

NWT LTER ADDENDUM

Thank you for this opportunity to write this addendum to our Niwot Ridge LTER renewal proposal. Todd Crowl's email of 21 May 2010 asks that: "First, we would like a comprehensive table showing the questions, hypotheses, variables collected and analyses for each of your research foci. Second, we would like a 5 page document detailing how the various research foci tie together conceptually". NWT LTER recognizes the need to continue the intellectual evolution of our site. The provost at CU-Boulder has committed a senior faculty position in support of NWT LTER (see attached letter). This new faculty position will (a) enhance the intellectual evolution of the site by having a specialty in ecological theory and synthesis, (b) be at the Associate Professor level, and (c) is designated to become the new PI for the NWT LTER by the time of our next site visit.

Integration and synthesis at the NWT LTER is shaped heavily by the interface of two conceptual models. The Landscape Continuum Model (LCM) (Seastedt et al. 2004) describes high-elevation systems as strongly influenced by both climatic and topographic drivers. The crux of the model are the strong linkages among landscape components as a result of transport processes caused by high-elevation systems' extreme topography. These transport agents cause biogeochemical amplification and attenuation of processes unique to alpine landscapes. Panarchy Theory also provides an appropriate conceptual framework to understand resilience, transformations, tipping points, and transition to novel ecosystems (summarized in Chapin et al. 2009). The LCM provides a particularly relevant and robust emphasis on connectivity, a critical dimension in Panarchy, and the NWT LTER thus provides a unique ecosystem to examine the interactions and controls of both conceptual models. Here, we assume that readers are familiar with these concepts and how they differ from classical succession or classical disturbance theories. A key point is that transformations are most likely to occur when a) external drivers exceed historical ranges of variability, b) when regional landscape characteristics match up with the characteristics of the focal system in its most connected, 'conservation stage', or c) when the system is subjected to new species containing novel traits capable of directly or indirectly altering the biogeochemical configuration of the system.

Synthesis opportunities at the NWT LTER are made possible through the combination of long-term monitoring, long-term experiments, process-based research activities, and punctuated disturbances. Our long-term data on climate and N deposition are exhibiting directional trends that exceed historical ranges of variability and that we hypothesize are pushing our high-elevation ecosystems into new states not shown in the historical record. To illustrate, forty-five years of glacial mass balance and climate data show that recent increases in summer air temperature have resulted in the mass balance of the Arikaree Glacier crossing a threshold from stable over the last 40 years to a large negative mass balance that will most likely result in the disappearance of the glacier in the next two decades (Figure 1) (Caine in prep). Deposition of dissolved inorganic nitrogen in wetfall (DIN = ammonium and nitrate) has increased by a factor of three over the last two decades, causing the Green Lakes Valley watershed (dominated by barren soils with little vegetation) to switch from an N-limited to N-saturated system (Williams et al. 1996) that is now phosphorus (P) limited (Elser et al 2009a,b). By contrast, most alpine tundra plant communities on Niwot Ridge are still N-limited (Williams et al. 2009), but have reached a tipping point because N deposition has reached critical loads (Bowman et al. 2006; Suding et al. 2008a).

For this addendum, we emphasize the strong connectivity between terrestrial and aquatic ecosystems, an inherent property of the LCM. Wind and water are the major vectors behind ecosystem connectivity in high-elevation catchments, and are responsible for redistribution of organisms and nutrients across regional and local spatial scales. We evaluate how landscape connectivity will change among four zones (Figure 1)—1) barren soils, 2) alpine tundra, 3) treeline ecotone, and 4) high elevation forests—in response to external drivers (increases in air temperature, dust deposition, and inorganic nitrogen (N) in dry and wet deposition), and to disturbance events such as the Mountain Pine Beetle (MPB) outbreak.

Here we focus on a subset of our proposed activities so as to clearly show how the research goals tie together conceptually. All identified regime shifts correspond to hypotheses and/or questions in the NWT proposal, which are highlighted in the accompanying table.

To emphasize how our research foci tie together conceptually, we restate our overarching hypothesis as: **Changes in the amount and timing of snow and snowmelt, along with increasing N deposition and increasing dust deposition, and punctuated disturbance such as the MPB outbreak, will decrease hydrologic connectivity among landscapes, leading to decreased biodiversity, less heterogeneity of high-elevation landscapes, and a decrease in ecosystem services.** This framework is an extension of the feedback loop model in our proposal that integrates the LCM, novel ecosystems, and Panarchy frameworks.

Working Hypotheses.

H1. Increased air temperatures in combination with increased dust and N deposition will result in a decrease in hydrologic connectivity across landscape units because of less snowfall and earlier snowmelt. Increases in N and dust deposition will disproportionately affect microbial populations in barren soils and lead to soil acidification.

For seasonally snow-covered catchments in mid-latitude mountains such as ours, it is essential to improve our ability to model the spatial distribution of snow and the timing and magnitude of snowmelt. These high-elevation catchments are “Water Towers”, characterized by the release of liquid water, solutes, and particulates from storage in the seasonal snowpack. Moreover, the timing, duration, depth, and extent of snow cover are major determinants of high-elevation plant communities (Figure 1). Our hydrological and hydrochemical models are reasonably well-developed (Liu et al. 2004; Williams et al. 2006, 2007; Molotch et al. 2008, Miller et al. 2009) and provide a sufficient platform to address questions concerning hydrological connectivity.

We hypothesize that increasing air temperatures in combination with increases in dust deposition, which lowers the albedo of snow, will result in an earlier snowmelt and a longer snow-free season, with the date of peak discharge also moving forward and total annual discharge decreasing (H1-a,b). We hypothesize that these changes in the timing and magnitude of snowmelt will result in higher infiltration rates, less surface and near-surface flow, and that the water table will be lower and “soils” saturated for a shorter time period, resulting in less flushing of soil nutrients and biota from terrestrial to aquatic systems (H1-c). In turn, our high-elevation lakes will become more disconnected from the terrestrial environment and the residence time of water in the lakes will increase (H1-d). Thus, terrestrial-aquatic connectivity will decrease as the date of snowmelt moves forward in time.

At higher elevations, permanently plant-free soils (barren soils) exist in a semi-equilibrium state with microbial heterotrophic activity hypothetically balancing ecosystem carbon inputs (Freeman 2009a,b). We believe that deep, late melting snow is what excludes plants from barren soil environments, limiting carbon availability and, ultimately, microbial growth (King et al 2008). We hypothesize that increases in ammonium from atmospheric deposition will shift the nitrifying community from dominance by *Archaea* to dominance by *Bacteria*, increasing the already high export of nitrate to surface waters (H1-e). *In situ* soil experiments suggest that more P in dust would also stimulate additional heterotrophic activity (King et al. 2008), reducing available carbon (H1-f).

In the long-term, we hypothesize that the loss of the late melting snow will result in these barren soil communities becoming plant dominated communities as seen in faster melting polar oases (Jones et al., 2000) (H1-g). We hypothesize that the tipping point for this change from microbial to plant-dominated ecosystems occurs when the snow-free season extends longer than 30 days. Thus, the displaced plant

communities on Niwot Ridge are expected to move up-gradient into what is now a barren soils ecosystem.

Our long-term data in combination with N-fertilization experiments here and in the Tatra Mountains of Europe have led us to develop a conceptual model of how soil buffering systems in high-elevation mountains respond to increasing N deposition (Bowman et al. 2008). We hypothesize that the cumulative effects of the increases in N deposition have enhanced sensitivity to continued inputs of N and brought the NWT LTER dangerously close to toxic conditions, such that a) soils in our N-treatment plots will become acidified, lowering soil pH, reducing cation exchange content, and increasing soil exchangeable aluminum and iron, and b) we will see a similar response when resampling soils previously sampled in the 1980's (Litaor 1987) (H1-h). We further hypothesize that soil acidification will be more pronounced in barren soils relative to alpine tundra because of the enhanced microbial production of nitrate from hypothesis H1-e.

H2. Changes in resource flow from H1 will result in a decrease in the spatial heterogeneity of plants and microbes: soils will become more “leaky” in alpine tundra causing a decrease in the DOC:NO₃ ratio of those streams, and plant and microbial diversity will decline.

We hypothesize that current levels of DIN in wet and dry atmospheric deposition are sufficient to drive a non-linear response in the composition of alpine vegetation and associated soil processes in directions predicted by long-term N fertilization experiments. We hypothesize that nitrophilic species, including *Carex rupestris* in the dry meadow and *Deschampsia* in the moist meadow, will replace slower growing forbs that stabilize N retention through production of more recalcitrant organic matter (H2-a). Similarly, soil/microbial changes will include: increased nitrate pools and leaching, decreased microbial biomass N, shifts in soil fungal and bacterial communities, changed extracellular enzyme activities, and increased turnover of light soil fractions (H2-b). A combined N deposition/warming experiment will be initiated in the summer of 2010, with full implementation in 2011, to evaluate how a warming climate will interact with increasing N deposition. The experiment will test the hypothesis that warming will enhance turnover of soil organic matter more than plant growth and uptake of N, leading to greater sensitivity to N deposition impacts (such as changes in biodiversity and acidification).

An exciting ‘natural experiment’ is that increases in nutrient availability in N-deposition and dust, along with changes in snowpack and air temperature, may be driving the expansion of shrubs such as *Salix spp* at Niwot Ridge (H2-c). We hypothesize that increases in *Salix* abundance leads to a positive feedback system, with increasing snow accumulation, which promotes higher winter soil temperatures, greater microbial activity and more plant-available nitrogen. We will expand on a project initiated in 2006 to further develop the snow-shrub feedback model developed in Arctic ecosystems (Sturm et al. 2005) to include a fully-factorial experiment to manipulate summer air temperature (via open-top chambers), snowpack (via replicate snowfences), and nitrogen availability (via N addition) to test the causal link between environmental changes, the increasing distribution of *Salix spp*, and the subsequent decline in the plant tundra community. The experiment will enable us to determine if increasing temperatures and feedbacks between temperature and snowpack or nutrient availability favor the growth and establishment of *Salix* over the existing herbaceous alpine community and if these changes can drive rapid conversion, including the loss of alpine species and increased *Salix* distribution. Additionally, historical changes in shrub cover will be evaluated using ten orthophoto mosaics which span seven decades — from 1938 to 2008 — at 1.0 m to 30 cm resolution (<http://culter.colorado.edu/NWT/orthoimagery/orthoimagery.html>).

The potential increase in the length of the snow-free season, in combination with the loss of hydrological connectivity and the expansion of shrubs, allows us to test a conceptual model developed by Suding et al. (2008b, pg 1127) for incorporating community dynamics into

predictions of environmental change. We hypothesize that these changes will likely result in the substantial reductions in the cover of snowbed, wet meadow, and moist meadow communities from their current areas (H2-d) (Figure 1). In contrast, the dry meadow and fellfield communities will expand in area. The rearrangement of these plant communities because of the loss of hydrological connectivity will result in a decrease in the landscape diversity of alpine tundra, and result in alpine tundra becoming more homogeneous. Spatially explicit statistical modeling will provide future projections, based on generalized linear and generalized additive models for species distribution over space and time, combined with topoclimatic predictor variables (MTCLIM, SnowModel). We will fold these models into an updated and spatially distributed SNOWPACK-BIOME-BGC. Historical changes will be evaluated as in H2-c above and used to back-cast model simulations.

Taylor and Townsend (2010) and Elser et al. (2009a,b) provide conceptual stoichiometric-based models that can be quantitatively tested with respect to changes in the DOC:NO₃ ratio of water bodies. We hypothesize that the increasing N deposition, coupled to the expansion of shrubs and changes in species diversity which are “leaky” with respect to N, will cause the average C:N ratio of microbial biomass to decline, and the carbon use efficiency of heterotrophs to increase, thus lowering the soil DOC:NO₃ ratio at which point nitrate concentrations in soil and surface waters begin to climb steeply. We predict that alpine tundra on Niwot Ridge, which is currently N-limited with a DOC:NO₃ ratio of about 40 (Figure 1), will become N-saturated and the DOC:NO₃ ratio in the aquatic system will rapidly decrease towards that of the Green Lakes Valley, which is around 3. Conversely, when alpine tundra moves into the current barren soils, these areas will have a carbon subsidy, and thus we predict the DOC:NO₃ ratio will increase in GLV surface waters (H2-e) at that time (Figure 1).

In our alpine lakes, several climate factors are changing in a direction that enhances algal growth (e.g. earlier ice-out, stronger thermal stratification), however for these changes to actually result in greater phytoplankton growth requires sufficient P supply. Thus, a key process that may regulate a lake ecosystem tipping point may be greater P input from geochemical weathering and directly from dust deposition. This hypothesis will be tested by adding P and dust to factorial in-lake incubation experiments (H2-f). In turn, we hypothesize that the longer residence time of water in lakes caused by the decrease in hydrologic continuity may cause lakes to switch from high-flow—low residence time systems to low flow—high residence time systems, enhancing the growth of zooplankton such as *Daphnia* (Figure 1). Thus, the decrease in hydrological connectivity may cause lakes to switch from “bottom up” to “top down” controls on phytoplankton abundance (H2-g).

H3: Directional drivers in combination with punctuated (rare) events alter historical disturbance regime in ways that enhance resource flux, shift species composition, and change the connectivity between landscape units.

The current structure of the alpine, treeline, and subalpine landscapes of NWTLTER are legacies of past, rare events. Glaciation, paleo-warming intervals, and very infrequent fires created the large-scale landscape features that now constrain community dynamics. These rare events, however, are not immune to change from directional drivers. We hypothesize that the relatively slow changes observed in community dynamics of the high elevation ecosystems are punctuated by rapid change caused by rare events, and several ‘rare events’ are currently underway.

Tipping points and ecosystem transitions can be generated by trophic interactions with directional drivers. At present, top-down (herbivore) controls are interacting with directional climate change to induce ‘new’ phenomena. Insect outbreaks such as the MPB represent a rare community-to-watershed scale disturbance that has interacted with regional climate drivers to generate a regional-scale forest die-back. We hypothesize that forest die-back caused by the MPB outbreak (which began last year at our site) will reduce water losses by canopy interception of snow and resulting sublimation in the winter and

evapotranspiration during the summer. The increased water content may lead to higher infiltration rates, more surface and near-surface flow, a higher water table and “soils” saturated for a longer time period, resulting in an increase in water export and more flushing of soil nutrients from terrestrial to aquatic systems (H3-a). In contrast to our alpine system, the MPB outbreak may initially increase the hydrologic continuity of the forested system.

We hypothesize that the interaction of climate with forest die-back will enhance the invasion of cold-tolerant species, particularly Timothy (*Phleum pratense*) (a non-native grass which has become a subdominant species in meadows around the Mountain Research Station), a non-native weevil *Rhinocyllus conicus*, and European earthworms. Subalpine forests will be replaced in part by novel meadows dominated by non-native grasses (H3-b). Similarly, in aquatic systems, we hypothesize that the combination of longer-residence times in lakes with directional climate and N deposition drivers will result in the invasive chytrid *Batrachochytrium dendrobatidis* increasing exponentially and creating a decline in amphibian populations (H3-c).

Gopher disturbances, well-documented at our sites (Sherrod and Seastedt 2001; Sherrod et al. 2005), are under frozen ground/snow controls. These animals only persist in thawed soils during winter and thawed soils are controlled by amount, timing, and duration of snow cover. These animals have large effects on soils and vegetation, and their response, more than the more subtle changes in herbaceous vegetation to N deposition or climate, can control alpine community structure. However, shrub invasion is hypothesized to ‘trump’ gopher activities, so we expect a sequence of transient activities (that will be measured by existing research and monitoring projects at NWT), to drive community change in the coming decades (H3-d) as gopher populations decline on Niwot Ridge but potentially move uphill as plants invade barren soils.

The extent to which disturbances, topography, climate, and N and dust deposition interact to control the treeline ecotone is an area of active research (Humphries et al. 2008; Liptzin and Seastedt 2009). We have found mechanistic processes that shape the ecotone—seed rain, seed germination, seedling establishment and subsequent tree growth form—are fundamentally the same for all forest-tundra ecotones across western North America (Malanson et al. 2007). Based on this conceptual understanding, we hypothesize that the treeline ecotone is in the process of in-filling, and as that progresses the ecotone will move uphill (H3-e) (Figure 1). We will evaluate this hypothesis using historical measurements at the ecotone (Humphries et al. 2008), new transects using the point-intercept method which are designed to support more quantitative analyses, and spatially distributed measurements of stand structure using LiDAR (currently supported by the NSF-funded Critical Zones Observatory program and by NEON in the future). These measurements support analytical tools such as Multiresponse Permutation Procedures (species richness differences), Jaccard’s coefficient for species difference among transects, and regression tree analysis.

The increased connectivity of the more fire-prone montane forest (which has been greatly influenced by human fire suppression activities) with the subalpine system (much less affected by human fire suppression activities) is hypothesized to enhance the likelihood of large-scale fire. The closed-canopy characteristics of the subalpine now exist lower down into the montane region. Combined with directional climate drivers that increase the aridity of this system, we expect higher fire return intervals because the fires will increase in areal extent. We remain poised to quantify fire effects, and potential unique and novel responses to either fire or the MPB outreach at the treeline ecotone. Similarly, new plants, invertebrates, and microbial symbionts and pathogens, are now in the regional species pool and will be influenced by direct and indirect human activities. We anticipate that these biota will interact with other changes in ways that will induce subtle to large changes in the biogeochemistry of these high-elevation ecosystems.

OVERARCHING HYPOTHESIS: Changes in the amount and timing of snow and snowmelt, along with increasing N deposition and increasing dust deposition, and disturbance such as the MPB outbreak, will decrease hydrologic connectivity among landscapes, leading to decreased biodiversity, less heterogeneity of high-elevation landscapes, and a decrease in ecosystem services.

<p>Working Hypothesis H1. Increased air temperatures in combination with increased dust and N deposition will result in a decrease in hydrologic connectivity across landscape units because of less snowfall and earlier snowmelt. Increases in N and dust deposition will disproportionately affect microbial populations in barren soils and lead to soil acidification.</p>		
Hypothesis/Question	Variables Collected	Activities
<p>H1(a). Snowmelt. Snowmelt will begin progressively earlier and result in a longer snow-free season.</p>	<p>Continue long-term measurements of snow properties (depth, density, duration, and area) and climate data. Measure dust content of snowpack. Retrospective analysis of snow covered area using Landsat back to mid-1970's.</p>	<p><u>Analyses/Modeling:</u> Determine day of the year for snowmelt center of mass (when half the snowpack had melted) using the energy-balance approach of Molotch et al. (2008).</p>
<p>H1(b). Discharge. Earlier snowmelt results in earlier peak discharge; lake ice-out also occurs earlier.</p>	<p>Continue long-term measurements of discharge and lake ice-out.</p>	<p><u>Analyses/Modeling:</u> Time series analysis of peak discharge, center of mass of discharge, total annual discharge, and lake ice out. Develop multiple linear regression models using air temperatures, snowfall, and elevation as explanatory variables to identify major controlling factors on snowmelt and discharge timing.</p>
<p>H1(c). Hydrological connectivity. Changes in the timing of snowmelt and discharge reduce overland and near-surface flows and increase sub-surface hydrologic residence times, reducing hydrological connectivity</p>	<p>Continue long-term climate, hydrological and hydrochemical measurements. Add additional soil moisture and soil lysimeter instruments, add groundwater wells.</p>	<p><u>Analyses/Modeling:</u> Combine snowmelt and energy balance models above with hydrologic mixing models and the Alpine Hydrochemical Model to improve understanding of surface/groundwater interactions and hydrological connectivity.</p>

<p>H1(d). Lake residence time. Residence time of water in alpine lakes will increase.</p>	<p>Continue long-term measurements of lake discharge, add measurements of stable and radiogenic (tritium) water isotopes.</p>	<p><u>Analyses/Modeling:</u> Use standard water residence time model; calculate water retention times with isotopes using the Michel and Kraemer (1995) model for years with isotopic data.</p>
<p>H1(e). Microbial shifts. Increases in availability of ammonium from atmospheric deposition will shift the nitrifying community from dominance by Archaea to dominance by Bacteria. These changes will be particularly strong in barren soils.</p>	<p>Clone libraries to identify and qPCR to quantify nitrifiers in barren soils, talus, and alpine tundra, and in response to experiments. Briefly, subunit <i>a</i> of bacterial ammonium monooxygenase (bAMO) genes will be amplified using primers amoA-1F and AMOa-2R, and archaeal ammonium monooxygenase (aAMO) will be amplified using Arch-AMOaF and Arch-AMOaR. Measurement of activities including gross nitrification, N mineralization and N fixation to determine how treatments affect processes.</p>	<p><u>Experiments:</u> <i>in situ</i> incubation of barren soils with factorial N, dust additions.</p> <p><u>Analyses/Modeling:</u> Sequences of AMO subunit <i>a</i> for both the Archaea and Bacteria will be collapsed into representative OTUs (1% distance) using Mothur (http://www.mothur.org/). All sequences will be aligned using MUSCLE before phylogenetic analysis. The Mx3000P software package (Stratagene) will be used to quantify initial copy numbers in the environmental samples via comparison to the standard curve for the gene of interest.</p>
<p>H1(f). Phosphorus influx. P in dust will stimulate growth of both heterotrophs and photosynthetic cyanobacteria.</p>	<p>Clone libraries as above. Soil respiration measured using an EGM-4 CO₂ analyzer. Measurements will be taken on an approximately log₂ timescale (Powers of 2 e.g. ½, 1, 2, 4, 8, 16, 32 hrs).</p>	<p><u>Experiments:</u> <i>in situ</i> soil respiration experiments will be conducted to assess the effects of added dust and pollen on microbial activity in talus soils. Pollen or dust, N and P will be added in a full-factorial design with three replicates for each treatment combination.</p> <p><u>Analyses/Modeling:</u> Gene analysis as above. Curves of CO₂ accumulation will be fit using the non-linear regression function of KaleidaGraph software and kinetic models as described in King et al. (2008).</p>
<p>H1(g). Barren soils transition to alpine tundra. Tipping point occurs when the snow-</p>	<p>Historical (beginning in 1936) changes in barren soils and plant cover, spatial distribution</p>	<p><u>Analyses/Modeling:</u> Time series analysis, overlay of snow covered area, barren soils, and plant cover</p>

<p>free season exceeds one-month for several years.</p>	<p>of snow covered area and snow depth (field measurements, remote sensing), barren soils, and plant-covered soils.</p>	<p>on DEM.</p>
<p>H1(h). Soil acidification. The increase in N deposition will acidify soils, reduce base saturation, and increase availability of mobile aluminum and iron.</p>	<p>Resample soils from the 1980's, sample soil properties of long-term N-fertilization plots. Analytes include soil pH, base cation concentrations, trace metals such as Al and Fe.</p>	<p><u>Experiments:</u> Long-term N fertilization plots in multiple vegetation types. <u>Analyses/Modeling:</u> The effects of the N treatments and resampled soils on the response variables (soil cations and pH, Al and Fe content) using least-squares linear regression and analysis of variance tests.</p>
<p>Working Hypothesis H2. Changes in resource flow from H1 will result in a decrease in the spatial heterogeneity of plants and microbes: soils will become more "leaky" in alpine tundra causing a decrease in the DOC:NO3 ratio of those streams, and plant and microbial diversity will decline.</p>		
<p>Hypothesis/Question</p>	<p>Variables Collected</p>	<p>Activities</p>
<p>H2(a) Alpine species diversity. N deposition and changes in air temperature will decrease alpine species diversity and shift composition towards fewer dominant graminoids and shrub species. Once the ecosystem crosses its critical N load (estimated between 4-10 kg N/ha/yr for vegetation change), species composition will shift in directions predicted by current long-term N fertilization experiments (eg increases of <i>Carex rupestris</i> in dry meadow and <i>Deschampsia</i> in moist meadow).</p>	<p>Annual measures of plant production and species composition both in experimental plots and long-term plots; long-term measurements of atmospheric deposition of N, climate variables.</p>	<p><u>Experiments:</u> Long-term N fertilization plots in multiple vegetation types; warming x N manipulations; species composition manipulations (removals) to access internal feedbacks. <u>Analyses/Modeling:</u> Assessment of non-linear responses over time and across different rates of N loading (after Bowman et al 2006); landscape modeling of N loading (based on differential accumulation of winter snow pack); causality network analyses among vegetation and soil time series.</p>

<p>H2(b). Soil processes. Warming air temperatures will enhance turnover of soil organic matter more than plant growth and uptake of N, leading to greater sensitivity to N deposition impacts.</p>	<p>Inorganic N pools, net N mineralization rates, tissue N content, soil carbon fractions, microbial activity (microbial biomass, fungal: bacterial) and function (extracellular enzyme activity); additional variables as above.</p>	<p><u>Same as above.</u></p>
<p>H2(c). Shrub Encroachment. Increased N deposition in combination with changes in snow amount will cause an increase in shrub growth in the moist and wet alpine plant communities.</p>	<p>Historical (beginning in 1936) changes in shrub cover. Shrub vs non- shrub variables: Snow depth and duration, snow albedo, morphology (canopy height relative to snow depth), soil temperature, carbon storage and plant production, N cycling (Inorganic N pools, N mineralization rates, microbial biomass N).</p>	<p><u>Experiments:</u> Factorial experiment manipulating snowpack (snowfences), temperature (ITEX chambers), nitrogen (N fertilization), shrub presence (transplant additions). <u>Analyses/Modeling:</u> Wind-blown snow landscape model to simulate snow transport and distribution (SnowModel) in different shrub expansion scenarios; radiative forcing due to surface albedo changes. Time series analysis of changes over time.</p>
<p>H2(d). Decrease in spatial heterogeneity of alpine tundra. The loss of hydrologic connectivity will cause a decrease in the areal extent of barren soils, snowbed, moist meadow, and wet meadow communities, and an expansion of more mesic portions of the dry meadow community.</p>	<p>Annual measures of species composition indicative of community types, snow covered area from remote sensing (LANDSAT and LiDAR), historical changes in land cover types.</p>	<p><u>Spatially explicit statistical modeling</u> Generalized linear and generalized additive models (GLM and GAM) for species distribution over space and time, combined with topoclimatic predictor variables (MTCLIM, SnowModel). Fold these models into an updated and spatially distributed SNOWPACK-BIOME-BGC.</p>
<p>H2(e). Soil nitrate export. Expansion of shrub and graminoid community will accelerate the change in tundra from N-limited to N-saturated, with increased export of nitrate to aquatic systems and decreases in</p>	<p>Complement existing long-term measurements of stream chemistry and factorial experiments above with addition of soil lysimeters, build on carbon use efficiency measurements above as well as lake mesocosm experiments</p>	<p><u>Analyses/Modeling:</u> Evaluate long-term trends in the DOC:NO3 ratio of surface waters using the nonparametric seasonal Kendall test. ANOVA tests on carbon use efficiency and changes in the stoichiometry of C and N.</p>

<p>carbon export.</p>	<p>below.</p>	
<p>H2(f). Enhanced phytoplankton growth. Greater fluxes of P into alpine lakes caused by accelerated weathering from melting of permafrost and deposition of P-rich dust rich increase phytoplankton productivity and concentrations of microbially-derived dissolved organic material, as well as drive shifts in algal species distribution.</p>	<p>Chlorophyll a, algal species distribution (using digital Flowcam), lake mixing (O18 isotopic measurements), light attenuation, thermal stratification, nutrients and water quality, DOM quality by spectral properties, e.g. fluorescence</p>	<p><u>Experiments:</u> Build on previous in-lake nutrient bioassay experiments using P additions and addition of dust. <u>Analyses/Modeling:</u> Classic 2-way ANOVA, RDA; use results to expand current lake algal-DOM model (Miller et al 2009) to include term for increased P driving increased algal growth, DOM production, and changes in DOM quality</p>
<p>H2(g). Lakes switch from “bottom up” to “top down” controls on phytoplankton. Earlier snowmelt will cause lakes to switch from high-flow—low residence time systems to low flow—high residence time systems, enhancing the growth of zooplankton such as <i>Daphnia</i>.</p>	<p>Measure rates of primary production and respiration in mesocosms, measure N-uptake in mesocosms using nitrate sensors, continue sampling of algal species distribution and abundance, add zooplankton distribution and abundance, investigate historical record of both in sediment cores.</p>	<p><u>Analyses/Modeling:</u> Use results to expand current lake algal model to include terms for algal growth controls by zooplankton grazing, with zooplankton growth controlled by algal abundance and lake residence time</p>
<p>H3: Directional drivers in combination with punctuated (rare) events alter historical disturbance regime in ways that enhance resource flux, shift species composition, and change the connectivity between landscape units.</p>		
<p>H3(a). Mountain Pine Beetle outbreak will enhance water export and nutrient export in forested areas.</p>	<p>Continue long-term monitoring of Como Creek water quantity and quality, install additional soil moisture sensors and soil lysimeters, wells, continue N-cycling measurements (inorganic N pools, N mineralization, microbial biomass C and N).</p>	<p><u>Analyses/Modeling:</u> Time series analysis, 2-way ANOVA. Combine hydrologic models from H1(c) with SNOWPACK/BIOME-BGC.</p>

<p>H3(b). Novel ecosystems. New, opportunistic species will exploit novel environment generated by climate x beetle-kill interaction.</p>	<p>Monitor changes in population densities of nonnative species (earthworms, beetles, plants) as a function of elevational gradient, community type. Continue long-term modeling of climate variables.</p>	<p><u>Analyses/Modeling:</u> Niche-based species distribution models based on generalized linear and generalized additive models with a binomial probability distribution and a logit link, based on topoclimatic predictor variables similar to H2(d).</p>
<p>H3(c). Invasive aquatic species. Increased hydrologic residence time and increased air temperatures will increase water temperatures, and the invasive chytrid <i>Batrachochytrium dendrobatidis</i> will increase exponentially and cause a decline in amphibian populations</p>	<p>Collect zooplankton and crayfish using NTL protocols; record prevalence of invasive chytrids. Regional synoptic sampling for amphibians and crayfishes.</p>	<p><u>Analyses/Modeling:</u> Spatially explicit modeling based on hydrologic and climate variables, and integrated into SNOWPACK-BIOME-BGC.</p>
<p>H3(d). Gopher disturbances. Gopher populations will decrease with a decrease in snow cover and decrease with expansion of shrubs, reducing nutrient redistribution.</p>	<p>Annual measurements of species richness and diversity; gopher populations, activity/disturbance. Soil properties include soil texture, clay content, total C, total N, total P, labile P, inorganic N pools.</p>	<p><u>Analyses/Modeling:</u> ANOVA, spatial modeling as in H3(b).</p>
<p>H3(e). Treeline. We hypothesize that the treeline ecotone will infill and become a closed canopy and that the ecotone will move uphill.</p>	<p>Continue long-term monitoring, add the Buckner point-intercept method, along with LiDAR measurements of stand structure (CZO currently, NEON in future).</p>	<p><u>Analyses/Modeling:</u> Multiresponse Permutation Procedures (species richness differences), Jaccard's coefficient for species difference among transects, and regression tree analysis.</p>

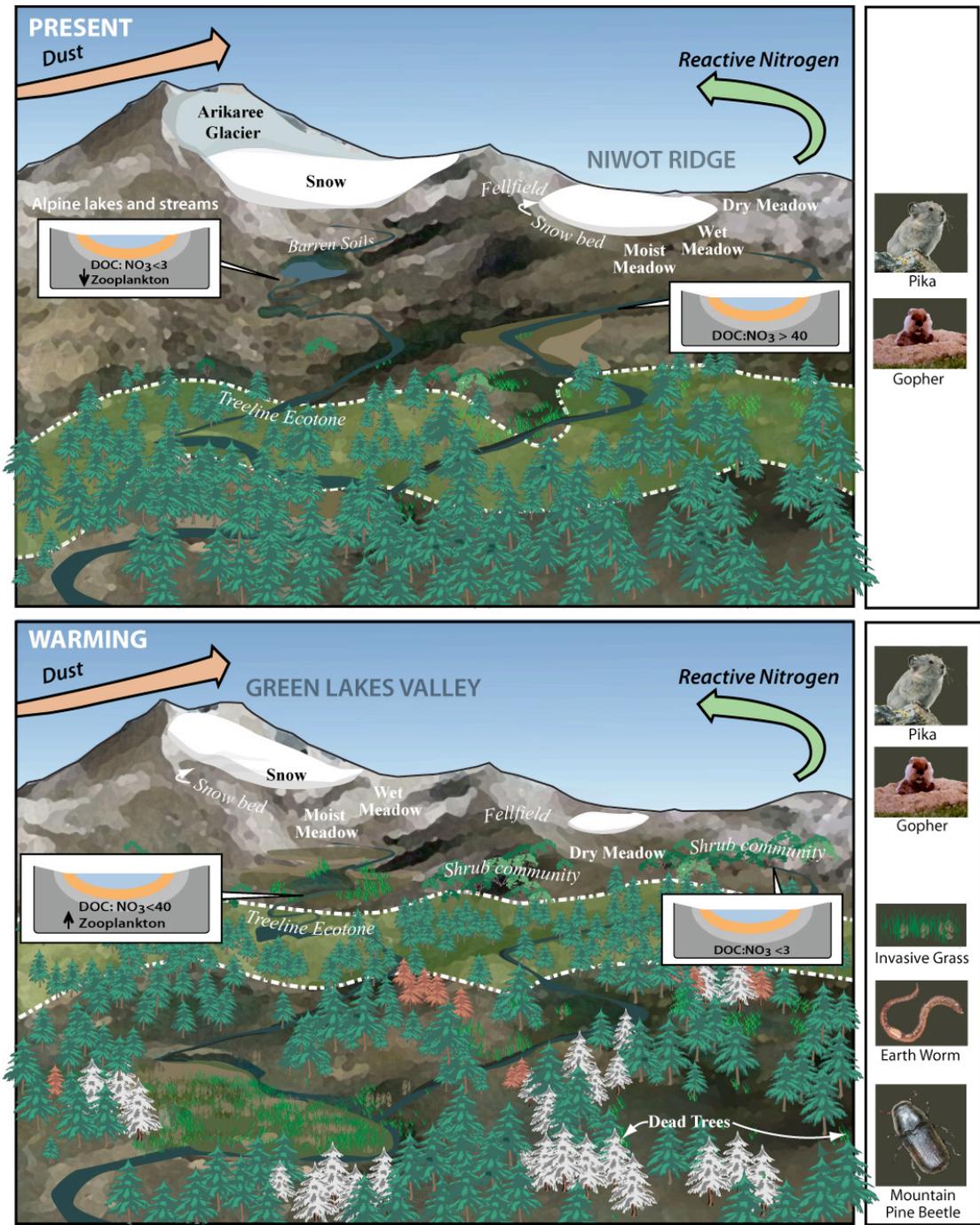


Figure 1. Major landscape types and plant communities at present and under a warming climate scenario. Alpine communities are controlled by the hydrological connectivity driven by the duration and timing of the seasonal snowpack and snowmelt. We expect that under a warming climate, along with increases in N deposition and dust, that we will lose the Arikaree Glacier in the Green Lakes Valley, snowmelt will occur earlier, snowline will move up in elevation, and hydrologic connectivity will decrease. In turn, species diversity will decrease, shrubs will expand, and the landscape will become more homogeneous. The Mountain Pine Beetle outbreak is expected to remove a large portion of the subalpine forest, facilitating the introduction of invasive species.

References Cited

- Bowman, W.D., Gartner, J.L., Holland, K., and Wiedermann, M. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: Are we there yet? *Ecological Applications* 16:1183-1193.
- Bowman, W. D., Cleveland C. C., Halada L., Hresko J. and Baron J. S. 2008. Negative impact of nitrogen deposition on soil buffering capacity. *Nature Geoscience*, 1: 767-770.
- Caine, Nel. 2010. The mass balance of Arikaree Glacier, Colorado Front Range: 1965:2010. *Annals of Glaciology*, In Preparation.
- Chapin, F.S., C. Folke and G.P. Kofinas. 2009. A framework for understanding change. Chapter 1 in: Chapin, F.S., C. Folke and G.P. Kofinas (eds). *Principles of Ecosystem Stewardship*. Springer Verlag, NY.
- Edgar, R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792-1797.
- Elser, J.J., Andersen, T., Baron, J.S., Bergström, A.-K., Jansson, M., Kyle, M., Nydick, K.R., Steger, L., and Hessen, D.O. 2009a. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* 326:835-837.
- Elser, James J., Marcia Kyle, Laura Steger, Koren R. Nydick, and Jill S. Baron. 2009b. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. *Ecology* 90(11):3062–3073.
- Freeman, K.R., Martin, A.P., Karki, D., Lynch, R.C., Mitter, M.S., Meyer, A.F., Longcore, J.E., Simmons, D.R., and Schmidt, S.K. 2009a. Evidence that chytrids dominate fungal communities in high-elevation soils. *Proceedings of the National Academy of Sciences* 106:18315-18320.
- Freeman, K.R., M.Y. Pescador, S.C. Reed, E.K. Costello, M.S. Robeson, and S.K. Schmidt. 2009b. Soil CO₂ flux and photoautotrophic community composition in high-elevation, 'barren' soil. *Environmental Microbiology* 11(3):674-686.
- Humphries, H.C., Bourgeron, P.S., and Mujica-Crapanzano, L.R. 2008. Tree spatial patterns and environmental relationships in the forest-alpine tundra ecotone at Niwot Ridge, Colorado, USA. *Ecological Research* 23:589-605.
- Jones, M. H., Fahnestock J. T., Stahl P. D. and Welker J. M. 2000. A note on summer CO₂ flux, soil organic matter, and microbial biomass from different high arctic ecosystem types in northwestern Greenland. *Arctic Antarctic and Alpine Research* 32: 104-106.
- King, A.J., Meyer, A.F., and Schmidt, S.K. 2008. High levels of microbial biomass and activity in unvegetated tropical and temperate alpine soils. *Soil Biol. Biochem.* 40(10):2605-2610.
- Liptzin, D. and Seastedt, T.R. 2009. Patterns of snow, deposition, and soil nutrients at multiple spatial scales at a Rocky Mountain tree line ecotone. *Journal of Geophysical Research* 114:1-13 G04002, doi:10.1029/2009JG000941.
- Litaor, M. I. 1987. The influence of eolian dust on the genesis of alpine soils in the Front Range, Colorado. *Soil Science Society of America Journal*, 51: 142-147.
- Liu, F. J., Williams M. W. and Caine N. 2004. Source waters and flow paths in an alpine catchment, Colorado Front Range, United States. *Water Resources Research*: 40.
- Malanson, G. P., Butler D. R., Fagre D. B., Walsh S. J., Tomback D. F., Daniels L. D., Resler L.M., Smith W. K., Weiss D. J., Peterson D. L., Bunn A. G., Hiemstra C.A., Liptzin D., Bourgeron P.S., Shen Z. and Millar C. I. 2007. Alpine treeline of Western North America: Linking organism-to-landscape dynamics. *Physical Geography*, 28: 378-396.
- Michel, R. L. and Kraemer T. F. 1995. Use of isotopic data to estimate water residence times of the Finger-Lakes, New York. *Journal of Hydrology* 164: 1-18.
- Miller, M. P., McKnight D. M., Chapra S. C. and Williams M. W. 2009. A model of degradation and production of three pools of dissolved organic matter in an alpine lake. *Limnology and Oceanography*, 54: 2213-2227.

- Molotch, N.P., Meixner, T., and Williams, M.W. 2008. Estimating stream chemistry during the snowmelt pulse using a spatially distributed, coupled snowmelt and hydrochemical modeling approach. *Water Resources* 44.
- Seastedt, T.R., Bowman, W.D., Caine, T.N., McKnight, D., Townsend, A., and Williams, M.W. 2004. The landscape continuum: A model for high elevation ecosystems. *Bioscience* 54(2):111-121.
- Sherrod, S. K. and Seastedt T. R. 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry* 55: 195-218.
- Sherrod, S. K., Seastedt T. R. and Walker M. D. 2005. Northern pocket gopher (*Thomomys talpoides*) control of alpine plant community structure. *Arctic Antarctic and Alpine Research* 37: 585-590.
- Sturm, M., Douglas, T., Racine, C., and Liston, G.E. 2005. Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research-Biogeosciences* 110(G1):G01004.
- Suding, K.N., Ashton, I., Bechtold, H., Bowman, W., Mobley, M., and Winkleman, R. 2008a. Plant and microbe contribution to community resilience in a directionally changing environment. *Ecological Monographs* 78:313-329.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Johannes, H., Cornelissen, C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., and Laure Nava, N. 2008b. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125-1140.
- Taylor, P. G. and Townsend A. R. 2010. Stoichiometric control of organic carbon-nitrate relationships from soils to the sea. *Nature* 464: 1178-1181.
- Tomback, D. F. and Resler L. M. 2007. Invasive pathogens at alpine treeline: Consequences for treeline dynamics. *Physical Geography* 28: 397-418.
- Williams, M. W., Baron J. S., Caine N., Sommerfeld R. and Sanford R. 1996. Nitrogen saturation in the Rocky Mountains. *Environmental Science & Technology* 30: 640-646.
- Williams, M.W., Knauf, M., Caine, N., Liu, F., and Verplanck, P.L. 2006. Geochemistry and source waters of rock glacier outflow, Colorado Front Range. *Permafrost and Periglacial Processes* 17:13-33.
- Williams, M.W., Knauf, M., Cory, R., Caine, N., and Liu, F.J. 2007. Nitrate content and potential microbial signature of rock glacier outflow, Colorado Front Range. *Earth Surface Processes* 32(7):1032-1047.
- Williams, M. W., Seibold C. and Chowanski K. 2009. Storage and release of solutes from a subalpine seasonal snowpack: soil and stream water response, Niwot Ridge, Colorado. *Biogeochemistry* 95: 77-94.