

## NWT LTER VII: Long-term research on the dynamics of high-elevation ecosystems – a framework for understanding ecological responsiveness to climate change

**1. INTRODUCTION.** The Niwot Ridge/Green Lakes Valley (NWT) LTER program is an interdisciplinary research program with the long-term goals of building a predictive understanding of ecological processes in high-elevation mountain ecosystems and contributing to broad conceptual advances in ecology. NWT also provides education, outreach, and knowledge to inform alpine resource management and conservation. Our proposal builds on a foundation of more than 35 years of research that includes decades-long experiments and monitoring designed to understand ecological dynamics and trajectories of change (Fig. 1).

Mountain ecosystems have been identified as among the most vulnerable to climate change (Jones et al. 2012, Field et al. 2014). Small changes in temperature can turn ice and snow to water, and sharp physical gradients can lead to rapid shifts in habitat zones over small distances (Suding et al. 2015, Williams et al. 2015b). Atmospheric deposition of base cations and nitrogen contribute to these changes, affecting nutrient limitation in this resource-poor environment (Bowman et al. 2014). The predicted vulnerability, however, is difficult to evaluate in a system characterized by spatial complexity and temporal variability. High topographic relief and variation in substrate age and depth associated with glacial and periglacial activity form the template for climate-related changes (Litaor et al. 2008, Leopold et al. 2015). Terrain and biota modulate climate effects spatially by dictating where the fierce alpine winds redistribute snow and temporally by influencing the onset and speed of snowmelt (Seastedt and Adams 2001, Scherrer and Körner 2011, Jepsen et al. 2012). The water from melting snow flows downhill, linking terrestrial habitats and connecting them with alpine lakes and streams (Miller and McKnight 2012, Knowles et al. 2015b). Long-term observations at NWT suggest that this complexity can lead to both rapid change and stability (Hu et al. 2010, Doak and Morris 2010, Spasojevic et al. 2013, Smith et al. 2015, Wilkening et al. 2015).

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 responsiveness or stability in ecological systems. Our objectives are to (a) continue to characterize how high-mountain environments are responding to climate, (b) test hypotheses about the underlying drivers and integration among these responses, and (c) forecast responses to future change. We take a conceptually integrative and empirically holistic approach, identifying underlying principles *across levels of ecological organization* (e.g., population, community, ecosystem, catchment), *across taxonomic groups* (e.g., trees, plankton, small mammals), and *across habitat types* (e.g., talus, tundra, lake, subalpine forest). We also explicitly incorporate spatial scale, focusing on *fine-scale* processes where local interactions predominate (up to a few meters on land or at a certain lake zone by depth), *microhabitat* variation that incorporates fine-scale heterogeneity (e.g., across tundra areas with and without shrubs, different zones within a lake), and integration at the *landscape* and *catchment scale* (from tens of hectares to many km<sup>2</sup>). We use modeling iteratively with observation and experimentation to generate testable hypotheses, refine and expand our models, and identify new observations and mechanisms to increase our predictive ability.

**1.1 CONCEPTUAL FRAMEWORK.** While variability in ecological responsiveness to climate characterizes complex landscapes worldwide, the mechanisms that cause these differences are poorly understood (Williams et al. 2008, Ackerly et al. 2015). **How do we explain such variability to better understand where and when changes in climate drivers result in ecosystem change? Why are some systems apparently insensitive to seemingly large shifts in climate?** Despite theory linking ecological stability



**Figure 1.** For more than 35 years, NWT long-term research has focused on ecological responses to climate in complex terrain.

with temporal variability and its relevance to climate change, we remain largely unable to predict dynamics in space: for instance, we are not able to predict where ecological processes will be relatively stable despite large shifts in climate or where large responses will occur.

Vulnerability theory considers response as a function of the magnitude of climate change experienced (exposure), the intrinsic ability to tolerate a given amount of change (sensitivity), and the capacity of the population or species to adapt or migrate (Dawson et al. 2011, Dickinson et al. 2014; Box 1). However, empirical tests of this framework are rare, as most research using the framework addresses modeling at the scale of species ranges. In LTER VII, we apply these ideas to spatial variation at the landscape scale, where complex terrain and biophysical effects of biota modulate climate, creating a heterogeneous template of climate exposure (Ashcroft et al. 2009, Maclean et al. 2015; x-axis in Fig. 2). At this scale, measurements of exposure and sensitivity are tractable within the context of long-term observation and experimentation.

To inform our expectations about how exposure and sensitivity integrate across levels of ecological organization and space, we evoke a second body of theory. Biodiversity theory predicts that diversity at one level should aggregate to stabilize properties or function at another (Tilman et al. 1998, Vasseur and Gaedke 2007, Gonzalez and Loreau 2009; y-axis in Fig. 2), as exemplified in the portfolio effect (Doak et al. 1998) and insurance hypothesis (Yachi and Loreau 1999). At the heart of this theory is the expectation of asynchronous dynamics – across vital rates within a population (Doak and Morris 2010, Villegas et al. 2015) and across species within a community (Ives et al. 1999, Loreau and de Mazancourt 2008; Box 1). In the same manner, spatial asynchrony across populations and communities should influence landscape and catchment stability (Thibaut and Connolly 2013, Wang and Loreau 2014). Despite the importance of this theory, rarely are responses integrated across populations, communities, and other ecosystem components. Empirical tests are quite challenging because they require measurements over decadal time scales and a range of expertise. Continued long-term observations and the interdisciplinary expertise at NWT will allow us to make a comprehensive test of this theory.

**1.2 RESEARCH QUESTIONS AND HYPOTHESES.** While it is well accepted that ecosystems respond to a changing climate in many ways, a major challenge is to predict where, when and with what magnitude responses are likely to occur. Our conceptual framework (Fig. 2) is built around four questions:

**Q1) SHIFTING LIMITATIONS: How do terrain-related differences in climate exposure affect ecological response?** Spatial and temporal variability characterizes virtually all ecosystems, with climate affecting resource availability and abiotic stress over the course of growing season and across years. Yet, heterogeneity in climate effects at the landscape scale has only recently begun to be considered and linkages to physiological limitations remain largely unexplored (Ashcroft et al. 2009, Ford et al. 2013, Ackerly et al. 2015). Varied climate exposure in complex terrain should influence the relative availability of different resources (Jepsen et al. 2012) and the occurrence or frequency of abiotic stress (Choler 2015). 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 hypothesize (**H1): Ecological**

#### Box 1: Ecological Responsiveness<sup>1</sup>

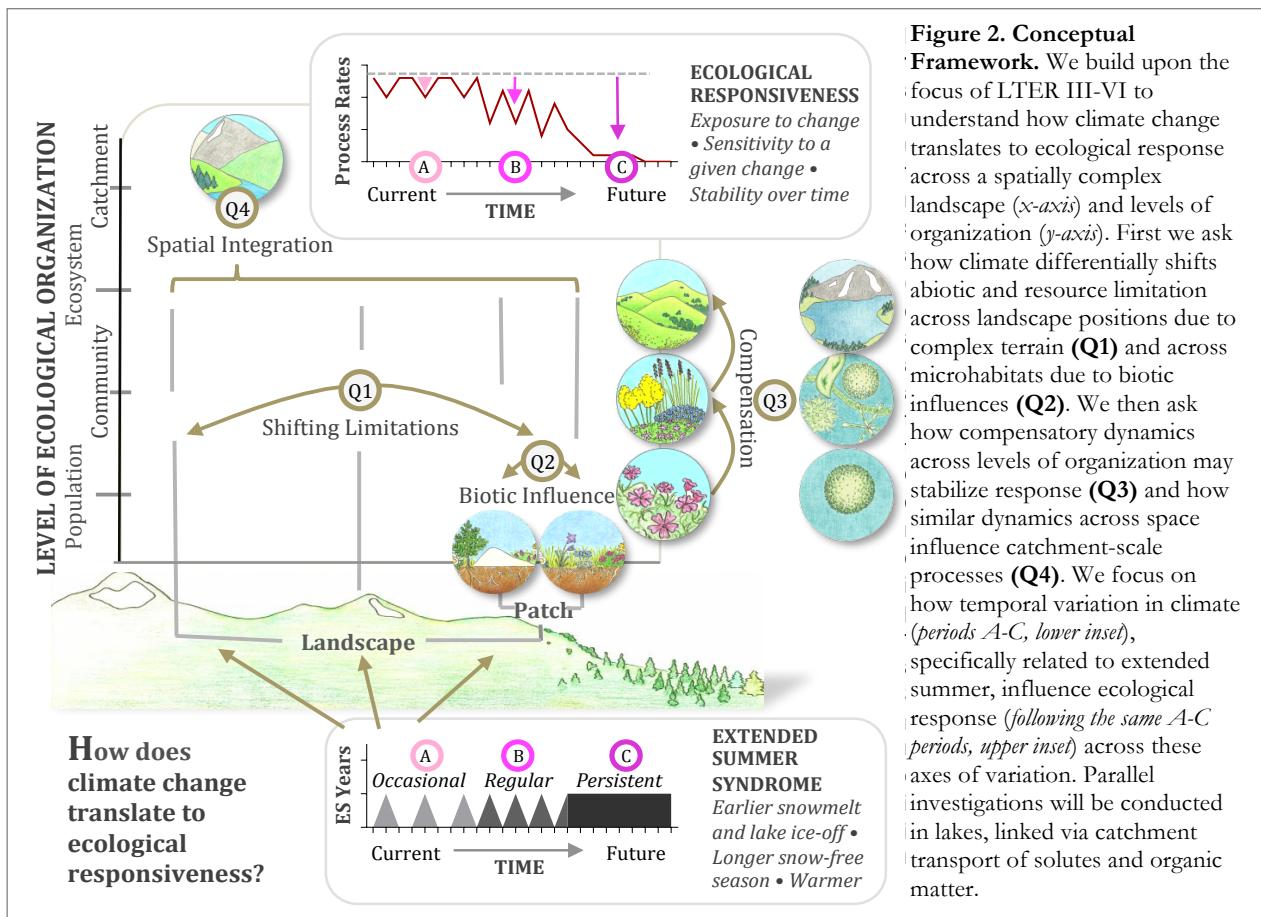
**Responsiveness** is the extent to which an ecological process changes owing to climate variation or change. We consider responsiveness to have three components:

- **Exposure** describes the magnitude of climate alteration experienced at a location, as modulated by terrain or structural effects of biota (e.g., a tree island).
- **Sensitivity** is the capacity to tolerate a given amount of change, determined by intrinsic aspects of species biology such as ecophysiology or life history. The inverse of sensitivity is resistance.
- In the longer-term, **adaptive capacity** involves genetic adaptation or migration.

**Responses** can be described relative to inter-annual climate variation or to more persistent directional change (**climate change**). We focus on three measures:

- **Relative change**, positively or negative, from average or baseline in a time series.
- **Stability** is variance over time in an ecological process rate (for a population, community, landscape).
- **Synchrony** describes the degree to which responses covary: for instance, among species within a community (all species do well in one year, poorly in another).  
**Asynchrony** describes negative covariance or opposing responses.

<sup>1</sup> After Dawson et al. 2011, Gonzalez and Loreau (2009).



**Figure 2. Conceptual Framework.** We build upon the focus of LTER III-VI to understand how climate change translates to ecological response across a spatially complex landscape (*x-axis*) and levels of organization (*y-axis*). First we ask how climate differentially shifts abiotic and resource limitation across landscape positions due to complex terrain (**Q1**) and across microhabitats due to biotic influences (**Q2**). We then ask how compensatory dynamics across levels of organization may stabilize response (**Q3**) and how similar dynamics across space influence catchment-scale processes (**Q4**). We focus on how temporal variation in climate (*periods A-C, lower inset*), specifically related to extended summer, influence ecological response (*following the same A-C periods, upper inset*) across these axes of variation. Parallel investigations will be conducted in lakes, linked via catchment transport of solutes and organic matter.

**responsiveness to climate will be strongest in locations where climate exposure results in a shift in limiting factors.** We expect these shifts to result in both positive and negative responses, and to influence process rates across levels of organization, including at the ecosystem (productivity), community (species turnover), and population (population growth rate) levels.

**Q2) 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 (Bowman 2000, Seastedt and Adams 2001, Suding et al. 2008, Cavieres et al. 2014). 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 (Williamson et al. 2010, Kissman et al. 2013). Biotic effects are also thought to create microrefugia in the face of a changing climate (Randin et al. 2009, Scherrer and Körner 2011). While the emphasis on these biotic effects has largely revolved around mitigating adverse or stressful conditions, we know much less about how these effects modify heterogeneity (Callaway 2007, Schob et al. 2012, Bulleri et al. 2016) to influence coexistence dynamics on larger scales (e.g. across microhabitats, patches, or zones; Chesson 2000). Thus, we hypothesize (**H2**): **Biophysical effects of biota will modify exposure to climate change, and heterogeneity in these effects will influence population persistence and coexistence dynamics.**

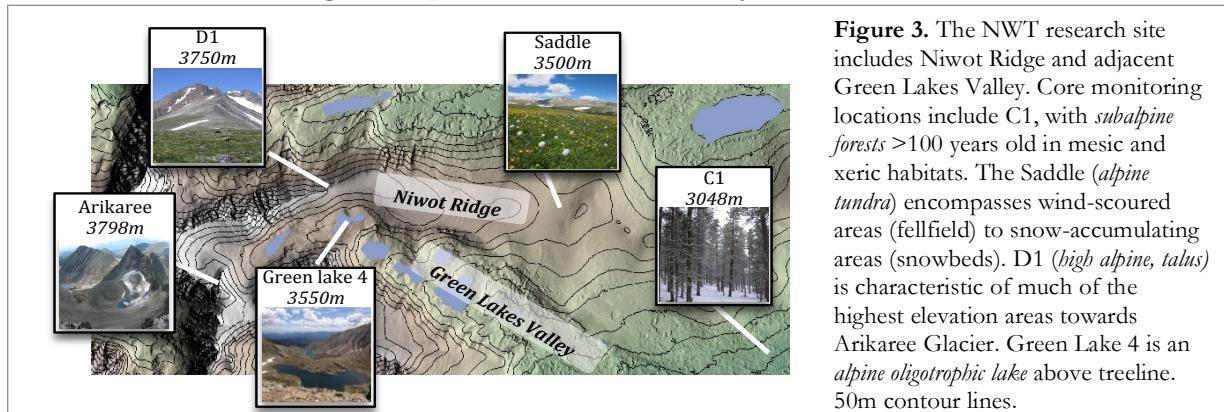
**Q3) COMPENSATORY DYNAMICS: Can opposing responses to climate variation – among populations, among species, and across geographic locations – lead to increased stability at higher levels of organization and at larger spatial scales?** While ideas of exposure and sensitivity have

been developed with the focus on species ranges, these processes should integrate across populations, communities, and other ecosystem components. Compensation describes a process where the decline of some species is offset by the increase of others. This can lead to a reduction in community-level variability relative to the alternative case, when populations fluctuate in synchrony (Gonzalez and Loreau 2009, Hallett et al. 2014). Similar dynamics, termed demographic compensation, occur when the decline of some vital rates in a population is offset by an increase of others, leading to a reduction in population-level variability (Villellas et al. 2015). Populations (or vital rates) should respond with greater synchronicity as climate conditions grow more extreme (Doak and Morris 2010). Thus, we hypothesize (**H3**):

**Asynchronous responses to climate within one level of organization will combine to reduce variability at a higher, aggregated, level. Climate change will increase synchronicity through shared tolerance and growth constraints.**

**Q4) 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 to streams and lakes (Lohse et al. 2009). Spatial variation in climate exposure and sensitivity may lead to compensation across landscape positions (Ford et al. 2013, Roth et al. 2014), where the decline in production or another ecosystem processes in one area is offset by the increase in other areas (Wang and Loreau 2014). This could lead to a reduction in catchment-level variability relative to the case where all areas of the landscape respond synchronously. However, climate also influences hydrologic connectivity across the landscape: some areas of the catchment may be connected via flow paths in some years but not in others (Williams et al. 2009, Darrouzet-Nardi and Bowman 2011). Because variation in ecological responsiveness has rarely been considered at the catchment scale (Currie 2011, Emanuel et al. 2011, Nippgen et al. 2015), we know little about how it interacts with connectivity to affect water quality and quantity leaving a catchment. We hypothesize (**H4**): **Climate-related changes in hydrological connectivity, by altering areas of the landscape that contribute to water and nutrient flux, will influence the degree to which landscape compensation stabilizes catchment response.**

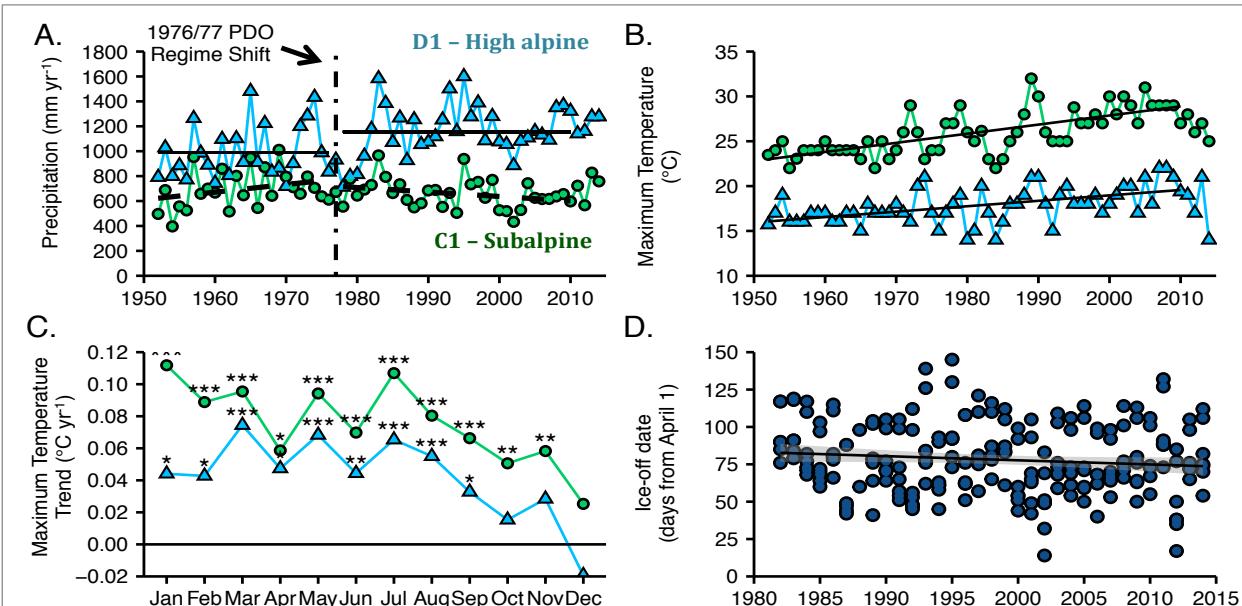
**1.3 LONG-TERM RATIONALE.** NWT is particularly well suited to ask these questions. Long-term monitoring at Niwot Ridge began in the 1950s with the installation of meteorological stations at the C1 subalpine forest site and the D1 alpine site, the longest high-elevation continuous climate record in the US (McGuire et al. 2012; Fig. 3). Research over the last several decades has demonstrated the importance of landscape complexity on processes in high-elevation systems (Williams et al. 2009, Darrouzet-Nardi 2010, Barnes et al. 2014, Schmidt et al. 2014), advances that have been fundamental to our understanding of mountain ecosystems worldwide (Fountain et al. 2012, Jones et al. 2012, Racoviteanu et al. 2013). Long-term experiments and observations confirm the interactive effects of climatic drivers across complex terrain (e.g., changes in snow, temperature and nutrients: Farrer et al. 2014, Farrer et al. 2015, Gasarch and Seastedt 2015b, 2015a). **We are now poised to address how this landscape complexity translates climatic drivers into ecological responsiveness and stability.**



We frame LTER VII in the scenario of ecological responsiveness to one specific aspect of climatic change in these snow-governed ecosystems: **the extension of summer**. In the recent IPCC report, winter snow cover was noted as one of the fastest changing climate features (Vaughan et al. 2013). Consistent with global patterns, spring temperatures are rising, snowmelt is earlier, and summers are warmer and drier at NWT (Kittel et al. 2015). “Dust on snow” events have also increased in frequency over the last decade; these events reduce albedo and further speed melting (Painter et al. 2007, Neff et al. 2008). Across high-elevation systems in Colorado, snowmelt is now three weeks earlier than it was in the 1970s (Clow 2010), similar to regional patterns (Stewart 2009, Pederson et al. 2011). Because climate projections for both moderate and high carbon emission scenarios indicate that these trends will strengthen (Kunkel et al. 2013), we expect to observe increases in frequency and intensity of extended summer conditions over the next six years. A goal of LTER VII is to better understand the ecological consequences of such changes.

**2. RESULTS OF PRIOR SUPPORT.** *Niwot Ridge - Green Lakes Valley (NWT) LTER Program, 2010-2016.* \$5,640,000. During LTER VI, NWT scientists and students authored 211 publications, including 181 refereed papers, 2 books, 8 chapters, and 17 theses/dissertations. NWT publications comprise contributions in a mix of discipline-specific to high-impact journals, and include contributions to special issues in *BioScience* on long-term research and in *Biogeochemistry* on cryosphere research. In 2015, NWT was the focus of the inaugural monograph in long-term alpine research (a special issue in *Plant Ecology and Diversity*), which featured 15 papers about our long-term research (Williams et al. 2015b). Since we launched our new website in early 2015, page views have averaged 780 per week. We have also been successful in utilizing supplemental funds to support the LTER Schoolyard book series, enhance our information management system, provide needed field equipment and, most recently, to establish a sensor network (we describe this last effort in section 3.4). Below, we highlight progress in specific areas, including ten selected publications (**in bold**), that represent the breadth of research during LTER VI and lay the foundation for our next phase of research.

**2.1 CHANGING CLIMATE AT HIGH ELEVATION.** Climate records indicate that NWT is experiencing warmer springs and summers and earlier lake ice-off (Fig.4; **Kittel et al 2015**). Annual precipitation



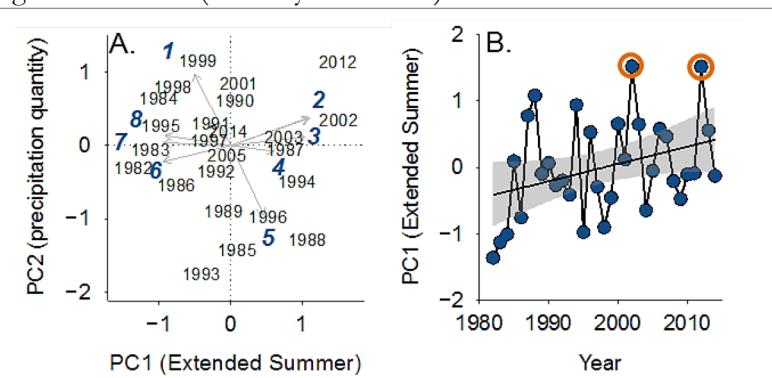
**Figure 4.** Climate trends since 1952 in the high alpine (D1 site, blue triangles) and subalpine (C1 site, green circles; Kittel et al. 2015; McGuire et al. 2012). **A)** Precipitation has been relatively stable, aside from a step increase in precipitation at D1 largely related to a PDO regime shift. **B)** Daily maximum temperatures have increased at both C1 and D1. **C)** The subalpine has warmed faster than the alpine; at both sites, warming has been most substantial in the spring and summer months (asterisks denote significant trends over time; \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ). **D)** Across the six lakes in the Green Lakes Valley, ice has melted an average of 7 days earlier since 1982.

(approx. 75% of which is snow) has increased in the alpine (D1 site) due to the exposure of high elevations to orographically-generated snow related to regime change in the Pacific Decadal Oscillation (PDO) in the late 1970s (Fig. 4A). After the step increase in the 1970s, snowpack has shown no discernable trend (consistent with regional patterns; Clow 2010). Subalpine precipitation patterns are unchanged since the 1950s. Regionally, projected trends in precipitation for both zones are uncertain, but directional changes, if any, are predicted to be small (Hoerling et al. 2013).

While changes in precipitation may reflect decadal-scale variation, there is growing evidence of persistent long-term warming trends at NWT (McGuire et al. 2012, Kittel et al. 2015; Fig 4B), consistent with high-mountain environments globally (Rangwala and Miller 2012, Pepin et al. 2015). A focus of LTER VII is the ecological consequences of such trends. The subalpine forest is experiencing daytime warming in the winter, spring and summer (Fig. 4C), with nighttime cooling in the fall months (not shown). Even in the higher, colder, alpine zone, daytime temperatures are warming in the spring and summer months (Fig. 4C). Along with warming, seasonal snowmelt (Clow 2010, Pederson et al. 2011) and lake ice-off (Fig. 4D; Caine 2010) have shifted earlier.

In addition to shifts in climate, atmospheric deposition of base cations (via dust) and nitrogen (via wet and dry deposition) are impacting NWT. Nitrogen deposition on Niwot Ridge is almost 40 times higher than background levels ( $\sim 8\text{kgN/ha/yr}$ ; Bowman et al. 2014). Dust deposition, which carries calcium and phosphorus, is among the highest in the US (Brahney et al. 2013). Because much of the deposition occurs during the snow-covered season, the redistribution of snow by wind can lead to large differences in nutrient inputs across the landscape (Freppaz et al. 2012).

In LTER VII, we consider this suite of climate-related trends as characteristic of **extended summer** (more precisely, extension and warming of the snow-free period ; Fig. 5A). We find extended summer climate conditions have significantly increased, with substantial interannual variation, since the start of the NWT program (Fig. 5B). Because our research questions in LTER VII relate to responses to these extended summer conditions, we assess patterns in our long-term data in relation to variation along this first PC axis.

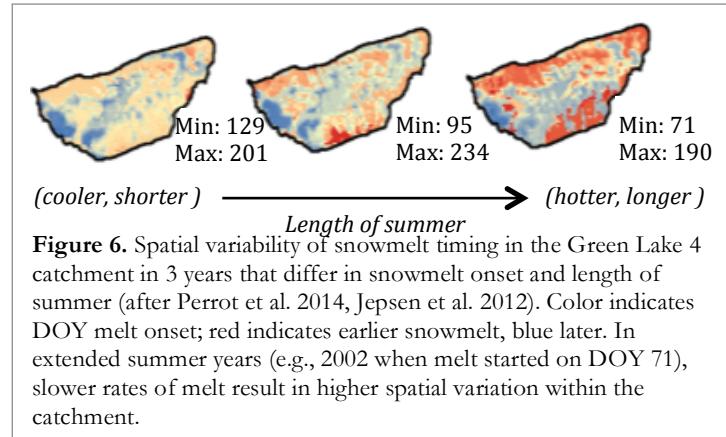


**Figure 5.** Trends in climate at NWT Saddle site as summarized by principal component analysis. **A)** Over 50% of the yearly variation is described by climate characteristics related to extended summers (PC1): high potential evapotranspiration (loading #3, in blue) and max temperatures (2), early warming (7,8; days to a 5-day running max temp of  $5^{\circ}$  or  $12^{\circ}\text{C}$ ) and ice-off (6), and a long growing season (4). The amount of precipitation (1) and moisture deficit (5) are described by the second axis. **B)** Since the start of the NWT program, extended summer climate has significantly increased over time. Notably, the most extreme extended summer years occurred in 2002 and 2012 (circled in orange). There is much variation across years, but this variation has not changed over our period of observation.

**2.2 BIOGEOCHEMICAL AND HYDROLOGICAL CONSEQUENCES.** Research at NWT has shown that extended summers are associated with the thawing of permafrost and stored ice at NWT (Caine 2010, Barnes et al. 2014). The Arikaree Glacier is losing large volumes of ice and is expected to disappear in the next two decades (Leopold et al. 2015). Long-term trends in stream water chemistry also suggest increased contributions of rock glacier meltwater (Leopold et al. 2011, Barnes et al. 2014). This thawing creates new subsurface flowpaths in areas that may not often receive flushing from snowmelt water, enhancing nitrification (Liu et al. 2004, Barnes et al. 2014). Thawing may also contribute to net carbon loss in tundra by stimulating carbon respiration (Blanken et al. 2009, Knowles et al. 2014). We expect, over six more years, that the signature of melting ice will grow even stronger.

We also find that extended summer increases catchment heterogeneity in snowmelt timing and flushing. As snowmelt flows through soils, it accelerates biogeochemical process rates (Darrouzet-Nardi

and Bowman 2011). In extended summer years, snowmelt starts earlier but the duration of snowmelt is longer (Jepsen et al. 2012, Burns et al. 2014), leading to increased spatial heterogeneity in melt date (Fig. 6). Increased variability in the timing of snowmelt within a catchment causes greater mixing of new snowmelt areas that flush solutes from hillslopes to streams and older snowmelt areas where nitrate has already been flushed (Perrot et al. 2014). The longer duration of flow allows for greater biological uptake and retention, reducing nitrate exports to streams. We aim to further address these consequences of heterogeneity at the catchment scale in our proposed work (H4).



**Figure 6.** Spatial variability of snowmelt timing in the Green Lake 4 catchment in 3 years that differ in snowmelt onset and length of summer (after Perrot et al. 2014, Jepsen et al. 2012). Color indicates DOY melt onset; red indicates earlier snowmelt, blue later. In extended summer years (e.g., 2002 when melt started on DOY 71), slower rates of melt result in higher spatial variation within the catchment.

**2.3 POPULATION AND COMMUNITY RESPONSES.** Earlier snowmelt and warmer summers have been linked to decreased primary productivity in subalpine forests (Hu et al. 2010) and meadows (Sloat et al. 2015), accelerated tree mortality (Smith et al. 2015), reduction in winter forage quality for pikas (Bhattacharyya and Ray 2015), and shifts in plant phenology (Smith et al. 2012). Positive responses to longer growing seasons have also occurred in some landscape positions at NWT due to the relaxation of energy limitation and benefits of drier conditions. For instance, a longer growing season enhances snowbed primary production (Carbognani et al. 2012; Fig 7A) and enables alpine plants to move up in elevation and colonize unvegetated talus areas (Gottfried et al. 2012, Bueno de Mesquita et al. 2015). Grasshopper populations benefit from increased time to complete their life cycle (Buckley et al. 2015). These varied responses reflect a widespread observation that responses to climate change can be negative or positive or largely undetectable, depending on the life history and traits of the organisms involved, scale of ecological organization, and spatial variability related to landscape position (Gilman et al. 2010, Ackerly et al. 2015). Four case studies from NWT illustrate these varied responses.

**2.3.1 Decline of pikas.** Pikas are widely considered a sentinel species for detecting ecological effects of climate change (Beever et al. 2011). Populations at NWT and across the Western US are projected to continue to decline (Ray and Beever 2012), and as a result, pikas have been considered for listing as threatened at the state and federal levels. Research at NWT has shown that pikas that inhabit warming sub-surface areas show signs of chronic stress (Wilkening et al. 2013, Wilkening et al. 2015). Pikas born early in longer summers approach adult weight sooner (Fig. 7B) and territorial adults may force them to disperse during warm summer months. In addition, the quality of forage cached for overwinter survival has declined at NWT due to climate-related shifts in plant composition (Bhattacharyya and Ray 2015). In the next six years, we may document the loss of pikas from a key monitoring site, the West Knoll, due to these changed conditions.

**2.3.2 Mixed responses in lakes.** For alpine lakes such as Green Lake 4 (GL4), climate-driven changes (earlier ice-off, summer warming) are associated with reductions in summer stream flow, increased surface water temperatures, stronger thermal stratification of the water column, and higher late-summer solute (including nitrate) concentrations (Miller and McKnight 2012). The resultant increase in lake water residence time increases utilization of resources (P, silica) by phytoplankton (Flanagan et al. 2009), and enhances autochthonously-produced dissolved organic material (Cory and McKnight 2005, Hood et al. 2005). Chlorophyll a levels consistently exhibit a deepwater maximum, but the intensity of these maxima respond positively to extended summer conditions (Fig. 7C). In contrast, extended summers affect community composition of phytoplankton more strongly in the epilimnion (0 to 3 m) than in the hypolimnion (~9 m), suggesting a modulation of UV stress.

**2.3.3 Little treeline advance, increased shrub colonization.** Projections of treeline often focus on warming; however, we find that water limitation may be a primary constraint on treeline expansion (Knowles et al. 2015b, Smith et al. 2015).

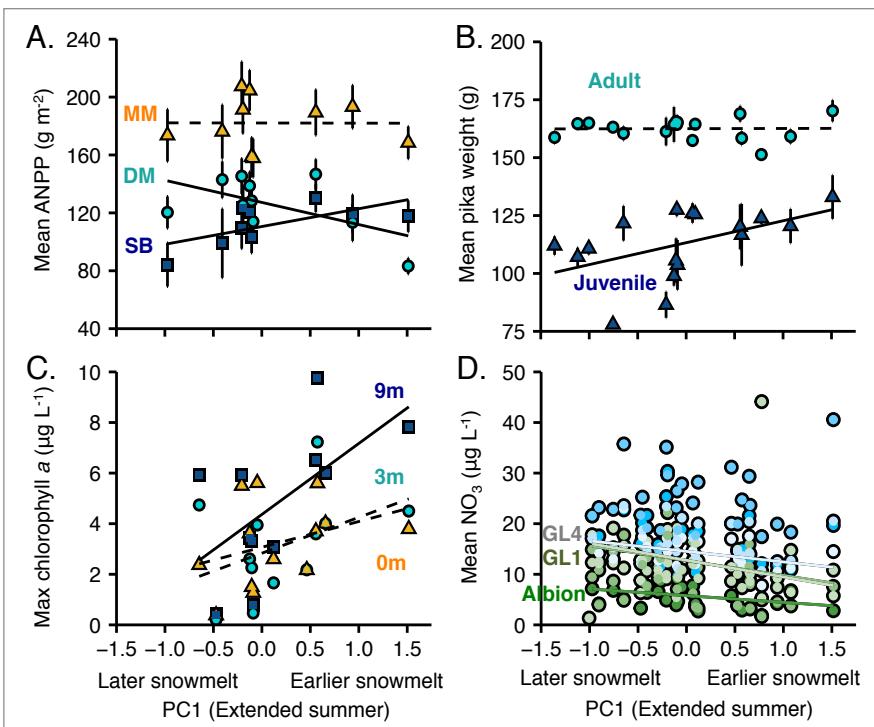
Forest expansion has been slow, mostly consisting of infilling lower elevation areas (Fig. 8). Shrubs (mostly *Salix* sp), however, have colonized alpine tundra at rapid rates (Formica et al. 2014), consistent with global patterns (Walker et al. 2006, Elmendorf et al. 2012). In the next six years, we will be able to better document patterns of shrub encroachment as well as identify areas of forest infilling.

#### 2.3.4 Uphill spread of tundra vegetation.

In many mountain regions across the globe, alpine plants are migrating uphill into areas that previously did not

support vascular plant life (Gottfried et al. 2012, Pauli et al. 2012). At NWT, vascular plant abundance is limited due to the short growing season (<20 days in some areas) in the mostly unvegetated talus fields above site D1. Aerial photograph analyses indicate 9-21% of these previously unvegetated areas have been colonized over the last four decades (Fig. 8B). Our work suggests that diverse and active microbial communities may be key players in these colonization dynamics (King et al. 2010). For instance, many heterotrophic microbial taxa (e.g., in *Helotiales*, *Rhodospirillales*) are associated with tundra vegetation at their uphill limits (King et al. 2012, Bueno de Mesquita et al. 2015), and likely facilitate the plant colonization of these sites as the growing season lengthens (Knelman et al. 2014, Bueno de Mesquita et al. 2015). The expansion of tundra vegetation into high elevation unvegetated areas should also increase terrestrial subsidies of dissolved organic matter into lakes and enhance aquatic primary production (Miller and McKnight 2012) and will affect catchment-scale processes such as water and nitrate retention. While we are currently are unable to detect a vegetation-related change reflected in our lake measures, tundra colonization is occurring at a rate that should enable detection over the next 6 years of the project.

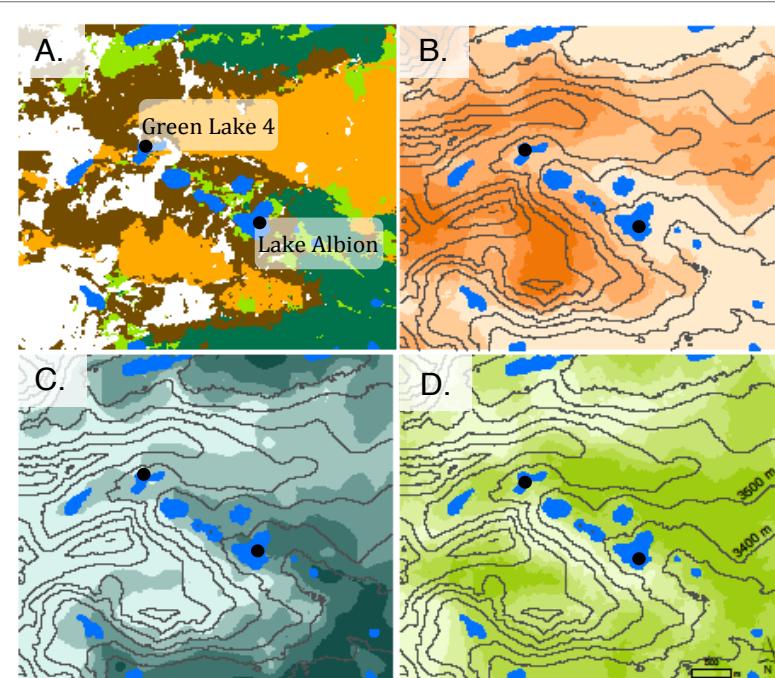
**2.4 OUTREACH AND EDUCATION.** Our outreach program has focused on two children books, *My Water Comes from the Rocky Mountains* and *My Water Comes from the San Juan Mountains*, as our primary educational tools. We have partnered with nine educational organizations and two school districts in the Front Range and Four Corners regions of Colorado to link our research to K-12 curricula. The books and associated classroom and teacher professional development curricula have reached an estimated 15,000 children and 90 teachers (Ray et al. 2015). In Boulder County, several of the components of the *My Water*



**Figure 7.** LTER VII will focus on ecological responsiveness to changes related to extended summer. **A)** Aboveground plant production in alpine tundra, where dry meadows (DM) show a negative response and snowbeds (SB) show a positive response with little effect in moist meadow (MM). **B)** Pikas are born earlier and approach adult weight sooner in years with longer summers. Earlier maturation may force dispersal during warmer summer months, as they are run off by territorial adults. **C)** Positive response in maximum chlorophyll a in Green Lake 4 at depth (9m), with limited response closer to the surface (at 0 or 3m depths). **D)** Average stream summer nitrate concentrations decrease with earlier snowmelt, particularly at lower elevations. Std errors describe spatial (in A) and individual (in B) variation.

curriculum have been adapted in a kit designed for teaching about weather and the water cycle. During each of the past four school years (2010–2014), we estimate the kits were used by 30–40% classrooms in the Boulder Valley school district. Our schoolyard LTER program is also enhanced by online curricula about hydrology and pika biology, available to teachers worldwide via [www.Science-Live.org](http://www.Science-Live.org). In addition, we supported development of a summer camp, “Our Watershed,” for 9–14 year olds from the Colorado Front Range and Denver Metro Area about water sources and uses in the Boulder Creek Watershed. After the massive flooding events of 2013, we developed STEM curricula for these communities’ schools around landscape vulnerability, adaptability and resilience. We have also engaged with the public by giving research tours and presentations to more than 800 individuals who have used the

Mountain Research Station facilities. Over 200 middle and high school students were welcomed annually into LTER laboratory facilities on the CU campus during open houses. In LTER VII we will continue many of these programs, with the specific focus on training students in community engagement (see 4.1).



**Figure 8. Land cover change at NWT.** **A)** NWT is largely composed of tundra (orange), forest (blue green), shrubs (green) and talus or barren soil areas (brown). White is persistent snow. Lakes (two focal lakes highlighted) receive water inputs from catchments that range from largely unvegetated (Green Lake 4) to largely vegetated (Lake Albion). **B-D)** Probability of expansion of tundra (**B**), forest (**C**) and shrubs (**D**) since 1972, based on aerial photograph time-series analysis combined with ground validation.

**2.5 RESPONSE TO MID-TERM SITE REVIEW.** Our July 2013 site review concluded that NWT “engages in an impressive range of high-quality research that is significantly advancing our understanding of high elevation ecosystems.” The team had three main suggestions, each of which has helped guide the development of our proposed work (we address suggestions about Information Management and Outreach separately). First, we **revisited the major conceptual ideas** that drive our research and translated these ideas into our proposed research direction. This has led us to focus on ecological responsiveness and its translation to direct testable hypotheses based on our long-term observations. As a consequence of this focus, we have initiated many lines of new work and expanded data sets since the site review. Previous investments have enabled us to complete several projects (we denote these in Table S3), allowing us to move forward with the focus of measuring ecological responsiveness. Second, we have focused on opportunities to **strengthen integration across studies and disciplines** to provide a rationale for our proposed work. Analysis of long-term observations has enabled us to ask common questions across levels of ecological organizations and systems. Third, our **new efforts related to modeling** provide a coordinated framework that extends from fine-scale biogeochemistry to landscape-scale snow accumulation to catchment-scale hydrology (Jepsen et al. 2012, Livneh et al. 2014, Fan et al. 2016). These efforts allow us to understand landscape complexity and ecological response in a hierarchical and spatially-explicit context; we will extend these efforts to lakes and subalpine forest in LTER VII. Collaborations with researchers at NCAR, CIRES, and Argonne and Lawrence Berkeley National Laboratories (Fan, Livneh, Kueppers, Wieder) have strengthened our modeling expertise. We have also initiated collaborations with ecologists to enhance **population biology expertise** (Doak, Emery, Farrer,

Harvey, Veblen). We elaborate more on the expansion of our research team in the project management section of this proposal.

**3. PROPOSED RESEARCH FOR LTER VII.** We propose a research program that utilizes long-term monitoring, experimentation, and a combination of heuristic and predictive modeling to examine how ecological responsiveness is affected by the interaction of climate, terrain, and biotic factors (Q1 and Q2, below), the compensatory mechanisms that contribute to these responses (Q3), and how these finer spatial scale responses integrate at the catchment scale (Q4).

### **3.1 SHIFTING LIMITATIONS: How do terrain-related differences in climate exposure affect ecological response?**

**3.1.1 Ecological theory and rationale.** 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 (Ashcroft et al. 2009, Ford et al. 2013, Ackerly et al. 2015). We build expectations about terrain-related differences in climate exposure from resource and abiotic limitation theory and variation in limitation caused by landscape processes (Seastedt et al. 2004, Turner 2010).

Recognition of the dynamic nature of resource limitation has shifted understanding away from the equilibrium ideas in Liebig's law of the minimum (Liebig 1840) and the multiple limitation hypothesis (Bloom et al. 1985) to ideas of transient maxima (Seastedt and Knapp 1993) where frequent and reoccurring shifts in limiting resources lead to nonequilibrium biotic responses. Recently, Farrior et al. (2013) argued that resource limitation may often be sequential, with one resource limiting at any point in time but several limiting over the course of a growing season. The best strategy to employ when resource limitation shifts through the growing season, or across years, is not well developed theoretically, although it is generally assumed that further investment in one allocation or foraging strategy is more possible than switching allocation strategies (Weiner 2004). 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 this rationale, we hypothesize (**H1**): **Ecological responsiveness to climate will be strongest in locations where climate exposure results in a shift in limiting factors.** We will evaluate H1 in three different systems at NWT: alpine tundra, lakes, and subalpine forest. We describe evidence from each system below.

**3.1.2 Evidence for H1. A. Alpine Tundra.** The environmental controls over alpine tundra productivity and compositional turnover can be roughly separated into physical (temperature and moisture) and nutrient (N and P) controls (Jones et al. 1998, Elmendorf et al. 2012, Ernakovich et al. 2014). At NWT, strong winds blow some slopes free of snow and carry snow to other areas, creating deep (>15m) drifts in sheltered leeward areas (Jepsen et al. 2012). Snowbeds may not melt out until late summer, whereas plant growth in snow-free areas can start as soon as temperatures warm in May (Carbognani et al. 2012, Wheeler et al. 2014, Harpold et al. 2015). The timing of snow disappearance and the date of peak soil moisture are highly correlated (Harpold et al. 2015); with earlier snowmelt, peak soil moisture occurs earlier in the year, followed by increased evapotranspiration and a longer dry period. Thus, we find moisture limitation to be most strong in wind-blown areas that receive little water from snowmelt and energy limitation to be strong in snowbeds that have short growing (snow-free) seasons (Freppaz et al. 2012, Natali et al. 2012).

Nutrient amendment experiments indicate that nutrient limitation (largely nitrogen, secondarily phosphorus) limits production most strongly in areas on the landscape that receive snowmelt from adjacent snowbeds (Bowman 1994, Bowman et al. 2012). In many areas, water and nitrogen tend to be co-limiting when both are manipulated (Farrer et al. 2015, Gasarch and Seastedt 2015a).

Extended summer conditions strengthen water limitation and relax energy limitation across alpine tundra. At the Saddle site, we find that species (Fig. 9) and production (Fig. 7A) respond more strongly to

extended summers in areas where these conditions result in changed snowmelt and soil moisture (wind-blown dry meadows, snowbeds) compared to areas where extended summers have little effect on the timing of snowmelt or soil moisture (moist meadows).

**B. Lakes.** The environmental controls over primary production and species composition in lakes can be roughly separated into abiotic (temperature, UV, flushing rate) and nutrient (nitrate, phosphorus, silica) controls, with the additional influence of grazing zooplankton (Flanagan et al. 2009, Miller and McKnight 2012). In alpine lakes located above treeline (e.g., GL4), the short growing season during ice-free conditions, high flushing rate during snowmelt, and intense solar radiation in mid-summer provide strong physical controls over productivity and planktonic community composition (Flanagan et al. 2009, Williamson et al. 2010, Miller and McKnight 2012; Fig. 10).

Lower-elevation lakes have increased water residence time, warmer water temperatures, and less intense solar radiation. In these lakes, nutrients (primarily phosphorus) and zooplankton more strongly control productivity and planktonic community composition (Gardner et al. 2008, Goldberg et al. 2015). While not primarily limited by nitrate availability, uptake of nitrate by phytoplankton causes greater in-lake retention, reaching about 30% of inflowing nitrate as the summer progresses and phytoplankton biomass increases (Bowman et al. 2014).

Extended summer conditions shift limitations in GL4 to be more similar to lakes lower in elevation, which have increased water residence times, warmer water temperatures, and higher average solute concentrations. These conditions stabilize the water column and facilitate increases in both phytoplankton biomass and the density of large-bodied grazers, such as *Daphnia pulicaria*, which tend to achieve higher densities in years with early ice-off and reduced flushing (Preston et al., in review; Fig. 10).

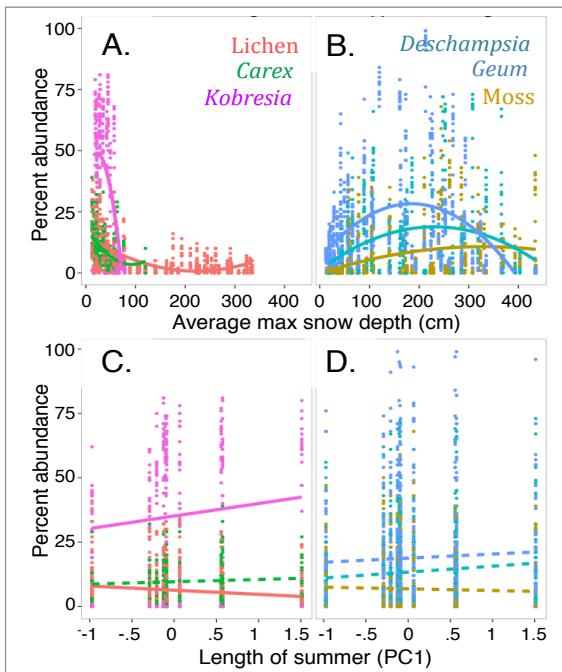
**C. Subalpine forest.** The environmental controls in subalpine forest are often considered to be energy, light, and water (Veblen 1986, Villalba et al. 1994), with treeline areas limited by energy and lower elevation forests limited largely by water and light. However, experimental common gardens at NWT show that warming reduces tree establishment in forest, treeline and alpine tundra, an effect partially offset by water additions (Moyes et al. 2013). Projections of population abundance through time suggest that water limitation will strongly limit population expansion across elevations (Conlisk et al, in review).

Extended summer conditions act to strengthen water limitations in most areas of subalpine forest. Smith et al (2015) found a two and a half fold increase in the average annualized tree mortality rates from the relatively cool and wet 1982–1994 period to the warmer and drier 2008–2013 period. While tree mortality initially lagged at some sites (more mesic locations, in canopy gaps), it became a more uniformly accelerating trend in the last decade. Longer growing season length reduced forest productivity due to tree growth dependence on snowmelt water through most of the growing season (Hu et al. 2010). We find little evidence for uphill expansion.

### 3.1.3 Predictions related to H1.

Based on theory and evidence from our past work (above), we predict:

**A. Alpine Tundra:** Ecological response to extended summer will be highest in areas where climate drivers shift limitation from nutrients to water (dry meadow), and from energy to nutrients (snowbeds). Moist meadow and wet meadow tundra will be less responsive due to persistent nutrient limitation.



**Figure 9.** Long-term plant composition at 88 permanent plots in the saddle grid indicates plant species (or lichen and moss) characteristic of areas that accumulate little snow (**A**) are more responsive to extended summer climate variation (**C**), compared to species characteristic of areas that accumulate more snow (**B, D**). Solid lines in (**C, D**) indicate significant relationships.

Relaxation of energy limitation will allow tundra to expand into higher-elevation unvegetated talus areas.

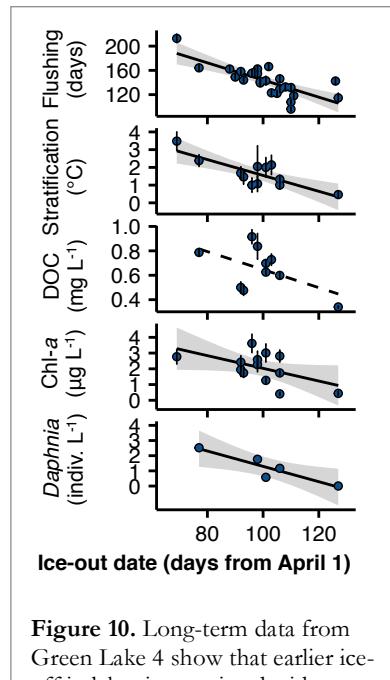
**B. Lakes:** Alpine lakes, typically limited by high flushing rates, intense UV radiation, and a short growing season (>250 days under ice), will exhibit the strongest responses to extended summer years as physical limitations shift to nutrient limitations. In lakes lower in elevation, extended summer climate variation may intensify nutrient limitations but will cause less response in production and species turnover.

**C. Subalpine forest:** Extended summer climate trends will intensify soil moisture limitation in subalpine forest and reduce already limited recruitment. Forests will not track climate warming trends due to moisture limitation, with treeline expansion only occurring in wet topoclimates (e.g. north facing slopes).

**3.1.4 Experiments and observations to test H1.** To test these predictions related to H1, we take a series of approaches, including a) continued monitoring, with expansion of ecological observations to encompass spatial variation; b) modeling limitation of plant growth and extension to lakes; and c) adding a consideration of physiological trait mechanisms. Lastly, to better understand mechanisms related to observed patterns, we propose d) experimental manipulations of extended summer conditions in tundra, forest, and lakes.

**A. Continued monitoring of tundra, forests, lakes, pikas and marmots.** Long-term observations are essential to relate ecological responsiveness in a process rate (e.g., production, compositional turnover, survival) to assessments of limitation using measures of soil moisture, nutrient availability, and growing season length. Based on climate trends, we anticipate the next six years of monitoring will include ES years, as well as years similar to the baseline climate over the last decades. In LTER VII we propose to expand some measurements to better encompass variation across the landscape as well as more explicitly link ecological response measures with biogeochemical measures. Observational measures we will initiate in LTER VII (Tables 1, 2) include: 1) pika and marmot population monitoring at a lower-elevation site in Green Lakes Valley; 2) addition of four forest stands to extend forest sampling to treeline; 3) forest production estimates comparable with our long-term tundra production estimates; and 4) demographic observations for four tundra focal plants to complement population demographic monitoring of tundra plants *Silene acaulis* and *Bistorta vivipara*, and trees *Abies lasiocarpa* and *Picea engelmannii*. To encompass a broader elevational gradient, we will expand our lake monitoring to include bi-weekly sampling in two lakes within the Green Lakes Valley (GL1 and Albion), and a 15-lake survey in Rocky Mountain National Park every 3 years. Targeted long-term monitoring of soil processes in select tundra and forest permanent plots (N cycling, soil moisture, microbial biomass and enzyme activities; Table 1h) will allow us to integrate biogeochemical processes with ecological responses.

**B. Modeling limitation of plant growth.** While resource limitation is a fundamental concept in ecology, there remains no one best way to identify limitation, or, in particular, no one best way to identify how different limiting resources shift in importance. Modeling allows us to create a framework for model-data iteration that we can use to refine understanding and make predictions. We take two approaches: 1) development of a heuristic biogeochemistry model specifically for NWT (**Niwot Biogeochemistry Model**, NBM), and 2) application of a well-tested global land surface model (**NCAR Community Land Model** version 4.5, CLM). NBM allows us to move quickly between observations, experiments, and modeling, but has greater site-specific data requirements for model forcing and parameterization (Fan et al. 2016). The CLM is a



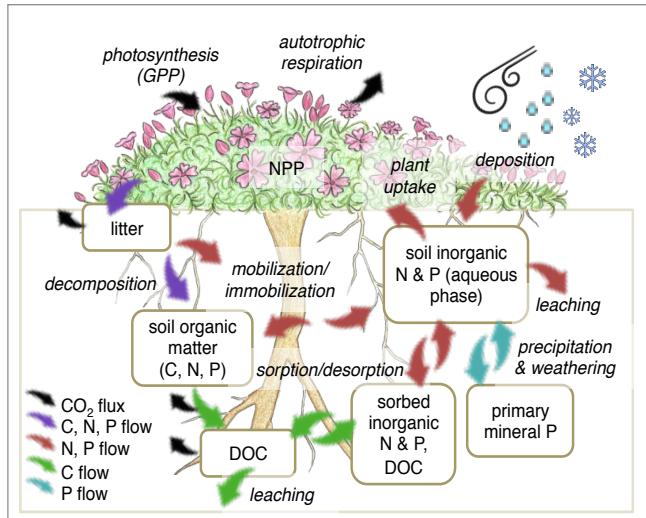
**Figure 10.** Long-term data from Green Lake 4 show that earlier ice-off in lakes is associated with increased flushing rates, stratification, and increased solute concentrations. Solid lines indicate significant relationships, shaded areas represent 95% confidence regions. Std errors describe within-season and across-depth variation.

larger model that has less flexibility, but requires only basic meteorological data taken from the site (Oleson et al. 2013). As a result, we use the NBM to describe shifting limitations at short time steps within well-instrumented habitats (e.g., dry meadow). In contrast, CLM allows us to describe topographic variation in space by modifying precipitation inputs and solar radiation in habitats where we have less empirical measures, enabling us to examine broader environmental gradients as well as to simulate experimental treatments (section 3.1.3). As neither of these approaches are spatially explicit, we also utilize a spatial watershed hydrology model (**DHSVM**) that we link with the NBM (described in section 3.4).

Shifting limitations in dry meadow tundra. We developed the NBM to integrate information on stoichiometric and physical constraints to alpine tundra plant growth, with a focus on first-order processes and the flexibility to add complexity through model-data iteration (Fan et al. 2016). NBM is similar to other models that focus on limitation such as the multiple-element limitation model (MEL; Rastetter et al. 1997). The model simulates the coupled cycling of ecosystem C, N, and P (Fig. 11), where C is separated into vegetation, litter, soil, and DOC pools with parallel organic N and P pools, and additional inorganic pools in aqueous and sorbed phases. We focus on dry meadows due to the extensive long-term data on soil processes and characteristics we have for this system. A goal in LTER VII is to better describe resource and abiotic factors in all our focal habitats, which would allow us to extend the scope of NBM. NBM results indicate strong shifts in the nature and intensity of resource limitations across years (Fig. 12A). For instance, in later snowmelt years, production strongly limited by available water only in the last weeks of the growing season, while in extended summer years, production is limited by water limitation throughout the entire period of growth. To validate model results, we compared model performance against observations from N, P, and N+P fertilization treatments in an experiment at NWT (Bowman et al. 1993); modeled NPP ratio among control, P fertilization, N fertilization, and combined N and P fertilization (1.0:1.0:1.2:2.4) was similar to variation in measured aboveground-biomass ratios (1.0:1.1:1.6:2.8; Fan et al. 2016).

Limitations across landscape positions. The CLM calculates fluxes in surface energy, hydrology (in snow and soil), and biogeochemistry with basic meteorological data taken from the site, enabling us to simulate different landscape positions by altering factors such as the amount of wintertime precipitation inputs. Currently, we use a single representation of an arctic C<sub>3</sub> grass and focus on how the timing and magnitude of snowmelt controls plant productivity; we plan to incorporate differences in plant physiological traits in LTER VII (see section below). Single point simulations were forced with data from ongoing eddy covariance-based flux measurements and meteorological measurements in tundra (e.g., Knowles et al. 2012). Simulated productivity results for each vegetation community were independently validated with NWT long-term snow and vegetation measurements (Spasojevic et al. 2013), where production measurements aligned within a standard deviation of empirical measurements; CLM and NBM also produced very similar results for dry meadows. Model simulations indicate shifts in limitations in two portions of the landscape: first, strengthening of water limitation and reduction of nitrogen limitation in dry meadows, and second, a relaxation of energy limitation in snowbeds (Fig. 12B).

Predictions generated by NBM and CLM are supported by long-term data (Fig. 12C). In 2012, snowmelt occurred in April, extending summer by more than a month (see Fig. 5). Compared to the long-

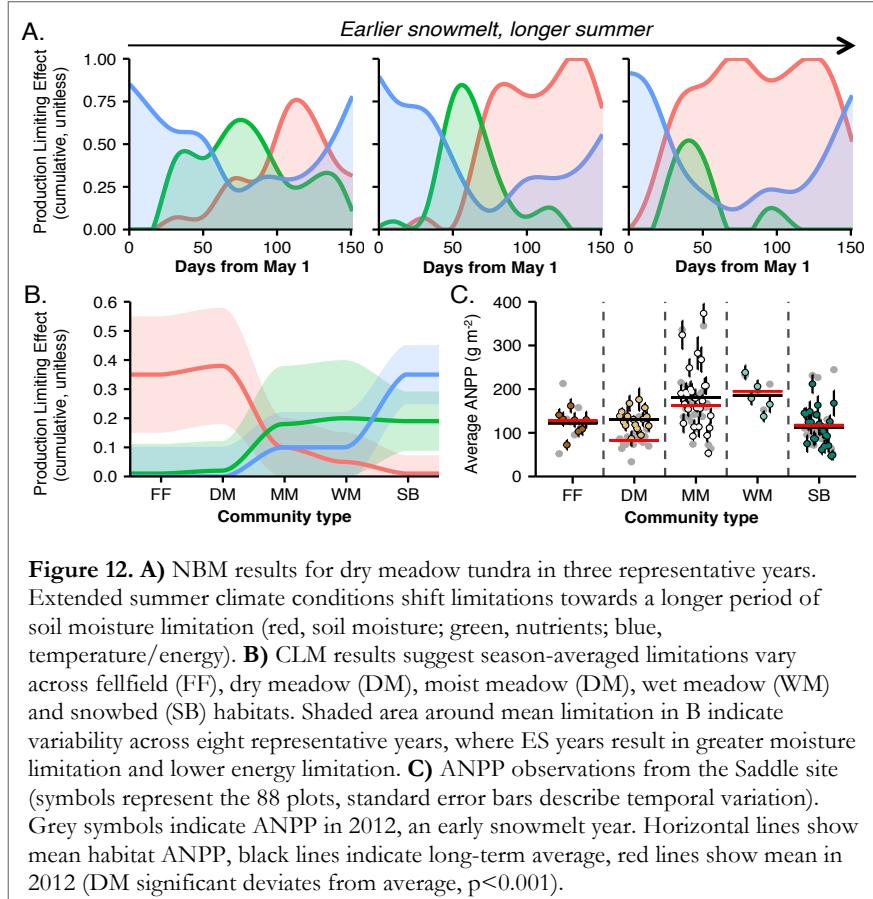


**Figure 11.** We developed the Niwot Biogeochemistry Model (NBM) as a heuristic tool to generate testable hypotheses about how climate affects resource and abiotic limitations via stoichiometric and physical constraints on alpine plant growth (Fan et al. 2016).

term average, aboveground production in 2012 declined in dry meadow by 40% and marginally increased in snowbeds (Fig. 12C), while there was little response in moist meadow. These patterns are also apparent in production trends across years, where dry meadow production significantly declines and snowbed production increases with ES (Fig. 7A).

#### Extension to lakes.

We will complement our terrestrial modeling work by building upon prior modeling of DOM dynamics in the alpine lake system. Our goal will be to create a model in parallel to the tundra model that uses the physical constraints associated with the hydrologic regime to drive phytoplankton growth. This model will be based on the initial modeling work by Miller et al (2009) that included stream inflows and thermal stratification. Similar to the NBM, we will simulate the coupled cycling of ecosystem C, N, and P, where C is separated into phytoplankton, zooplankton, sediment and DOM pools, with parallel organic N and P pools, photochemical, and heterotrophic oxidation of DOC, and grazing as a lagged response to primary production. This modeling effort will allow us to evaluate the potential importance of photochemical release of P from terrestrial DOM in enhancing phytoplankton growth in the subalpine lakes. As with the terrestrial model development, we will use this model to make predictions about how high-elevation lake ecosystems will respond to changing climate conditions, with particular focus on water residence time.



**Figure 12.** **A)** NBM results for dry meadow tundra in three representative years. Extended summer climate conditions shift limitations towards a longer period of soil moisture limitation (red, soil moisture; green, nutrients; blue, temperature/energy). **B)** CLM results suggest season-averaged limitations vary across fellfield (FF), dry meadow (DM), moist meadow (MM), wet meadow (WM) and snowbed (SB) habitats. Shaded area around mean limitation in B indicate variability across eight representative years, where ES years result in greater moisture limitation and lower energy limitation. **C)** ANPP observations from the Saddle site (symbols represent the 88 plots, standard error bars describe temporal variation). Grey symbols indicate ANPP in 2012, an early snowmelt year. Horizontal lines show mean habitat ANPP, black lines indicate long-term average, red lines show mean in 2012 (DM significant deviates from average,  $p < 0.001$ ).

**C. Addition of physiological/trait mechanisms.** While our modeling work (described above) assumes that vegetation type and its functional response does not change in response to climate, a goal in LTER VII is to evaluate the mechanisms related to climate sensitivity and compositional turnover. Starting with a focus on alpine plants, we will measure a suite of traits across the tundra indicative of a spectrum of functional strategies related to resource use (Baptist and Aranuelo 2012), including leaf carbon isotope composition ( $\delta\text{-}^{13}\text{C}$ ), specific leaf area, and leaf chlorophyll content (Table 1). By combining existing information about species' exposure to climate effects with a suite of plant traits related to carbon and nitrogen metabolism (Baptist and Choler 2008, Spasojevic and Suding 2012), we will be able to incorporate plant traits into our NBM and CLM model simulations. This can be further developed to link with demographic responses (a focus of H3) to predict survival and growth as well as simulate feedbacks between vegetation and the atmosphere as at the catchment scale (a focus of H4).

**D. New experiments: manipulation of extended summer conditions in terrestrial and aquatic systems.** We propose parallel manipulations in lakes and tundra/forest to allow integration of our long-term measures with focused manipulations of specific climate drivers and to address effects of more persistent climate change.

Terrestrial manipulation of growing season length. While we suspect that earlier snow melt and longer growing seasons are key drivers in response to extended summer conditions, we will initiate a manipulative experiment in LTER to better understand the mechanisms of response. Using black sand application, we will reduce snow albedo and speed melt rates without concurrently affecting snowpack depth (after Blankinship et al. 2014). While many methods for manipulating snowmelt timing have been attempted (Steltzer et al. 2009, Wipf 2010), few do so without altering soil water input. Although this might be realistic in some ecosystems, records at NWT indicate that the change in snowmelt timing is largely occurring independently of precipitation amount (Fig. 5). The application also approximates a dust deposition event, now a common occurrence at NWT (Neff et al 2008). The ease of application allows us to conduct these manipulations across the spatial complexity that characterizes NWT.

At peak snow pack (generally early May each year; Erickson et al. 2005), we will spread a thin layer (200-500 cm<sup>3</sup>/m<sup>2</sup>, based on model simulations of albedo effects in CLM; Fig. 13) of inert black vitreous sand (manufactured by Mission Laboratories, Los Angeles, CA, composed primarily of silicon dioxide, iron oxide, and calcium oxide) over the snow. Pilot studies in 2015 indicated the black sand application extended growing season by 7-10 days (9-13% increase) with no effects on soil temperature. We will also add the sand to control plots after snowmelt to account for any soil albedo or microbial substrate effects. Our CLM simulations also suggest that early melt should increase the frequency of frost events, which can damage buds and reduce root reserves (Inouye 2008, Wipf et al. 2009, Galvez et al. 2013; Fig. 13).

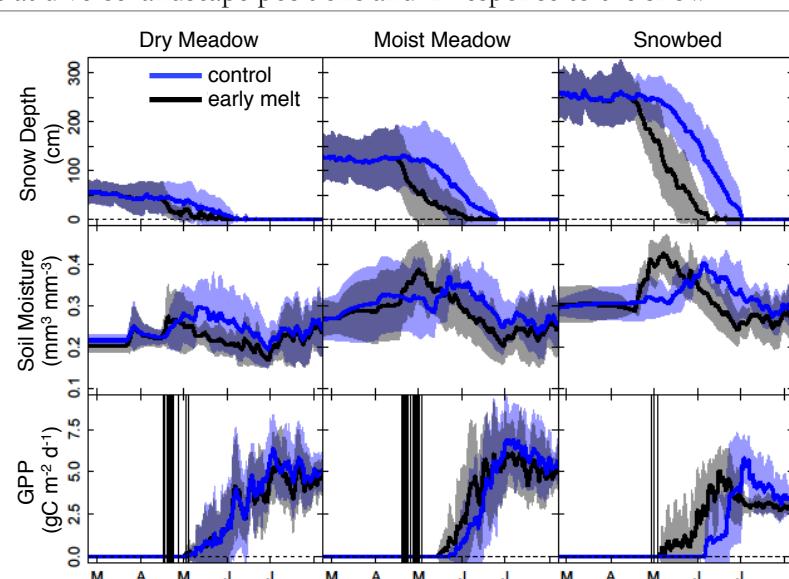
To understand how effects differ across complex terrain, we will conduct these manipulations in a spatially distributed design within subalpine forest, open canopy treeline, dry meadow tundra, moist meadow tundra, snowbed tundra, and unvegetated talus. Within each habitat type, we will establish 6 replicate blocks (for a total of 36 blocks; Fig. 14). Within this experimental set-up, we will measure ecological responses with methods that allow for comparison with our long-term monitoring (our response measures are listed in Table 1, denoted by +*Exp*). Campbell loggers will record soil temperature and soil moisture as well as light availability and snowfree date. We will continue these manipulations yearly in order to examine persistent changes in growing season length.

Data collected on a subset of alpine plant species and on subalpine forest trees will enable demographic modeling of populations at diverse landscape positions and in response to the snow manipulation (Conlisk et al. 2013).

We will use output from the catchment hydrological model, DHSVM (described in section 3.4) to specify environmental parameters (soil moisture, temperature, snow-free season length) continuously over the landscape, allowing us to develop range-shift models.

Based on our predictions related to H1, we expect a longer growth season to reduce primary production in dry meadow and subalpine forest and increase production in snowbeds.

Compositional turnover and changes in vital rates will be greatest in these habitats. Moist meadow and wet meadow tundra will be less responsive. Manipulations will increase



**Figure 13.** CLM simulations of the effects of the experimental black sand treatment in dry meadow, moist meadow, and snowbed habitats, simulated by reducing albedo. Interannual variability in model runs is shown by shaded areas, the x-axis is time (months). Vertical lines indicate days when soils in the experimental treatment are significantly colder (below freezing) compared to the snow-covered control scenario.

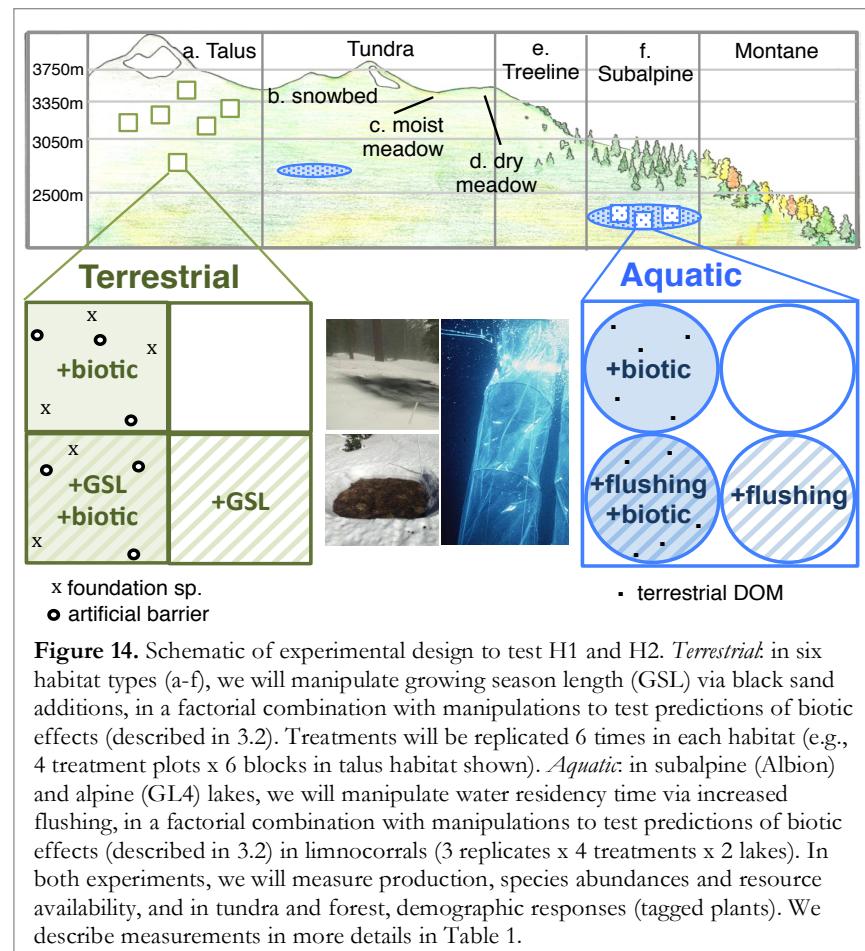
population growth and production in talus habitats.

Lake manipulation of water residence time. To parallel manipulations conducted in the terrestrial environment, we will use experimental limnocorals in Lake Albion (subalpine) and Green Lake 4 (alpine) to evaluate the effects of changes in flushing rate and water residence time (Fig. 14). The experiment will be a 2 x 2 design (with flushing rate as one factor; the other a manipulation of terrestrial DOM as described in H2) with 3 replicates of each treatment in each lake for a total of 24 limnocorals. We will suspend corals from PVC rings mounted in floating wooden frames. They will be constructed out of UV-transparent plastic to facilitate natural light regimes, and each will be 2-3m deep and 1-2m in diameter (~6300 L). Corral

temperatures will be buffered by the thermal mass of the surrounding lake. The corals will be open to the atmosphere to avoid depletion of inorganic carbon, and associated spikes in pH. We will fill the limnocorals with lake water to establish natural background nutrient concentrations; standardized aliquots of filtered phyto- and zooplankton communities will be seeded into each coral to help limit stochastic variation in initial conditions.

To manipulate residence time and simulate extended summer conditions, we will pump lake water into the bottom of each limnocoral using solar-powered pumps mounted on a frame: one treatment will approximate residence time in the lake for the current year, whereas the other will decrease residence time by 25% to approximate an extended summer year. Onset HOBO loggers will record both surface and bottom temperatures, providing a more finely resolved record of thermal stratification. We will run the experiment over a 21 day period, sampling every three days from two depths in each coral as well as the host lake (following long-term protocols; Table 1f). We will also measure the depth-specific UVR attenuation curve in each coral. Based on our predictions related to H1, we expect that reductions in flushing rate will increase production and shift planktonic communities more at high elevation (GL4) compared to lower in elevation (Lake Albion). We expect that zooplankton abundance will also increase in treatments with reduced flushing rates, increasing grazing intensity.

**3.1.5 Context of H1 within LTER VII.** In H1, we capitalize on long-term observations to test our hypothesis that ecological responsiveness to climate will be strongest in locations where climate exposure results in a shift in limiting factors. We use four related approaches: a) integrating ecological responses with resource availability and changes in abiotic factors using correlational approaches, b) modeling limitation in different locations and in different climate years, c) measurements of physiological traits, and



**Figure 14.** Schematic of experimental design to test H1 and H2. *Terrestrial*: in six habitat types (a-f), we will manipulate growing season length (GSL) via black sand additions, in a factorial combination with manipulations to test predictions of biotic effects (described in 3.2). Treatments will be replicated 6 times in each habitat (e.g., 4 treatment plots x 6 blocks in talus habitat shown). *Aquatic*: in subalpine (Albion) and alpine (GL4) lakes, we will manipulate water residency time via increased flushing, in a factorial combination with manipulations to test predictions of biotic effects (described in 3.2) in limnocorals (3 replicates x 4 treatments x 2 lakes). In both experiments, we will measure production, species abundances and resource availability, and in tundra and forest, demographic responses (tagged plants). We describe measurements in more details in Table 1.

d) comparisons with responses to experimental climate manipulations. Coordinated climate manipulation of extended summer across habitat types will additionally allow integration of long-term measures with focused manipulations of specific climate drivers. An additional six years of data will allow us to better explore the consequences of intense ES events and discern how time lags influence response.

### **3.2 BIOTIC INFLUENCE: How do biotic effects influence climate exposure and ecological responsiveness?**

**3.2.1 Ecological theory and rationale.** At a finer scale than landscape effects of complex terrain, biota can also influence climate exposure through effects on the physical environment (Wright and Jones 2004). In tundra, 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 (Bowman 2000, Seastedt and Adams 2001, Suding et al. 2008, Cavieres et al. 2014). We refer to species that may have these effects as *foundation species* (Schob et al. 2012, Bulleri et al. 2016). In alpine aquatic environments, terrestrial subsidies of DOM can protect phyto- and zooplankton from harmful UV radiation and help offset nutrient limitations related to high flushing rates (Williamson et al. 2010, Kissman et al. 2013). These effects can be viewed as an additional modulation of climate exposure, at a smaller scale than the geographic terrain effects in H1, but potentially shifting resource or abiotic limitations similarly and affecting heterogeneity across areas that differ in the degree to which these effects occur. As in H1, climate modifications via biotic effects can result in positive as well as negative responses (although facilitation is often evoked; Pugnaire and Luque 2001, Kikvidze et al. 2011).

While the emphasis on biotic effects has largely revolved around mitigating adverse or stressful conditions, we know much less about these effects modify fine-scale variability (Bulleri et al. 2016). A cornerstone of niche theory is that heterogeneity in environmental conditions (e.g., the creation of microhabitats) promotes coexistence on larger scales (e.g. across microhabitats; Chesson 2000). Foundation species can be one factor that enhances environmental heterogeneity (Callaway 2007, Schob et al. 2012). However, biotic effects also can reduce heterogeneity, ameliorating environmental differences among micro-habitats (Bulleri et al. 2016). We expect the biotic effects in terrestrial habitats to increase heterogeneity and beta-diversity, while effects in lakes will reduce heterogeneity and beta-diversity across depths within a lake. The difference in expectation is that one mechanism (DOM subsidies) will increase environmental similarity across depth zones within a lake; the other (*foundation species*) will increase dissimilarity across patches. We also note that the biota that cause these effects also respond to climate, for instance by changing in abundance, resulting in cascading effects (Thomsen et al. 2010).

Based on this rationale, we hypothesize (**H2: Biophysical effects of biota can modify exposure to climate change, and heterogeneity in these effects will influence population persistence and coexistence dynamics**). We detail evidence related to these effects in terrestrial systems (*foundation species*) and aquatic systems (DOM subsidies) in the sections below.

**3.2.2 Evidence for H2.** *A. Structural effects of biota in terrestrial areas.* Just as topography and complex terrain modulate the effects of climate, the physical structure of a plant can strongly influence abiotic and resource limitations. Cushion plants comprise an important group of foundation species in alpine tundra (Elliott 2012, Pauli et al. 2012), whose compact surface structure can change surrounding microenvironments, regulate maximum and minimum temperature, improve soil humidity and nutrient availability, and reduce wind scour of snow and soil (le Roux and McGeoch 2010, Roy et al. 2013, Cavieres et al. 2014, Ballantyne and Pickering 2015). Similarly, tree islands at treeline act as a wind break with the leeward side accumulating snow (Seastedt and Adams 2001); spatially aggregated patterns of seedling establishment indicate positive effects on recruitment via snow retention (Humphries et al. 2008). Studies of tree seedling establishment above the tree limit at NWT suggest that shrubs may facilitate tree establishment (Daly and Shankman 1985), likely due to their effects on snow retention and temperature moderation (Sturm et al. 2005). In addition to biophysical effects, our work suggests that changes in plant species composition and abundance are often accompanied by changed microbial interactions, including root endophytes facilitating the colonization of tundra plants in the talus (King et al. 2012) and shrub

facilitation of ectomycorrhizal conifer establishment above the present treeline (Reithmeier and Kernaghan 2013).

*B. Terrestrial DOM subsidies in lakes.* Expansion of alpine vegetation into the unvegetated talus (e.g., Fig. 8; King et al. 2012) will increase terrestrially-derived DOM inputs into alpine lakes, helping to attenuate UV stress and promote ecosystem productivity (Williamson et al. 1996, Kissman et al. 2013, Rose et al. 2015). UVB radiation creates an extreme vertical stress gradient in the water column that affects both primary producers and consumers (Williamson et al. 1996, Cooke et al. 2006, Sommaruga and Augustin 2006, Kessler et al. 2008). The depth to which UVB penetrates is controlled, in part, by the concentration of chromophoric DOM (CDOM) (Williamson et al. 1996). When DOC concentrations are low (<2mg/L), as is common in alpine lakes, even small fluctuations in DOC can exert strong effects on plankton (Williamson et al. 1999, Williamson et al. 2010). As the initial snowmelt pulse of CDOM is flushed from these alpine lakes, autochthonous production of CDOM by phytoplankton becomes important and causes a shift in DOM quality (Hood et al. 2005). This CDOM from microbial phototrophs is paler (e.g. less chromophoric) than plant/soil-derived CDOM (Hood et al. 2005, Miller and McKnight 2010; Fig. 15).

In contrast, much of the DOM in montane and subalpine lakes derives from terrestrial sources. These patterns have important implications for light penetration generally and UV stress specifically in both phyto- and zooplankton communities. For instance, we estimate that the median UVB attenuation depth ( $Z_{\text{a320}}$ ) in GL4 was 3.7 m (2.7 to 21.6 m 95% CI). In contrast, median  $Z_{\text{a320}}$  in the subalpine Lake Albion was both shallower and less variable (1.5 m median, 0.7 to 2.9 m 95% CI). Correspondingly, among 13 lakes sampled in Rocky Mountain National Park during the 2015 ice-free season, DOC concentrations decreased significantly with lake elevation.

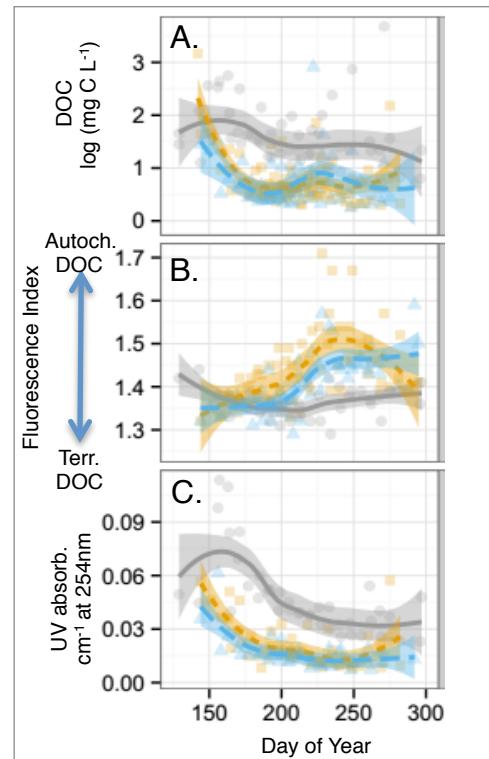
Alongside their UV-protecting influence, DOM inputs can also increase water temperature, alter PAR, and provide subsidies that promote the growth of phytoplankton or zooplankton. For example, nutrients (N and P) associated with DOM can promote autotrophic production (Granéli et al. 1999, Klug 2002) and can enhance zooplankton growth indirectly by stimulating the microbial loop (Berggren et al. 2010). While predicting the net effect of these mechanisms can be challenging (e.g., Kissman et al. 2013), both pathways are likely to increase zooplankton abundance, enhance grazing pressure, and shift phytoplankton community composition.

### 3.2.3 Predictions related to H2.

Based on theory and evidence from our past work (above), we predict:

*A. Biotic influence of snow accumulation in terrestrial areas.* In both tundra and upper-elevation forests, the presence of individuals that provide physical shelter from wind, causing accumulation of snow and organic matter (e.g., cushion plants, shrubs, trees), will attenuate climate exposure. As a result, we predict that the fine-scale effects will increase diversity (via environmental heterogeneity) across microhabitats and increase population persistence as climate changes (via microrefugia).

*B. Biotic influence of terrestrial DOM in lakes.* Lakes at high elevation rely more on autochthonous (lake-derived) organic carbon than lakes at lower elevation, which receive greater terrestrially-derived subsidies of organic carbon. Changes in land cover due to uphill tree, shrub, and tundra advances will increase



**Figure 15.** Seasonal variation in DOC (A), Fluorescence Index (B), and UV absorbance (C) in subalpine (Albion in gray) and alpine (GL4 in orange and GL5 in blue) lakes. High elevation lakes experience a short window early in the season when terrestrial DOM subsidies raise DOC levels to those in the subalpine; as the season progresses DOC concentrations decline as subsidies are replaced by autochthonous DOC.

terrestrial subsidies of DOM into alpine lakes, helping to attenuate UV stress and relax constraints on UVB-sensitive phyto- and zooplankton. Terrestrial DOM can also provide subsidies of biolabile carbon and nutrients that promote both primary and secondary production. These shifts will increase the importance of trophic interactions, possibly shifting the phytoplankton community composition toward species that are more resistant to grazing.

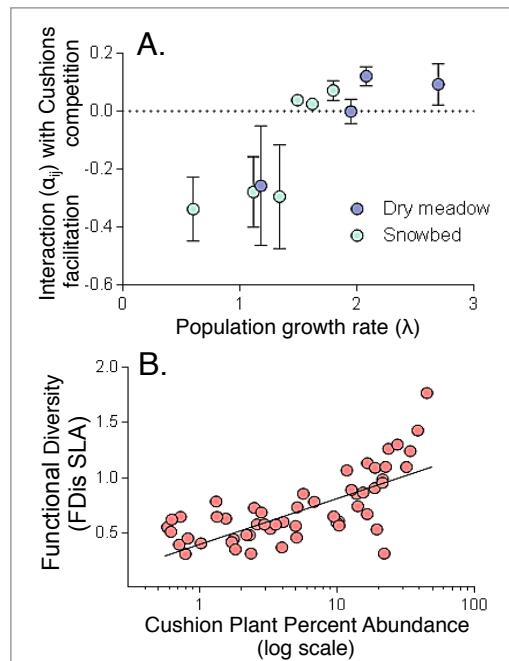
**3.2.4 Experiments and observations to test H2.** *A. Long-term observations to describe positive and negative associations.* Our long-term observations are ideal for identifying positive and negative associations among species, as well as for identifying how associations vary across environmental gradients. We note that while observational approaches do not definitively assess the relative importance of interactions, they can help confirm patterns in species groups that we expect to have large biotic influences (e.g., cushion plants, trees at treeline) and assess patterns more broadly for a wide range of taxa and habitat characteristics; we then propose more targeted manipulative approaches to assess subsets of these interactions in detail (below).

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. For instance, we can analyze population change (as annual cover changes) in our long-term vegetation dataset at the Saddle site (Farrer et al. 2014; Fig. 16) by modifying a simple population model (Watkinson 1980, Rees and Westoby 1997, Harpole and Suding 2007, Levine and HilleRisLambers 2009, Yenni et al. 2011) such that:

$$N_{i,t+1} = \frac{(\lambda_i + \beta_i GSL_{t+1})N_{i,t}}{1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t}}$$

where  $N_i$  is the cover of species  $i$  and is a function of  $\lambda_i$ , the intrinsic rate of increase of species  $i$ , divided by the summed intra ( $\alpha_{ii}$ ) and neighbor ( $\alpha_{ij}$ ) interaction terms, where a negative  $\alpha_{ij}$  indicates facilitation. Because growing season length may differentially affect species' carrying capacities and growth rates, we include  $\beta_i$  to modify  $\lambda_i$  based on snowmelt date in a given year (standardized around 0); this term could reflect other variables related to climate exposure across landscape (discussed in H1) and more fine-scale data collection will allow us to modify interaction terms by terms related to biotic effects on snowpack and growing season. The structure of this model is flexible, allowing us to investigate temporal lags, other important climate drivers, and many types of biotic effects. We can also use this approach to project population changes to simulations of future environmental changes (as in Farrer et al. 2014).

Interaction strengths inferred from long-term abundance and cover data support the expectation that foundation species affect population growth rates of associated species and enhance diversity. For example, when we examine how other tundra species interact with cushion plants (where  $\alpha_{ij}$  describes the interaction of a focal species with cushion plants) across temporal and spatial variability in snowpack, we find evidence of positive effects of cushion plants, particularly for less dominant species that tend to have lower population growth rates when alone (Fig. 16A). These effects occur in both dry wind-blown sites and



**Figure 16.** Population models based on long-term abundance data can help identify positive and negative interactions. **A)** Cushion plants facilitate plant species in dry meadow and snowbeds (negative interaction coefficients, std errors: spatial uncertainty). **B)** Facilitation is consistent with the pattern of increased functional diversity (shown: dispersion of specific leaf area) with cushion abundance.

snowbed sites; fine-scale environmental measures and linkages with the NBM will allow us to better understand effects in these two very different habitats. At the community level, these interactions result in greater taxonomic and functional diversity associated with cushion plant abundance (Fig. 16B).

These models require a long time-series of repeated measurements, preferably across a range of environmental conditions, and can also be applied to experimental manipulations of climate (Farrer et al. 2014). We plan to fit similar models to the GL4 dataset to assess phytoplankton dynamics. The Saddle and GL4 data sets are both now long enough to enable the analyses we propose; six more years of data will enable better use of our modeling frameworks and allow us to document effects on time scales longer than one year. For data sets that lack a long temporal component, we will make more targeted campaigns to identify spatial associations among taxa. For instance, we intend to build on the long-term record of GL4 by increasing comparative sampling among lakes over elevation gradients (both in Green Lakes Valley and watersheds in Rocky Mountain National Park), and implementing a broader taxonomic (e.g., zooplankton) and temporal (e.g., winter samples from GL4) sampling program.

*B. Adding biotic manipulations to the terrestrial growing season length experiment (in 3.1).* In combination with the extended summer manipulations (described in section 3.1.4, above), we propose to manipulate biotic interactions by focusing on how physical protection from wind can affect biotic interactions. In factorial combinations with the black sand treatment, we will plant foundational species as well as construct artificial structures that simulate the presence of the individual. Thus, the experimental design will be a 2 x 2 manipulation with black sand and biotic manipulations performed across 6 habitat types (6 replicates per treatment in each habitat) with 24 total replicates per treatment and 144 plots (Fig. 14).

In the biotic manipulation treatment, we will establish subplots to investigate how the presence of foundation species may modulate climate effects: in tundra and unvegetated talus areas, we will transplant cushion plants into treatment plots as well as construct barriers that approximate the height and diameter of an established cushion plant (5-10 cm tall, 15 cm wide). In treeline and forested sites, we will construct barriers that approximate the height and diameter of an established small tree (20 cm tall, 30 cm wide). The barriers and transplants will be located in subplots within the larger experimental plots; we will add seed to circumvent dispersal limitation both in areas of the biotic manipulation and control subplots in this treatment. To simulate the physical effects of a plant, we will construct structures following Rachal et al. (2015), using galvanized hardware cloth attached to steel rods to form a cross.

We expect that, if foundation species increase heterogeneity in climate exposure, we will observe increased snow, later melt, and enhanced soil moisture associated with individuals that provide physical shelter from wind (e.g., cushion plants, shrubs, trees). These effects will be particularly strong in windblown areas such as treeline, dry meadow and talus. In these areas, we expect that the fine-scale effects will increase diversity (via environmental heterogeneity) across micro-habitats and increase population persistence (via microrefugia) as climate changes.

*C. Adding terrestrial DOM subsidy manipulations to the water residence time experiment (in 3.1).* Changes in land cover due to uphill tree, shrub, and tundra advances are expected to increase terrestrial DOM subsidies in lakes. We will mimic this phenomenon within the limnocorral experiment described previously by adding highly concentrated DOM from GL1 (accessible by vehicle) obtained using a preparative scale reverse osmosis unit and transported in carboys to the corrals. The DOM-enhanced treatment concentrations will be targeted to approximately 2 mg/L, thereby reducing UVB attenuation depths from ~ 9 m to ~1 m, which is within the estimated range of seasonal variation in GL4. The concentrate will be replenished weekly to maintain the elevated concentration. Thus, the experimental design will be a 2 x 2 x 2 manipulation with flushing (ambient vs. 25% elevated) and terrestrial DOM enhancement (ambient vs. 2 mg/L) performed in two lakes that differ in elevation (3 replicates per treatment in each lake) for a total of 24 limnocorrals (Fig. 14). Response variables in this experiment will be measured at 0.5 and 1.5 m depth in the limnocorrals (after Table 1). Additionally, we will measure DOC concentrations, UV absorbance at 254 nm (SUVA), 320 nm (UVB), and 380 nm (UVA), and the fluorescence index (FI) (Hood et al. 2003).

We expect that, if added terrestrial DOM ameliorates UV levels, we will observe an overall increase in phytoplankton and zooplankton biomass with a shift toward less UV-tolerant taxa, particularly in the shallow (0.5 m) water samples relative to 2 m (e.g., Leech and Williamson 2001, Kessler et al. 2008). Based on empirical observations from GL4, we also expect reduced UVB stress to lead to increases in chlorophyll a and a shallower chlorophyll a maximum. These effects should be most apparent at ambient flushing rates and in the manipulation performed in GL4 (i.e., a lake-by-treatment interaction), with fewer effects of added DOM in Lake Albion (which already has high DOC concentrations from surrounding vegetation). Alternatively, if DOM primarily acts as a nutrient or biolabile subsidy (Graneli et al. 1999, Klug 2002), we expect general increases in both phytoplankton and zooplankton without any depth-specific differences or consistent shifts in species composition toward lower UV tolerance.

We also expect to observe a shift from allochthonous DOM to algal-derived DOM within the low-flushing condition in GL4, similar to field observations (Fig. 15). Such a shift toward more labile DOM will potentially amplify trophic forcing. We will assess the degree of top-down regulation of phytoplankton and chlorophyll a by zooplankton based on the time-lagged correlations between standing biomass in adjacent trophic levels (Frank et al. 2007, Bunnell et al. 2014).

**Table 1.** Long-term observations as part of NWT's signature datasets that will be used to test predictions in H1-H3, including new measurements in LTER VII as well as corresponding measures (+Exp) in experiments (see 3.1 and 3.2). RMNP = Rocky Mountain National Park. SUVA = 254 nm specific UV absorbance

Dataset	Response (+Exp?)	Measurement Details
<b>A. Tundra vegetation</b>	Aboveground biomass, plant species composition. + <u>Exp</u>	88 1m <sup>2</sup> plots, spaced at 50m intervals, pt quadrat species cover. 2 adjacent 0.1m <sup>2</sup> plots harvested for aboveground biomass. Established 1989, continue annually (n=88) (Spasojevic et al. 2013). <i>New in LTER VII:</i> Trait measures related to water use, C and N metabolism, including delta-13C, SLA, C:N (Baptist and Choler 2008, Spasojevic and Suding 2012).
<b>B. Experimental resource manipulations</b>	Aboveground biomass, plant species composition.	3 experiments, all established prior to 2004, continue annually across dry meadow and moist meadow communities (Bowman et al. 2014, Farrer et al. 2015, Gasarch and Seastedt 2015a)
<b>C. Pika population</b>	Population persistence, survival.	Representative population sampling (since 2004)(n=6-30 indiv/yr), historical 1980s full population sampling (Erb et al. 2014, Wilkening et al. 2015). <i>New in LTER VII:</i> (a) add comparative lower-elevation site in GLV, (b) snow depth monitoring in West Knoll and GLV sites.
<b>D. Tundra plant population</b>	Population vital rates. + <u>Exp</u>	4 populations/spp, stems(ramets) + new recruits tagged (n= 24 populations, ~200/pop). <i>Silene</i> and <i>Bistorta</i> since 2007 (Doak and Morris 2010). <i>New in LTER VII:</i> <i>Carex</i> , <i>Deschampsia</i> , <i>Geum</i> , <i>Kobresia</i> populations.
<b>E. Tree stand and population</b>	Survival, stand and understory production, seedling recruitment, stand production, + <u>Exp</u> , for <i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	8 stands (>200 years old), xeric to mesic (n=8 stands, ~400 trees >4cm DBH/stand). Mapped and monitored 7 times in the last 34 years (Smith et al. 2015), continue every 3 years. <i>New in LTER VII:</i> (a)Add 4 stands at upper treeline, (b) include 24 seed traps (0.24 m <sup>2</sup> ) and annual tree seedling surveys (6.8 m <sup>2</sup> ) in each stand, (c) understory production harvests (as in A) and stand production estimates using allometry, (d) measures of tree ring delta 13C (moisture stress)(Bradford et al. 2008).
<b>F. Lake production and composition</b>	Production (chl-a), composition (phytoplankton, <i>Daphnia</i> ), Depth-specific light, SUVA. + <u>Exp</u>	Weekly for 6 weeks following ice out, 3 depths at lake center (Miller and McKnight 2012). GL4 since 2000, continue annually. <i>New in LTER VII:</i> Extension to collect winter samples through the ice from GL4, consistently sample GL1 and Albion (every other week), measurements of depth-specific UV attenuation, permanent thermistor chain in GL4, and extend basic sampling to 15 RMNP lakes every 3 yrs (two sampling dates/yr, n=90).
<b>G. Flux towers</b>	Ecosystem CO <sub>2</sub> , water vapor, energy.	Alpine eddy covariance flux towers started in 2007 (Knowles et al. 2012, Knowles et al. 2014). CI towers part of AmeriFlux (Burns et al. 2014).
<b>H. Soil nutrient and microbial processes</b>	Microbial biomass, N pools, lysimeter water chem, enzyme activity + <u>Exp</u>	<i>New in LTER VII:</i> Select tundra and forest plots, three times annually. Methods after Fisk et al. 1998, King et al. 2008, Hinckley et al. 2014a. Nested sets of lysimeters (at each habitat type, multiple depths) to measure soil water fluxes and chemistry.

**Table 2.** Long-term observations as part of NWT's signature data sets that integrate climate drivers with ecological response. We partner with other programs to obtain measures such as CO<sub>2</sub>, ozone, and atmospheric deposition.

Dataset	Locations	Measurement Details
A. Climate	C1 and D1 (1952-) Saddle, GL4, Albion (1982-)	Climate measures are taken on chart recorders (as in the 1950s) and with data loggers (Kittel et al. 2016).
B. Snow	Saddle grid (88 plots), GLV snow survey (1992-)	Saddle grid plots (bi-weekly), intensive snow survey in GLV at peak SWE (Jepsen et al. 2012). +Exp
C. Soil	Saddle, C1 sites (2000-)	Soil temperatures, soil volumetric moisture (hourly). +Exp
D. Stream, lake, snow chemistry	Various sites within the GLV (1982-)	Major cations and anions (including nitrate, Si, SRP), pH, conductance, dissolved organic nutrients (DOC, DON, DOP), and isotopes <sup>180</sup> O, <sup>2</sup> H (Williams et al. 2006).
E. Streamflow	Sites within the GLV (1981-)	Hourly/daily streamflow discharge records (Knowles et al 2015b).
F. Lake ice-off	Sites within the GLV (1981-)	Date at which each lake in the GLV becomes ice-free (Caine 2002)

**3.2.5 Context of H2 within LTER VII.** In H2, we will focus on ecological responsiveness to climate variation by adding manipulations and observations of biotic effects. Because biotic interactions can vary widely across taxa and systems, we take a two-pronged approach in evaluating how such interactions may influence ecological responsiveness. First, we capitalize on long-term data to model interaction coefficients. Second, we experimentally test two specific mechanisms which have been hypothesized modulate climate effects: structural effects that affect the redistribution of snow by wind in tundra and treeline environments, and terrestrial DOM subsidies in lake environments. Responses to these experimental manipulations can be linked to observational patterns via our modeling techniques.

### 3.3 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?

**3.3.1 Ecological theory and rationale.** Ecologists have long debated whether ecological trade-offs at one level of organization can lead to stability at others (Elton 1958, May 1972, McNaughton 1977). One key area of debate is whether compensatory responses of components of a community (e.g., species in species-rich communities) can cause stability in functional response (e.g., biomass) at the ecosystem level (McNaughton 1977, Tilman 1996, Ives et al. 1999, Cottingham et al. 2001, Gross et al 2014), often known as portfolio effects. More recently, these ideas have been developed at the population level, where opposing vital rate trends across population segments or environments, a phenomenon also called demographic compensation, may buffer a population to climate change (Schindler et al. 2010, Schindlet et al. 2015, Villegas et al. 2015). Variation in environmental conditions and responses among communities may stabilize ecosystem processes across the landscape (Wang and Loreau 2014).

A key challenge in understanding the consequences of climate change is to determine when compensatory dynamics stabilize populations and ecosystem properties despite climate fluctuations, and when fluctuations result in sharp transitions in population viability or ecosystem function. Ecological responses to shifts in abiotic and resource limitation depends in the short-term on plasticity and local adaptation at the population level and shifts in species abundances and diversity at the community level; in the long term these effects are also mediated by local extinction, migration, and evolutionary responses to selection (Hector et al. 2010, Zhu et al. 2012, Roth et al. 2014, Gomez et al. 2015). H3 addresses the degree to which individual fitness, population growth rates, ecosystem function and landscape-scale processes are buffered against climate variation and the limits to this buffering as climate change surpasses the ability of the resident biota to respond.

While there have been substantial efforts to understand compensatory dynamics, dynamics have been studied at one level of organization. Ecologists still lack a clear framework to integrate across organizational scales and degrees of environmental change. First, questions remain about when and why the ability to buffer will break down. Specifically, will currently observed asynchronous responses to climate persist under novel climate conditions, such as climate-driven shifts in resource limitation or increased frequency of climate extremes? Second, questions remain about the relative importance of buffering at each scale, and how much higher-level buffering results can be predicted by lower level buffering (e.g., at the individual, genotype or population levels). Especially because exposure to climate change effects may vary across the landscape (H1), it is possible that a loss of asynchrony at one scale may be balanced by greater asynchrony at another scale. For example, preliminary results suggest that extended summer forces synchrony in biomass production response within a habitat type, but at the landscape scale this may be balanced by greater asynchrony in response between habitat types (e.g., higher biomass in the snowbed and lower biomass in the dry meadow; Fig. 7A).

Based on this rationale, we hypothesize (**H3**): **Asynchronous responses to climate within one level of organization will combine to reduce variability at a higher, aggregated, level. Climate change will increase synchronicity through shared tolerance and growth constraints.**

**3.3.2 Evidence for H3.** A range of organisms at NWT exhibit demographic compensation under the moderate climate variation we are currently observing. For example, opposing vital rate trends across climate variation may allow alpine and subalpine species to have stable population growth rates despite climate change (Villellas et al. 2015). Doak and Morris (2010) found that trade-offs related to growth and survival rates buffer negative effects of a warming climate for *Silene acaulis* and *Bistorta vivipara*. Both species showed lower survival and recruitment but higher growth of individual plants, possibly owing to longer, warmer growing seasons. Because most demographic rates that improved in moderately warmer years declined in the warmest years, model projections indicate that more extreme climate variation may disrupt this trade-off and lead to population declines (Doak and Morris 2010). Similar dynamics have been observed in the subalpine forest, where rapid initial growth is correlated with reduced longevity for both subalpine fir and Engelmann spruce (Bigler and Veblen 2009). The two species differ in how these demographic parameters influence population growth: subalpine fir has high fecundity but low longevity; Engelmann spruce has low fecundity but high longevity (Veblen 1986). Pika populations also appear to have trade-offs between survival and recruitment, where extended summers are depressing survival while boosting recruitment (Jeffress et al. 2013, Erb et al. 2014); as dispersal becomes more limited by summer warming, we expect climate change to depress both survival and recruitment and lead to reduced population growth rates.

The degree to which species have differing responses to climate appears to vary considerably among communities at NWT. Strong asynchronies to climate variation characterize phytoplankton taxa in GL4 (Flanagan et al. 2009); these differential responses result in greater than expected stability in total community biovolume (Fig. 17). The fast turnover rates of phytoplankton may enable taxa to quickly respond to environmental conditions; and, in tandem, allow us to detect alternative responses via time series that encompass many generations (Rusak et al. 1999). For alpine plants, species asynchrony appears to be weaker than demographic trade-offs where the major compositional trade-off due to climate variation for tundra plants is between non-vascular plants (moss, lichen) and vascular plants (Fig. 17). Synchronous responses among most alpine species may also be indicative of temporal lags in climate responses and their intrinsic sensitivity: these are slow-growing perennial species, and much of the growth in one year is from carbon stored in previous years (Mooney and Billings 1960, Meloche and Diggle 2003, Farrer et al. 2015). A longer compositional record in LTER VII will enable us to further explore these longer temporal signatures of climate variation. Similar analyses are underway in the subalpine forest, where spatio-temporal synchrony/asynchrony in establishment, propagule production, and mortality can be evaluated in the existing permanent plots and newly installed large permanent plots.

Climate may also change another type of asynchrony, between species in a mutualistic relationship (e.g., plant-pollinator), via effects on phenology (Iler et al. 2013, Forrest 2015). While this framework could be expanded to include such interactions, we first start with investigations within one trophic level.

### 3.3.3 Predictions related to H3.

Based on theoretical expectations and our prior work, we predict:

*A. Buffering via portfolio effects.* Differential responses at the population level (e.g., in demography between growth and survival vital rates or size classes, and among genotypes) and the community level (e.g., in composition between abundances of different species, functional groups) will increase the stability of aggregate functions (e.g., population growth rate, mean fitness, community biomass) to climate variation.

*B. Loss of buffering.* Climate change will erode these differential responses, causing a transition from compensation-related stability to synchronous responses. Forced synchrony will be strongest in areas exposed to a shift in resource limitation (after H1). In contrast, we expect asynchrony across landscape locations to stabilize landscape or catchment-level response.

### 3.3.4 Observational, experimental and model integration to test H3.

This hypothesis will integrate long-term observations and new data collections described in H1 and H2 (sections 3.1 and 3.2). We will use two simple approaches to provide a framework for analysis of these ideas in the context of climate change. First is the **General Decomposition of Variance**. This well-known result of a Taylor expansion (and often referred to as the Delta method) shows that the variance of a function,  $f$ , which depends on multiple underlying random variables  $x_i$ ,  $x_j$ , etc., can be approximated as:

$$var(f) = \sum_i \left( \frac{\partial f}{\partial x_i} \right)^2 var(x_i) + \sum_i \sum_{j \neq i} \left( \frac{\partial f}{\partial x_i} \right) \left( \frac{\partial f}{\partial x_j} \right) SD(x_i)SD(x_j)corr(x_i x_j)$$

Here,  $var(x)$  and  $SD(x)$  represent the variance and standard deviation of a variable or function, while  $corr(x_i, x_j)$  is the correlation of two variables. This approximation emphasizes that negative correlations between the factors that underlie some aggregate function can reduce variance in that function, while positive correlations exaggerate variability. This relationship also provides a framework to conduct nested variance decomposition for multiple ecological levels. For example, variance in the growth rate of a population can be estimated from the variance and covariance of stage specific demographic rates (Tuljapurkar and Orzack 1980) while variance in the total biomass of a community can be estimated from the variances and covariances in the growth rates of each species present in that community. Linking across levels then allows an estimation of how much variation at higher levels results from each of the multiple lower levels of organization. By decomposing variance at each organizational level for our control versus black sand plots over time, for example, we will be able to differentiate whether the temporal scale at which buffering occurs shifts under extended summer conditions. Similarly, using variance decomposition within and among lake treatments in the limnocorral experiment and by depth will enable us to better understand whether variance among phytoplankton taxa contribute to variance in biovolume.

Importantly, variance decompositions also provide a way to define buffering. In the equation above, the least buffering will occur when the underlying variables ( $x_i$ ,  $x_j$ , etc.) are strongly positively correlated; in other words, when the underlying variables respond in synchrony to environmental drivers. In contrast, buffering is manifested when we see weak positive and especially negative correlations between the underlying variables; that is, when the underlying variables are asynchronous. Following an operational definition of portfolio effects, buffering can therefore be quantified as the difference between observed SD of an aggregate property (e.g., a population or community biomass) and its predicted value from the empirical relationship between  $\log(var)$  and  $\log(\text{mean values})$  for the component entities (e.g., individuals or species) contributing to the aggregate (Anderson et al. 2013). We employ this approach because it is conservative, empirical, and can be rescaled to the non-logged standard deviation scale, which allows intuitive understanding of the magnitude of buffering effects (Fig. 17). In addition to this approach, we will also use randomization methods to quantify the effects of particular species, patches or vital rates in promoting stability in the face of environmental variation (Villellas et al. 2015).

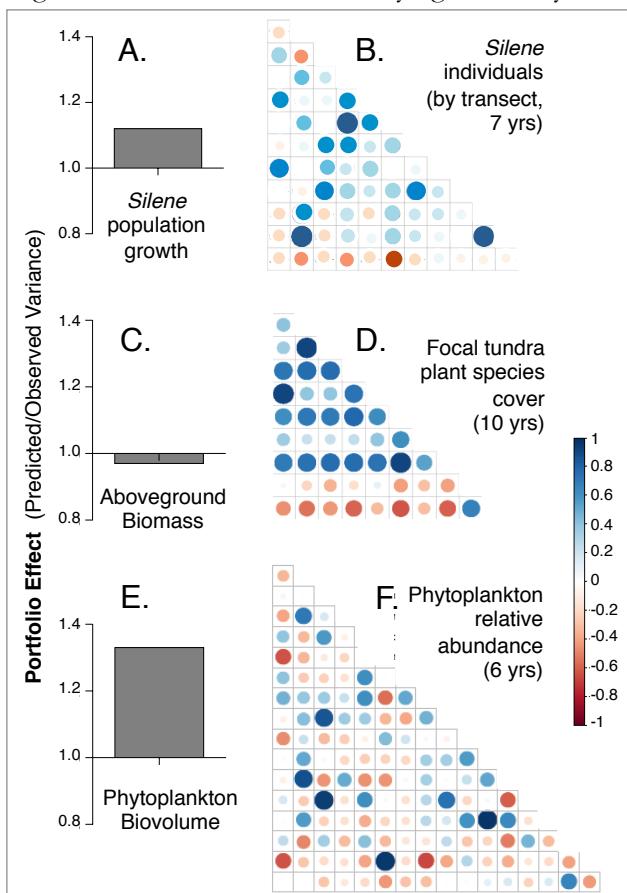
A second key result of the same Taylor expansion approach is a **Mechanistic Variance Model**, which can be used to estimate the buffering that will occur when each of multiple underlying processes are themselves functions of one or more climate drivers. Using the same nomenclature as above, but assuming variance and covariance of  $x_i$ ,  $x_j$  depend only on growing season length ( $GSL$  or, for lakes, water residence time), we can rewrite the variance of  $f$  as:

$$var(f) = \sum_i \left( \frac{\partial f}{\partial x_i} \frac{\partial x_i}{\partial GSL} \right)^2 var(GSL) + \sum_i \sum_{j \neq i} \left( \frac{\partial f}{\partial x_i} \frac{\partial x_i}{\partial GSL} \right) \left( \frac{\partial f}{\partial x_j} \frac{\partial x_j}{\partial GSL} \right) var(GSL)$$

Note this decomposition can be expanded to include multiple other underlying variables that will determine the performance of different populations, species or functions. This approach to the analysis of compensation is key to our proposed work because we do not expect that covariances or variances will stay the same in the face of shifting mean climate. Using data on how different underlying rates vary with mean climate, evaluation of the derivatives in the above equation for different average  $GSL$  values will allow us to estimate how buffering at different scales will change with shifting climate.

We will focus on key species and processes to fill in the larger picture of when and why buffering will occur and when it will fail. We will continue long-term monitoring of species abundance and production across tundra, subalpine and lake habitats (Table 1), coupled with fine-scale environmental monitoring and analysis of demographic responsiveness of tundra and tree focal species.

The extended summer experiments will allow us to track compensation across replicate locations (plots, limnocorals) in space to determine synchrony simultaneously across populations, communities and ecosystems. We predict differential responsiveness to climate variation to be strongest at the demographic level, and that trade-offs at one level of organization will be reflected at larger scales of ecological organization. In addition to responses to natural variation in climate over the course of our long-term measures, the extended summer experiments described in sections 3.1 (H1) and 3.2 (H2) can be used to describe limits to buffering capacities with continued climate change. For example, pairwise synchrony calculations between control and black sand plots early in the experiment will indicate if buffering is rapidly lost in areas that experience a shift in resource limitation. We will continue our black sand manipulations for the LTER VII's 6-yr duration. As a result, pairwise comparisons of control and black sand plots over the course of the experiment will enable us to identify whether frequent extremes result in a pronounced increase in synchrony within populations and communities.



**Figure 17.** Portfolio effects occur when temporal variance at one level (population growth in A, biomass in C, E) is buffered by asynchrony in its components. Right panels (B,D,F) are correlation matrices (with each row individuals in B, species in D, F), colors indicate direction and strength of correlations (ranging from  $r=1$  to  $r=-1$ , blue indicates positive correlation). Portfolio effects are calculated by comparing observed variance in an aggregate measure (population growth in A, biomass in C, E) with predicted variance based on mean-variance relationships among its components (B,D, F). For example, in A, we find less variance than expected in population-wide growth rates of *Silene*, indicating that asynchronies in individual growth stabilizes overall population growth rate.

**3.3.5 Context of H3 within LTER VII.** Understanding compensatory dynamics in H3 is essential to the integration of our first two hypotheses (H1, H2) with our fourth hypothesis at the catchment level (H4). We expect differences in local limiting factors (H1) will predict buffering resulting from community differences in response to climate. If different communities have different limiting factors, we expect them to be less strongly correlated in responses than communities with the same limiting factors. These dynamics will also relate to changes in biotic interactions (H2), as species interactions are a second mechanism that leads to negative or positive correlations and synchronous (or asynchronous) responses (Loreau and de Mazancourt 2008).

We acknowledge that the most basic version of this framework for integrating and analyzing buffering effects across levels of ecological organization is simplified. In particular, a phenomenological analysis of synchrony, as outlined above, does not explicitly acknowledge the role of species interactions (e.g., competition, facilitation, herbivory). However, these effects can be included in this framework by combining with estimation of interaction coefficients (in H2), similar to our treatment of causal factors such as climate in H1. We will also undertake the construction of stochastic demographic (integral projection) models for our focal species, as well as models for community dynamics. These more complex modeling frameworks, which can accommodate more realistic and complex interactions and nonlinear causality, are a key intermediate step in an analysis of buffering, and can be analyzed for buffering effects in parallel with simpler statistical breakdowns. Perhaps the most important complication for long-term predictions is that the dominance and identity of species in any one area or community will shift with directional trends in climate, in ways that will likely alter buffering. Specifically, predictions related to climate effects in H3 relate to longer-term continued change as the ecological processes in H1 and H2 break down. Estimation of these processes will require long-term measures within our experimental framework, which we hope to obtain as we move into LTER VII.

### **3.4 CATCHMENT INTEGRATION: How do asynchronous responses across a landscape affect catchment-scale processes?**

**3.4.1 Ecological theory and rationale.** Variability in hydrologic fluxes (e.g., snowmelt) provides a strong spatial and temporal context for much of our fine-scale focus of H1-H3 (Jepsen et al. 2012, Barnes et al. 2014, Perrot et al. 2014). Flow paths, water sources, and residence times will dictate connectivity between high and low elevation ecosystems (e.g. alpine to montane) as well as between terrestrial and aquatic ecosystems (e.g. hillslopes to streams and lakes) (Williams et al. 2011, Mladenov et al. 2012). For instance, flow paths are highly variable and dependent on snowmelt dynamics, where some catchment areas may never contribute to streamflow and other areas may contribute in some years and not in others (Lohse et al. 2009, Nippgen et al. 2015, Williams et al. 2015a). Changes in climate-driven connectivity will affect how streams and lakes respond to terrestrial ecological responses, via such influences as transpiration, nutrient uptake and microbial transformations (Darrouzet-Nardi et al. 2012, Barnes et al. 2014, Hinckley et al. 2014a).

Because the importance of different areas in space can vary over time, spatially explicit approaches are necessary to integrate processes and temporal dynamics in response to climate conditions at the catchment scale (Peters et al. 2007, Molotch et al. 2008, Currie 2011). For instance, it is unclear how the integration of ecological responsiveness within a catchment (e.g., H1-H3) influences responsiveness at the catchment scale (Currie 2011, Emanuel et al. 2011, Nippgen et al. 2015). While asynchronous responses at different locations within a catchment might enhance buffering, shifts in hydrological connectivity (where some areas of the catchment may contribute in some years but not in others) may influence the spatial aggregation of varied responses and are not well-described using space-averaged conditions (McClain et al. 2003, Williams et al. 2009, Darrouzet-Nardi and Bowman 2011). Thus, we expect certain climatic conditions will change the extent to which asynchrony across landscape position influence processes such as water flow and nutrient retention. Such alternative responses may also decouple fluxes of water and nutrients from other processes such as NEE and primary production. With continued climate change,

longer-term changes in vegetation cover will influence water quality and quantity (Brown et al. 2005, Knowles et al. 2015b), depending on the spatial patterns of vegetation change within the catchment.

Based on this rationale, we hypothesize (**H4**): **Climate-related changes in hydrological connectivity, by altering areas of the landscape that contribute to water and nutrient flux, will influence the degree to which landscape compensation stabilizes catchment response.** Below, we focus on how changes in hydrological connectivity interact with heterogeneity in ecological responses, as well as how longer-term feedbacks in land cover change may affect this interaction.

**3.4.2 Evidence for H4.** For over two decades, NWT has used nutrient, chemical and isotopic analyses of stream, talus groundwater, and snow samples and hourly streamflow records at numerous sites along the hydrological axis of the Green Lakes Valley (Table 2) to understand mass fluxes of nutrients (Ley et al. 2004, Williams et al. 2007, Molotch et al. 2008, Williams et al. 2009, Mladenov et al. 2012) and their influence on organic matter and phytoplankton in the Green Lakes (Flanagan et al. 2009, Miller and McKnight 2012). Spatio-temporal patterns in snowmelt largely dictate stream nitrate concentrations, with early-onset snowmelt areas controlling the flushing of ions and nutrients from the snowpack and soils (Perrot et al. 2014). Endmember mixing analysis of hydrochemical and O<sup>18</sup> observations indicate source waters also shift throughout the growing season and across years.

Snowpack accumulation and snowmelt timing, in addition to being strong controls on discharge and nutrient export, are also strong controls on the annual carbon budget within a catchment (Fig. 18). Measurements of NEE using a pair of eddy covariance towers located near the Saddle suggests that the winter plays a dominant role in the annual carbon balance, with more carbon being released by winter respiration than absorbed during the summer growing season (Knowles et al. 2014). Interestingly, extended summer years (such as 2012; Fig. 18) appear to decouple the relationship between snow accumulation and the carbon balance, suggesting differences in carbon-related (e.g., NEE) and more hydrology-related responses (e.g., discharge).

Vegetation modulates many hydrological and biogeochemical processes. In higher-elevation catchments, where much of the basin is unvegetated, wet and dry deposition of labile carbon is leading to increased relative abundances of nitrifying bacteria and rates of nitrification, particularly during snowmelt (Mladenov et al. 2012, Schmidt et al. 2014). Nitrate exported in stream waters in these higher-elevation areas is primarily from nitrification by microbes, and secondarily from inputs of atmospheric nitrate in precipitation (Williams et al 2015a). In lower-elevation catchments, tundra and forest vegetation reduce the influence of microbial nitrification in stream export (Darrouzet-Nardi et al. 2012). Wetter areas appear to disproportionately contribute to nitrogen transformations and carbon flux (Darrouzet-Nardi and Bowman 2011, Knowles et al. 2015a); in particular, mid-elevation krummholz and moist meadows export N as nitrate shortly after the onset of snowmelt, but this nitrate is rapidly consumed as the stream flows through the subalpine forest. We expect the influence of these wetter areas to be particularly important in years with early snowmelt and extended summers.

**3.4.3 Predictions related to H4.** Based on our past work on hydrological connectivity and landscape-scale productivity responses, we make two predictions:

- A. *Restricted connectivity will restrict buffering.* Restriction of hydrological flushing will cause wetter areas to disproportionately contribute to nutrient export at the catchment scale during periods of extended summer climate conditions.
- B. *Longer-term feedbacks with vegetation change.* With continued climate change, vegetation transitions at the treeline and tundra ecotones will create longer-term vegetation changes that will influence water quality and quantity.

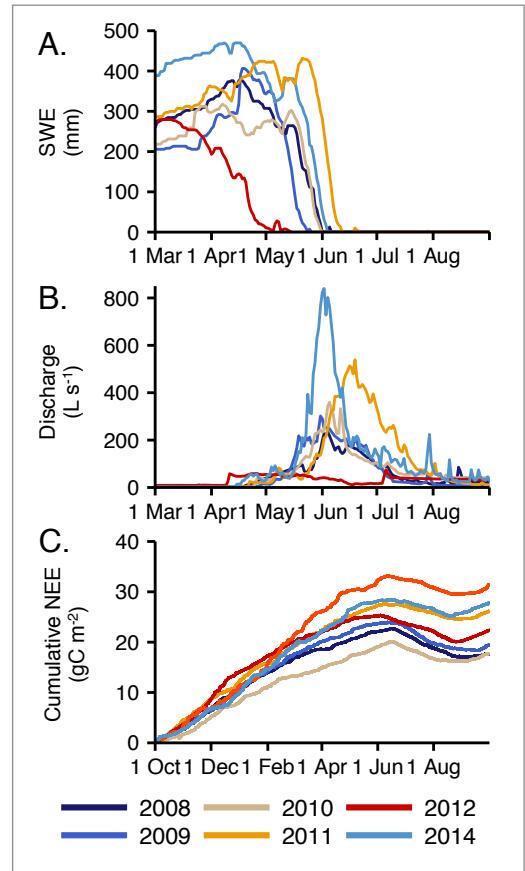
**3.4.4 Observations and modeling to test H4.** A. *Continued hydrological and snow measurements, extensions to sensor network and remote sensing.* We will continue monitoring of stream and snow chemistry, as well as precipitation inputs, focusing on major cations and anions, pH, conductance, reactive silicate (Si), dissolved organic nutrients (DOC, DON, DOP), and isotopes <sup>18</sup>O, <sup>2</sup>H, combined with streamflow monitoring at focal sites (Table 2). We will use endmember mixing models, which partition different

sources of water to the streams, to determine years and times within a year when baseflow/soil water dominates (as in Liu et al. 2004). To better link these hydrological measurements with the terrestrial systems, we will extend our microbial process measures into terrestrial areas (Table 1).

Additionally, we are installing a wireless sensor network across the spatial variability that characterizes a high-elevation catchment to provide real-time field measurements of snow depth, soil moisture and temperature, and plant productivity (NDVI cameras). We focus on a catchment that extends from the Saddle site into the Green Lakes Valley through subalpine forest to the saddle stream water sampling site (north of Lake Albion), using a wireless networked system that has been successfully deployed as part of the American River Hydrologic Observatory and Southern Sierra CZO (Kerkez et al. 2012). To place the empirical measures in a broader watershed context, we will 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 (Trujillo et al. 2012).

**B. Spatially-explicit modeling at the catchment scale.** To better understand how physical hydrologic controls on flushing behavior and connectivity are modulated by ecosystem biophysical responses to changes in climate, we characterized the spatio-temporal distribution (2001 – 2014) of snowmelt and hydrologic fluxes at an hourly time step using a 20-m resolution gridded **Distributed Hydrology Soil Vegetation Model** (DHSVM; Wigmosta et al. 1994). Model forcings, which are dependent on terrain geometry such as solar radiation and wind speed, were derived from a combination of observed conditions and geometric terrain reflectance models (Dozier and Frew 1990) and indices of terrain induced wind convergence-divergence (Winstral et al. 2002). Simulated runoff was evaluated against observed runoff at the outflow of GL4 and at nested gauged catchments, against observed soil moisture, SWE and snow depth at climate station sites, and against estimates of evapotranspiration (ET) and potential ET at flux tower locations. We use the snow water equivalent reconstruction algorithm of Jepsen et al. (2012) to validate DHSVM simulations of snow depth and SWE.

We illustrate how DHSVM will allow us to examine effects of ecological responses at the catchment scale with a land cover change scenario based on the predicted probability of alpine tundra cover expansion at high elevation (where 50% of the barren soils were colonized by tundra vegetation, with probabilities determined by important environmental controls of previous tundra expansion over the past three decades, Fig. 8). Analysis of the annual cycle reveals that the vegetation expansion reduced soil evaporation due to shading. While vegetation expansion also increased water loss due to transpiration, the net effect was an increase in surface layer soil moisture and increased streamflow, with peak increases in the late summer and early fall (Fig. 19). We will use the generalized likelihood uncertainty estimation procedure (GLUE) to evaluate the uncertainty and output error from a variety of sources (Chu et al. 2010).

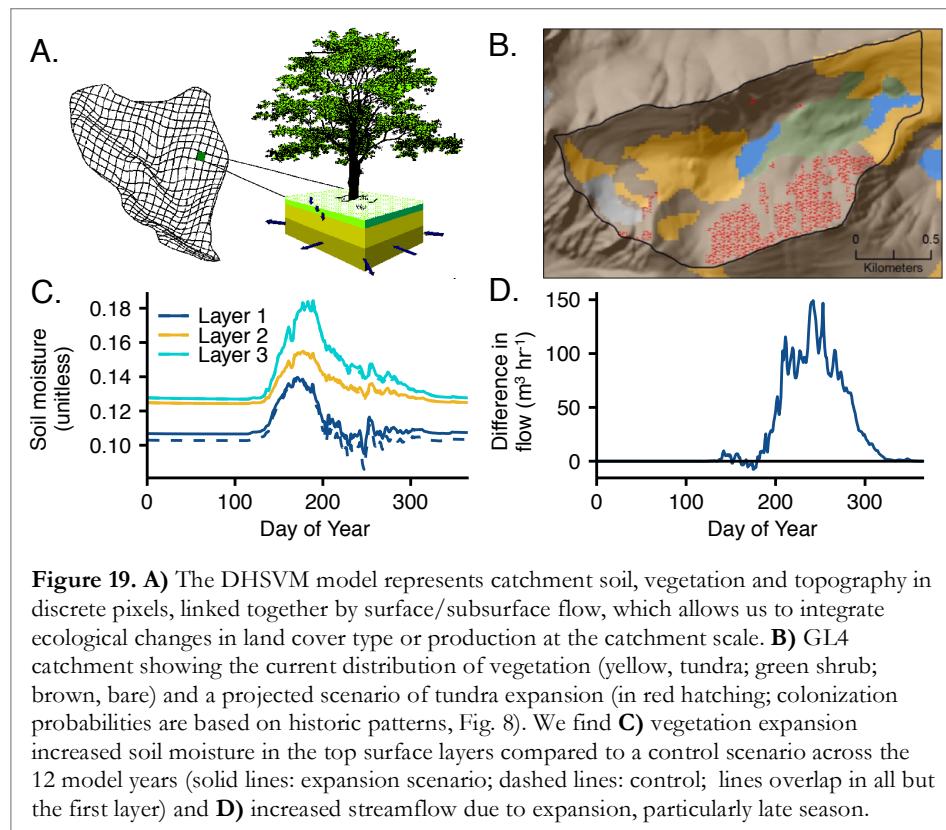


**Figure 18.** The evolution of snow-water equivalent (SWE) at Niwot (A) relates to both the (B) catchment hydrograph and (C) cumulative 24hr mean net ecosystem exchange in the tundra using eddy covariance. Top panels (A,B) shown for the period 1 March to 1 September; the bottom panel (C) includes winter to show the importance of snow on winter respiration. In most years, SWE is predictive of discharge and NEE. However in an extreme year such as 2012, extended summer decoupled those relationships (Knowles et al 2015b).

*C. Integrating spatially-explicit hydrology into fine-scale biogeochemical modeling.* To enable comparison of ecological responses and catchment export of water and nutrients, we will iteratively force the biogeochemical model used to quantify limitations in H1 (NBM, Fig. 11; Fan et al. 2016) using fluxes of water from DHSVM at 20-m spatial resolution for the period 1996 – 2021 in gridded landscape simulations. This approach will allow us to explore how 1) shifts in the timing of the snowmelt and space (e.g., Fig. 6) will affect fine-scale ecological responses, hydrological connectivity among fine-scale patches or zones, and integration at the catchment scale; 2) understand the relative importance of responses in different parts of the landscape to catchment-level flux of water and nutrients; and 3) evaluate the impacts and correlations between these terrestrial hydrologic changes and lake-water residence times and phytoplankton response. In addition, we will simulate vegetation change over longer time scales (e.g., upward expansion of tundra, regression of treeline) based on our long-term observations (e.g., Fig. 8) to test how process interactions over longer temporal scales will feedback to influence export of water and nutrients. The spatially-explicit integration of fine-scale estimates of ecological responses will also enable evaluation of patterns of biomass production, compositional turnover, and population growth at the catchment-scale.

Our approach will allow us to test our prediction that fine-scale responses to climate variation, as predicted by H1 for dry meadow tundra, may never contribute to catchment-scale responses due to a simultaneous reduction in hydrological connectivity (Williams et al. 2015a). Empirical analyses will provide important model verification and will evaluate consistencies between model and observational catchment-scale eco-hydrologic behavior. Uncertainty in model results will be used to guide our ongoing field measurements. We will continue to use a generalized likelihood uncertainty estimation procedure (GLUE) to identify uncertainty and output error in our modeling efforts (Freer et al. 1996).

*D. Integrating hydrological and biogeochemical modeling efforts with new field tracer studies.* In conjunction with the sensor array measures (in 3.4.4A, above), we will use targeted tracer additions to identify critical catchment locations that contribute greater runoff as well as those that generate less; that is, we will assess catchment connectivity under different conditions. We will take an iterative model-observational approach. In phase 1 of this coupled modeling-observation work, we will force DHSVM using dynamic inputs (meteorology) and static fields (topography, soils, vegetation), and validate model soil moisture, streamflow, and fluxes to local observations. Preliminary simulations will be used to identify locations of high and low connectivity. These end member locations will guide field deployment of the first set of tracer analyses. A dual tracer approach will include application of lithium bromide as a conservative tracer of hydrologic flow paths and  $^{15}\text{N}$  (likely as nitrate) to follow the fate of atmospheric N deposition into ecosystem pools and near-



**Figure 19.** **A)** The DHSVM model represents catchment soil, vegetation and topography in discrete pixels, linked together by surface/subsurface flow, which allows us to integrate ecological changes in land cover type or production at the catchment scale. **B)** GL4 catchment showing the current distribution of vegetation (yellow, tundra; green shrub; brown, bare) and a projected scenario of tundra expansion (in red hatching; colonization probabilities are based on historic patterns, Fig. 8). We find **C)** vegetation expansion increased soil moisture in the top surface layers compared to a control scenario across the 12 model years (solid lines: expansion scenario; dashed lines: control; lines overlap in all but the first layer) and **D)** increased streamflow due to expansion, particularly late season.

surface hydrological flow paths (after Hinckley et al. 2014a, Hinckley et al. 2014b). The tracer will be applied during spring snowmelt within 4m x 4m area plots established at each location of interest identified by the hydrological modeling as well as some experimental plots (described in section 3.1). We will use soil water content sensors as well as multiple lysimeters at the rooting zone/saprolite interface. We will sample soil water (from lysimeters) multiple times a week to assess the transport of tracers during snowmelt. At the end of snowmelt, we will recover tracers in soil cores within and outside (downgradient) of the plot. In addition, we will measure  $^{15}\text{N}$  in new plant tissues and microbial biomass above and belowground to assess biological uptake of N, which is critical information for the biogeochemistry model described in H1. We will use the resulting transport data and measured biological N uptake to verify DHVSM results and refine estimates of connectivity. In the second, iterative project phase, simulated and observed results will be used to identify new catchment locations for further observation and study. This phase will enable testing of new hypotheses and refining our scientific lines of inquiry using new tracer studies, and hydrologic and biogeochemical models.

**3.4.5 Context of H4 within the LTER VII Framework.** Our fourth hypothesis represents a critical new line of thinking for LTER VII because it links much of the fine-scale work in the terrestrial sphere with the aquatic through water quality and quantity. To make this linkage, we must be able to scale up to the catchment scale and then relate these dynamics to responsiveness in the lake ecosystems. This inquiry also enables a longer-term linkage by incorporating vegetation/land cover change at the catchment scale. By nesting the fine-scale biogeochemical model (NBM in H1) within the gridded hydrological model (in H4), we will be able to project consequences of climate change at both scales simultaneously. We hope, ultimately, to also incorporate population dynamic estimations of interaction strength (in H2) and estimations of buffering effects (in H3) as part of the nested analysis. For example, we can evaluate the relative importance of these interactions in the context of nutrient export using a non-linear hierarchical regression tree model (Meromy et al. 2013, Simons-Legaard et al. 2015). The resultant statistical model will reveal the hierarchical importance of the various abiotic and biotic factors influencing nutrient export.

**3.5 SYNTHESIS.** In LTER VII, we will employ a three-pronged approach (modeling, observation, experimentation) to predict when shifts in resource and abiotic limitation may indicate responsiveness (H1), when biotic interactions may be important to consider (H2), and when compensation (and the erosion of compensatory mechanisms) are key (H3). Spatially-explicit linkages that consider larger-scale processes will aid in understanding the catchment consequences of different patterns of responsiveness (H4). This work will help improve and test ecological theory related to how we predict ecological responsiveness to understand where and when changes in climate drivers result in ecosystem change.

Through the work outlined in this proposal, we will build a predictive framework where point-scale biogeochemistry (Niwot Biogeochemistry Model, Community Land Model) translates climate exposure across complex terrain to shifts in abiotic and resource limitation (the x-axis of Fig. 2). We will build on this information about abiotic and resource controls with inclusion of sensitivity (species traits) and adaptive capacity (the potential that these traits can shift due to adaptation or compositional change) in the NBM framework. Experimentation will allow us to better identify drivers as well as understand the temporal evolution of these responses (in particular how more persistent climate change will overcome species tolerances and diminish compensation). While we first approach this work at the ecosystem level (prediction of primary production, for instance), parallel investigations will allow us to understand demographic responses for a subset of species. Interaction strengths among species can be related to climate exposure via inclusion of environmental terms in population dynamic models; these terms will be informed by the NBM and can be expanded to include considerations of resource and abiotic limitation. Biotic influences, then, can be described by both alpha terms (as described in H2), as well as by effects of resource or abiotic limitations (a modification of NBM), linking the two modeling frameworks.

Decomposition of Variance and Mechanistic Variance models link these processes across level of organization (the y-axis on Fig. 2). Lastly, by integrating the NBM into the spatially explicit DHSVM (H4), and using predictions of the Mechanistic Variance Model across locations in the landscape to inform input

into the DHVSM model, we will integrate responses across complex terrain at the catchment scale. Model-observation iteration is an important component of each of these steps, building complexity as needed to inform our predictions.

**3.5.1 Related research projects.** Many complementary projects on NWT support research related to LTER (e.g., Suding and Schmidt have a currently funded NSF-DEB project on whether microbes facilitate the upward expansion of tundra plants) and provide insight into mechanisms that underlie long-term changes in the structure and function of high-elevation systems (e.g., Kueppers just completed a DOE-funded experimental warming project about treeline). None, however, are essential to the research proposed here. In LTER VII, we will help continue and expand rich datasets that had been ongoing previously without LTER support, most notably population dynamics datasets of *Silene* and *Bistorta*, collected since 2007 with NSF LTREB support (Table 1d; Doak and Morris 2010) and forest stand mortality since the early 1980's (Table 1e; Veblen et al. 1986, Smith et al. 2015). The Boulder Creek Critical Zone Observatory (CZO) and Southern Rockies/Colorado Plateau core National Ecological Observation Network (NEON) site are co-located at the site, and enable a breadth of research directions above the scope of one LTER site. NWT is also a location of CO<sub>2</sub> and ozone monitoring (by NOAA), a NADP site (monitoring wet atmospheric deposition), and benefits from being co-located with the US-NR1 AmeriFlux tower site near C1 (Table 1g).

**4. BROADER IMPACTS.** There is a paucity of information for mountain catchments, and in particular a lack of long-term data collection in alpine areas. Niwot Ridge is a major multidisciplinary, long-term field site representing high elevation areas on the North American continent. Only a few other North American sites exist (e.g., White Mountain Research Center, the Loch Vale Watershed, and the Rocky Mountain Biological Laboratory) that routinely conduct high elevation ecological research. As such, research at Niwot Ridge provides a crucial reference point for regional, national, and global networks that measure geophysical and biological changes and feedbacks, and that experimentally assess the mechanisms involved in these relationships.

The western United States is strongly dependent on wintertime precipitation and snowpack accumulation to sustain a multitude of ecosystem goods and services (Magoun and Copeland 1998, Barnett et al. 2005, Bales et al. 2006). The alpine/subalpine systems in the Colorado Front Range provide important and critical ecosystem services, including cultural (aesthetic value, recreation/ecotourism), provisioning (freshwater), regulating (water regulation, climate regulation [C storage]), and natural hazard regulation (fire, insect outbreak). In the Rocky Mountains, changing climate and population growth are both increasing the demand on water resources (Vorosmarty et al. 2000, Mackun and Wilson 2011). Earlier snowmelt has implications with regard to streamflow generation, as snowmelt strongly affects soil moisture conditions and modulates water table heights (Huntington and Niswonger 2012, Godsey et al. 2014). In addition, high-elevation environments, and particularly the alpine zone, are often conservation priorities due to their high species richness, high level of endemic species, and threat of species losses due to climate change. Some species, such as American pikas, have been considered for protection under the Endangered Species Act. Dissemination of research, through publishing in both applied and general journals and presenting research at regional, national, and international conferences, will ensure NWT research helps inform these issues.

**4.1 OUTREACH AND EDUCATION.** Historically, NWT Education and Outreach has largely been opportunistic: we have offered programming and curricula in response to requests from teachers, students, and the public. In response to the midterm site review, we have developed a plan to focus the outreach program in LTER VII on training in science communication, outreach, and education. This strategy will allow us to support our graduate students in becoming scholars who are able to communicate the results of their research in an impactful way, prepare them for careers as engaged scholars, and make NWT research accessible and relevant to public audiences of all ages.

**4.1.1 A focus on engaged scholarship.** Annually, 4-6 graduate students at CU receive research assistantship funding through the NWT LTER. In LTER VII, we will ask these students to complete a one credit-hour course offered by Rose (outreach coordinator) and Suding focused on science communication and “engaged scholarship.” Engaged scholarship encourages a link between the classroom and its surrounding community through experiential learning focused on teaching, research, and service. Because of the growing interest in science communication, we expect that this course will attract students from several science, education and journalism programs at CU. Partnerships with several on-campus organizations and institutes will allow us to introduce students to experts in science communication and outreach (e.g., CU Museum of Natural History, CU Science Discovery, CU Engage, Bartlett Center for Climate Communication, and the Center for Environmental Journalism). Formative and summative evaluation of graduate students will measure the impact of the course, and we will work with students to develop evaluation tools that they can use to assess the efficacy of their outreach activities. The seminar will also involve a class capstone project (we list some examples in Table 3). We view these capstone projects as the initiation of most of these endeavors, with partnership among on-campus organizations, our outreach coordinator, and many of the graduate students continuing for several years.

**Table 3.** Examples of capstone projects, aimed at training graduate students to communicate the results of their research in an impactful way and make NWT research accessible and relevant to public audiences of all ages. The objectives, scope, and length will depend on interests of the students and partners involved.

Project	Audience	Possible Scope
Expanding <i>My Water Comes from the Rocky/San Juan Mountains</i>	3rd, 4th, and 5th grade classrooms	Soon after the publication of <i>My Water</i> , NWT researchers helped develop an activity-based curriculum guide. The curricula and associated kit were used heavily. The project would revisit the existing “My H2O” activities and curricula, updating them to match current standards and needs of teachers.
Interpretive plan for the MRS and Niwot Ridge	General public, MRS guests	The Mountain Research Station (MRS) is easily accessible to the public via a state road that passes by a popular camping and fishing area. This capstone project would initiate the development of an interpretive plan for the MRS and surrounding sites. Students would determine the scope of information needs to be conveyed to visitors about NWT, and design and implement a visitor assessment study.
Interpretive materials for the MRS	General public, MRS guests	Students would use their peers’ work from the project above to create content for the permanent interpretive signage, exhibits, guided and self-guided tours, website, and other potential materials recommended by the previous year’s participants.
Field trip activities and tours for K-12 visitors to NWT	K-12 students, teachers	This project would collect existing activities and curricula for NWT field trips and catalog them in an accessible web-based format. Determine content areas and primary school age group needs. Develop materials to prepare visiting teachers and students and a handbook to prepare LTER staff and students to deliver tours.
Developing the Luminous ID app for mobile devices	General public, K-12 students, teachers	The Luminous ID alpine plant field guide app, designed by an LTER graduate student and post-doc, allows anyone with a mobile device to take pictures of certain alpine flowers and have the plant’s identification automatically confirmed. This project would expand the Luminous ID app to become a tool allowing users to identify a broad subset of flowering and non-flowering alpine plants, lichens, and animals.
Engaging elementary school girls in LTER science	4th and 5th grade girls	Girls at the Museum Exploring Science (GAMES) is a unique program designed to encourage interest and excitement about science in 4th and 5th grade girls through after-school visits to the CU Museum of Natural History. This project would develop field-based research experiences for an expansion called MORE GAMES - "Moving On to Research Experience".

**4.1.2 Synergistic initiatives.** In addition to the projects described above, we will mentor two REU students per year in independent research. Our objective is to engage students in independent research in a manner that encourages them to pursue science careers. Students will join other students participating in an REU site grant at the Mountain Research Station run by Co-PI Bowman. We will expose students to a wide range of research activities, from plot based one-day inquiries to decadal projects involving multiple sites. In partnership with CU Science Discovery, we will also team local high school students each summer with LTER mentors to conduct field-based research projects. Our graduate students will also continue to share their work via a week-long intensive camp for high school students taught by Dr. Rose.

## INFORMATION MANAGEMENT PLAN

**Goals and milestones.** The primary goals of the Information Management (IM) program are to ensure the quality, security, integrity, and availability of data collected at NWT LTER. All current IM procedures are consistent with revised IM Network Guidelines. Major milestones for improvement of data management at NWT (described in detail below) are to: (1) complete an integrated system that streamlines additions/updates to metadata and data and synchronizes them across NWT platforms; (2) acquire/develop methods to combine variables across data sets to facilitate synthetic analyses; and (3) require involvement of the IM with NWT-funded research projects at their inception and as they continue. Milestones (1) and (2) involve collaboration with other LTER IMs, especially through participation in the National Information Management Organization (NIMO; proposal submitted) to leverage knowledge available in the LTER network through a new LTER data center. We expect that milestones (1) and (3) will be accomplished in the first year of the grant, whereas milestone (2) will involve an ongoing process over several years.

**Organization and response to review.** NWT LTER supports a position dedicated to IM. Part-time employees conduct data entry and assist with other data management tasks as needed. Our data management system has several integrated components. The central repository for metadata and data is a custom relational database (implemented in Microsoft SQL Server 2008). Our primary data dissemination method is web-based. We deliver the data and metadata to users through website downloads as ASCII text files. Our website data pages also display the metadata information for each data set. A major concern raised during NWT's site review was the need to separately update components of this system that are intended to be synchronized, e.g., metadata for a data set in the database, text file, and webpage. We are addressing this concern by integrating the components of the system (see details below) so that additions and updates to the data and metadata in the database are propagated with scripts to the ASCII files and the website content management system (CMS). We are also improving Perl scripts for automated generation/update of EML (Ecological Metadata Language) and preparation of data packages for ingestion into the LTER Network's Provenance Aware Synthesis Tracking Architecture (PASTA). The strategy of our data management program and our policies are described at <http://niwot.colorado.edu/data/landing>.

**Non-spatial data.** Non-spatial (tabular) data is viewed as comprised of one of three “types”: 1) electronically provided data collected by equipment; 2) data recorded on hard-copy field forms or charts; or 3) electronically provided data not directly downloaded from electronic equipment. Raw data of all types are archived in an unmodified state in a secure location on our Linux server. Quality assurance/quality control (QAQC) information is also archived along with the data.

Scripts have been developed to conduct many routine processing steps to prepare raw data for distribution. For electronically recorded sensor data, we have implemented the GCE Data Toolbox to conduct preliminary QAQC and reformatting of raw data, including data collected at hourly or finer intervals, which are difficult to manually QAQC. We have developed a set of flagging criteria that are the basis for generating data sets posted on our website. The use of the Toolbox will allow us to produce high quality data in a timely and efficient manner. In addition, the Toolbox is also used to generate and display near-real-time graphs of hourly sensor data from NWT climate sites; these are accessed from the main page of our website (<http://niwot.colorado.edu>). We will continue to take advantage of support and knowledge available in the Toolbox users' community as we further develop our implementation.

For non-sensor climate, snow, and vegetation data recorded on field forms, data entry is conducted using Visual Basic or Excel forms, which are customized to mirror field data forms exactly, thus reducing errors and entry time. The forms employ lookup tables as well as a re-key function to decrease entry mistakes. Manual checking of data is also performed. These data are moved to the Linux server, processed with scripts, and then archived. Field forms, charts, maps, photographs, and paper

documents are all stored at INSTAAR or at the Mountain Research Station's Marr Lab. Programs and procedures are documented, including all updates, and securely archived.

Additions and updates to our data and metadata will be incorporated into the database, and changes will then be exported to other components of the system. The database formerly contained only metadata, and was updated with a combination of scripts and manual entry of information. We are incorporating new tables to contain the data in the database, and establishing automated procedures for exporting updated data and metadata to the other components of our system. This was recommended during the site review, and provides a starting point for synthesis efforts. We will make use of NIMO's skill exchange system and development of centers of excellence to increase NWT's efficiency in completing tasks and avoiding duplication of effort.

Tabular data that have been exported from the database for download from the website are organized and stored as comma-delimited ASCII text files. Each tabular data file has an accompanying metadata text file (see metadata section below). Versions of all data and metadata files are maintained to track changes over time and prevent accidental loss of information. Finalized tabular data sets are searchable via the main data page on the website (<http://niwot.colorado.edu/data>) and are available for download from each data set's individual webpage. For some data sets, the metadata note the existence of finer temporal resolution data that are not available online, but may be obtained from the data manager. The use of the Toolbox has made it easier to process and make available such data sets. Tracking of data downloads occurs using Google Analytics. Online access is provided to 150+ tabular and 50+ spatial data sets.

**Geospatial data.** Spatial data sets are searchable and can be downloaded from an FTP site accessed via our redesigned spatial data webpage (<http://niwot.colorado.edu/data/geospatial>), which maps data locations over base imagery. The spatial webpage provides access to 58 data sets. EML 2.1 has been generated for all spatial data sets, and all have spatial data packages that have been uploaded to PASTA.

Several high-resolution LiDAR flights have been flown for both the Green Lakes Valley and the larger Boulder Canyon area, including some in cooperation with the Boulder Creek Critical Zone Observatory (Figure 1). These data sets are available through OpenTopography (<http://opentopo.sdsc.edu/gridsphere/gridsphere?cid=datasets&loc=Colorado>), based on an MOU between LNO and OpenTopography that was facilitated by NWT.

Available imagery includes a set of high-resolution orthophoto mosaics and accompanying DEMs and accessory map layers for NWT, including twelve "timeslices" encompassing the past seven decades. These map layers are available from our FTP site and have been used for change detection (e.g., Formica et al. 2014's study of alpine shrub expansion).

**Data publication schedule.** Data sets are updated as often as possible and have a lag time of one month to one year (see supplemental table for listing of ongoing data sets). Some data sets are received by the IM within one year, but may not be posted to the website until two years after collection, such as graduate student thesis data and special measurement campaigns. The following long-term data sets are available (posted to NWT website and in PASTA) within 6 months of collection: signature climate data (data logger and chart-based), snow data, water quality data, phytoplankton and zooplankton data, and vegetation net primary productivity data. The following long-term data sets are available (posted to the NWT website and in PASTA) within 1 year of collection: Kiowa lab water chemistry data (time required for sample analysis and conducting QAQC), stream discharge data, vegetation species composition data, animal species composition/physiological data, and data sets submitted by individual investigators.

**Incorporation of new data sets.** We plan to collect several new data sets for LTER VII (Table S1), using IM protocols for existing data sets to collect and/or process the new data. We acknowledge that incorporation of new data collection efforts requires that we complete some existing data projects. These are indicated in Supplemental Data Table S3.

We will explore methods for the delivery of model output data, which presents challenges in terms of the volume of data produced, including spatial data, as well as providing comprehensive information about the models used to generate the data, such as assumptions, uncertainties, parameter sets, input data, sensitivity and validation analyses, and access to model versions. Publications arising from model implementation generally contain some but not all of this information.

**Table S1.** New data sets planned for LTER VII, including model output. New data sets will be collected and/or processed using existing IM data protocols wherever available. Column labeled “Project Desc Ref” refers to the Project Description. Core data areas: A=Primary production, B=Population studies, C=Movement of organic matter, D=Movement of inorganic matter, E=Disturbance patterns.

Project Desc Ref	Core Data Area	Data Set/Model	Measurements/ Simulations	IM Protocols (existing and new to be developed)
<b>Table 1a</b>	B	Tundra vegetation (Saddle grid)	Trait measures related to water use, C and N metabolism	Use protocols for processing saddle grid plot data.
<b>Table 1c</b>	B	Pika population sampling (GLV)	Weight, stage, sex, reproductive status, temp., foot length, parasites	Use protocol for west knoll pika population sampling.
<b>Table 1d</b>	B	Tundra plant population (Saddle to D1)	Stems (ramets) and new shoots tagged	Use protocol for <i>Silene</i> and <i>Bistorta</i> sampling for 4 additional alpine species.
<b>Table 1e</b>	B	Tree stand and population (near C1 in subalpine forest)	Mapping, monitoring, seed traps, seedling surveys, understory and stand production	Use protocols for tree mapping and monitoring. Use tundra production protocol to sample understory production.
<b>Table 1f</b>	A,B	Lake production, composition (RMNP)	Chl-a, phytoplankton & <i>Daphnia</i> comp., depth-specific light, SUVA	Use protocol for GL4 and Albion to sample 15 RMNP lakes.
<b>Table 1h</b>	C,D	Soil and microbial processes (Saddle, C1)	Microbial biomass, N pools, lysimeter water chemistry, enzymes	Use protocols for water chemistry and lysimeter data collection and processing.
<b>Sec 3.4</b>		Wireless sensor network (Saddle to GLV)	Snowmelt, soil moisture, temperature, NDVI	Use protocols for climate/soil data loggers for downloading, archiving, and processing.
<b>Sec 3.1 and 3.2</b>	A	Black sand terrestrial experiments (36 sites)	Soil temperature and moisture, light availability, snowfree date, GPP	Use protocols for climate/soil data loggers for downloading, archiving, and processing.
<b>Sec 3.1 and 3.2</b>	A,B,C,D	Lake limnocorral experiment (24 corrals)	Water temperature, light, chl-a, chemistry, DOM, phytoplankton & zooplankton comp.	Use protocols for water chemistry, phytoplankton, and zooplankton sampling.
<b>Sec. 3.1</b>	A,C,D	Niwot Biogeochemical Model (NBM); Community Land Model (CLM) output	C, N, P fluxes, NPP	We will develop new protocols, archiving model parameters and outputs of specified simulations.
<b>Sec 3.4</b>	A,C,D	Distributed Hydrology Soil Vegetation Model output	Gridded soil moisture, SWE, snow depth, runoff	We will develop new protocols, archiving model parameters and outputs of specified simulations.

**Combining data for analyses.** Incorporation of data sets into our relational database will permit development of specialized queries to combine variables from different data sets for analyses. A second approach will use the GCE Data Toolbox as a platform for combining variables from climate data sets that are currently incorporated into the Toolbox for QAQC and reformatting. Toolbox advantages

include built-in functions for many types of data aggregation and tracking of all changes to data sets. We will also explore the use of R for data manipulation with assistance from the LTER IM community (especially through NIMO) and knowledgeable INSTAAR graduate students. Any scripts we acquire or develop, including R, Matlab, Perl/CGI, and PHP, for data combination, synthesis, or display will be made available to users through links in the metadata and will be archived in a central repository available from the NWT website. An example is NWT's modification of Toolbox Matlab code for generating near-real-time climate graphs. Also, NWT-developed code may be contributed to NIMO's library of scripts, if deemed appropriate. NWT IM personnel will participate in one or more 'center of expertise' working groups sponsored by NIMO for particular science themes to improve data discovery and harmonization for synthesis research projects.

**Metadata.** Metadata information is collected and maintained for all data sets (where metadata are defined as all information such as materials, methods, parameter units, etc. that are necessary for proper interpretation of a data set). Metadata are acquired in several ways. Individual investigators fill out required fields in our metadata spreadsheet (available on our main website page: <http://niwot.colorado.edu>). For long-term data sets, QAQC notes are incorporated into the appropriate metadata fields.

Metadata categories and content are mirrored in our relational database, ASCII text files, and website CMS fields. The central repository for metadata is our SQL Server database. Scripts are used to update metadata text files and CMS content when changes are made to the metadata content in the database. File versioning is used to maintain all versions of metadata text files. Website users can view metadata information on a data set's webpage or can download metadata text files with the same content.

We generate EML 2.1 for all tabular and spatial data sets; NIS-compliant data packages for all data sets have been ingested into PASTA. Until 2013, we generated EML at level 2.0.1 and our data sets lacked URLs at the data set level. A major effort was undertaken to upgrade the large number of tabular and spatial data sets to their current EML level. EML is generated using scripts from the relational database. We will also explore using the GCE Toolbox to generate EML for climate data sets.

**Involvement of data management in research.** A strong link between the information manager and NWT researchers exists through regular meetings with the lead PI, and through intercommunication at NWT meetings. We are strengthening this link through interaction with NWT's Scientific Steering Committee. The IM will participate in the annual meeting of this committee, prior to the main field season, to plan allocation of funds to research projects. Submission of proposals by researchers will give advance information to the IM about the types of data sets that will be produced that year. Researchers whose projects are approved by the committee will be explicitly required to provide data to the IM using recommended protocols/formats (in consultation with the researcher) and within agreed-upon time periods. Permission to conduct research will be contingent on fulfilling these requirements. In addition, annually submitted Mountain Research Station (MRS) Research Applications help to alert the IM to new projects and any changes that may occur in existing ones. The IM also supplies assistance in developing field forms for recording data.

A link to our metadata spreadsheet is prominently displayed on the main page of our website so that it is readily available to researchers to provide metadata information for data sets. Incentives for researchers to submit their data include independent archiving to a computer that is regularly backed up, script writing for data processing, the ability to direct other researchers to their data for quick access, and the availability of DOIs for data sets through ingestion into PASTA. We will update our metadata preparation procedures as needed to reflect best practices developed under the auspices of NIMO.

**Website.** The website has undergone a complete redesign in the ExpressionEngine (EE) content management system (CMS), which offers many useful features at a reasonable cost. EE was selected as our CMS in part because of the availability of extensive local expertise. EE fields that display content on the website are easy to populate and update, and for several types of content, such as metadata and

publications, automated procedures are being developed for uploading updated content into the CMS. Website usage is tracked using Google Analytics. The new design provides improved accessibility for data, publications, and information regarding NWT LTER. The design meets LTER website design and content criteria, and promotes enhanced data discoverability through greater search capabilities, including categorization of data sets by type, discipline, etc., and linking of related data sets. Our spatial data sets are accessed separately through a recently upgraded webpage (<http://niwot.colorado.edu/data/geospatial>) that displays these data over base imagery and allows zooming in to specific areas of interest.

Graphs and tables of hourly real-time meteorological data are prominently featured on the main page, and continue to be a valuable source of information for local researchers; these graphs are also well-liked by the general public, as measured by Google Analytics webpage visits.

The TundraCam has been a popular NWT web destination (<http://instaar.colorado.edu/tundracam/index.php>). A new camera installed in the fall of 2012 with a new software interface continues to perform well under challenging conditions in the alpine zone; we receive many emails expressing appreciation for the TundraCam.

Several ancillary websites have been developed for specific projects, such as the website for the “My Water Comes from the Mountains” children’s book series (<http://niwotlter.colorado.edu/MyWater>). A website developed for the Rocky Mountain Lake Algae outreach effort contains images, taxonomic information, and data for hundreds of algae taxa, mostly from lakes in the NWT LTER site, but also from nearby Rocky Mountain National Park (<http://niwotlter.colorado.edu/MyWater>). This website receives a high number of visits. The Alpine Microbial Observatory (AMO) website complements NWT microbial research (<http://amo.colorado.edu>).

**Hardware.** We describe IM hardware in the Facilities and Equipment section of the proposal.

**Security.** Data files are protected with Linux permissions and group designations to prevent unauthorized manipulation. File versioning is used to maintain a complete record of authorized modifications to data and metadata files and to retrieve earlier versions when necessary. Incremental backups are performed nightly to a ReadyNAS NV+ desktop server that is in a different location than the Dell Linux server. The Windows PC is backed up nightly to two external hard drives. The FTP server is backed up to an external hard drive as needed when files are updated or added.

**Communications.** We have fourteen sites in NWT’s environmental sensor network that record digital information, ranging in elevation from 2199 to 3814 m. We have recently upgraded our Campbell Scientific data loggers to newer generation Cr1000, 3000, and 5000 models. The upgrades add flexibility to our data collection methods and make the network more robust, increasing reliability and decreasing gaps in data due to data logger malfunctions. Nine sites currently download data automatically on an hourly or more frequent basis using Campbell Scientific LoggerNet software. The remaining sites must be visited to retrieve data, and data is collected weekly to monthly at these sites. The connection from Niwot Ridge to CU Boulder consists of a fiber-optic line from the Mountain Research Station to the Tundra Lab, and a wireless connection from the Tundra Lab to the world with a bandwidth of 3 mbs.

Following extensive damage to stations from multiple lightning strikes, we re-grounded our alpine sites and added newer technology (in the form of Spline Ball Terminals on structures and sensor towers, and grounding augmentation fill to account for our dry rocky soils) to replace existing lightning rods and grounding soils. The re-grounding has added robustness to the network, lessening data and remote communication loss from lightning damage. The Subnivean meteorological station suffered a total loss due to a direct lightning strike in August 2012, but has been completely rebuilt with new sensors and the improved grounding methods and is back in operation.

**Publications.** All current and in-press publications are listed in the Publications section of the website (<http://niwot.colorado.edu/publications/>); all bibliographic fields in the CMS are searchable.

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