Dataset design for community survey data” workshop attended by Humphries in Albuquerque, June 6-8th. Humphries also attended a session at the ESIP meeting in July that addressed the use of R in creating EML. (2) Acquire/develop methods to combine variables across data sets: A consistent set of variable names has been developed for use in all NWT climate data sets. Existing data set variable names have been edited for cross-data set agreement. (3) Require involvement of IM with projects at inception and as they continue: The proposal process has provided information to the data manager about new data sets being produced, in addition to information available through annual Mountain Research Station (MRS) Research Applications.

We are continuing to work on implementing the GCE Data Toolbox as our primary tool to handle raw NWT sensor data, including automated harvesting of logger data, application of quality assurance/quality control (QAQC) criteria, and production of data sets at different time intervals. For the new wireless sensor array, we are developing Toolbox capability to harvest and archive data, as well as display data in near-real time on our website. The ability to download logger data to our server using Campbell software has made integration with the Toolbox more seamless.