COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

PROGRAM ANNOUNCEMENT/SOLICITATION NO./DUE DATE

NSF 22-543 **03/23/2022**

☐ Special Exception to Deadline Date Policy

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NSF PROPOSAL NUMBER

2224439

FOR CONSIDERATION BY NSF ORGANIZATION UNIT(S) (Indicate the most specific unit known, i.e. program, division, etc.)

DEB - LONG TERM ECOLOGICAL RESEARCH

DATE RECEIVED	NUMBER OF COPIES	DIVISION ASSIGNED	FUND CODE	UEI (Unique Entity Identifier)	FILE LOCATION
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NAME OF PRIMARY PLACE OF PERF

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ADDRESS OF PRIMARY PLACE OF PERF, INCLUDING 9 DIGIT ZIP CODE

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TITLE OF PROPOSED PROJECT

LTER: Long-term research on the dynamics of high-elevation ecosystems: A framework for understanding rates of ecological response to climate change

SHOW LETTER OF INTENT ID IF APPLICABLE

REQUESTED AMOUNT	PROPOSED DURATION (1-60 MONTHS)	REQUESTED STARTING DATE	SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
$ **7,650,000**	**72** months	**12/01/2022**	

THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW

☐ BEGINNING INVESTIGATOR
☐ DISCLOSURE OF LOBBYING ACTIVITIES
☐ PROPRIETARY & PRIVILEGED INFORMATION
☐ HISTORIC PLACES
☒ VERTEBRATE ANIMALS IACUC App. Date ____
PHS Animal Welfare Assurance Number **pending**
☒ TYPE OF PROPOSAL **Research**

☐ HUMAN SUBJECTS Human Subjects Assurance Number ____
Exemption Subsection ____ or IRB App. Date ____
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Non-Collaborative

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PROJECT SUMMARY

OVERVIEW

The Niwot Ridge/Green Lakes Valley (NWT) LTER is an interdisciplinary research program that strives to develop a predictive understanding of ecological processes in high-elevation mountain ecosystems. Through research, education and outreach, NWT engages diverse scientists, students, and citizens in the scientific exploration of mountain ecosystems, and shares information with stakeholders to inform resource management and conservation. In NWT VIII, we build on over four decades of research that has documented striking variation in the rates at which ecological processes have responded to climate change. Integrating long-term data, manipulative experiments, and models, we will systematically evaluate the mechanisms driving variation in the rates at which organisms, communities, and ecosystem processes respond to warming, and the consequences of this variation in forecasting ecosystem function at landscape scales. We will leverage the natural topographic complexity and biodiversity of high-elevation mountain terrain to disentangle the abiotic and biotic drivers of variation in ecological response rates across a wide range of organisms. This work will provide broad synthetic conceptual advances in ecology, ecosystem science, and global change biology while improving specific understanding of alpine and subalpine ecosystems.

INTELLECTUAL MERIT

While it is well-established that climate change drives ecosystem change, there is tremendous variation in the rate at which ecological systems have responded, complicating attempts to forecast future ecological states and changes in ecosystem function. In NWT VIII, we propose a conceptual framework that explicitly evaluates the ecological mechanisms that determine the speed with which biota and ecosystem processes respond to climate change. We focus on rising air temperature as a key climate driver that risen substantially at NWT and in mountain systems worldwide, and that may have particularly critical consequences for organisms adapted to high-elevation, cold-dominated environments. Leveraging the topographic complexity of NWT terrain, we will examine how rates of ecological responses to rising air temperature are mediated by spatial heterogeneity in temperature exposure and other abiotic factors (e.g., exposure, precipitation, growing season length, nutrients) and by biotic processes that unfold over this physical template (e.g., life history strategies, community dynamics, ecosystem legacies). The specific objectives of NWT VIII include (1) continuing to characterize how high-elevation mountain systems are responding to climate change, (2) testing hypothesized mechanisms that explain variation in the rate at which ecological responses track rising air temperature, and (3) exploring how the aggregated effects of variable rates of response to warming alter forecasts of ecosystem function across mountain landscapes.

BROADER IMPACTS

Long-term data collection in remote alpine areas is relatively rare, but provides invaluable information for the conservation and management of mountain catchments and the resources they provide to society. Located in the Front Range of the Colorado Rocky Mountains, NWT is uniquely positioned to generate knowledge that impacts a large human population while engaging diverse audiences in ecology, conservation, and mountain science. In NWT VIII, we will continue to provide high-quality outreach and education activities to communities in our region, train and engage graduate students in science communication, grow our efforts to recruit and support participants from underrepresented groups in science, and deepen our relationships with local organizations that share a common interest in our local mountains and the critical services they provide. We will play a key role in an ambitious research study that evaluates the potential for an immersive, field-based graduate orientation program to reduce barriers in graduate school for students from historically excluded groups. We also propose new K-12 programming that emphasizes “constructive hope,” integrates art into our science curriculum, and makes the NWT landscape accessible to students in their classrooms. Finally, we will lead a consortium of local stakeholders to develop a stronger collective understanding of the impacts of climate change in our local mountains. Our commitment to increase inclusion and equity at NWT, within our community, and across STEM disciplines is core to all of these efforts.

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LTER: Long-term research on the dynamics of high-elevation ecosystems: A framework for understanding rates of ecological response to climate change

1. INTRODUCTION. The Niwot Ridge/Green Lakes Valley (NWT) LTER is an interdisciplinary research program that strives to develop a predictive understanding of ecological processes in high-elevation mountain ecosystems. NWT also provides education and outreach activities that engage diverse scientists, students, and citizens in the scientific exploration of mountain ecosystems, and shares information with stakeholders that are invested in resource management and conservation in the Front Range of Colorado (**Fig. 1**). Our proposal builds on more than 40 years of long-term monitoring, manipulative experiments, and modeling to document, explain, and predict patterns of change in mountain ecosystems while contributing to synthetic conceptual advances in ecology, ecosystem science, and global change biology.

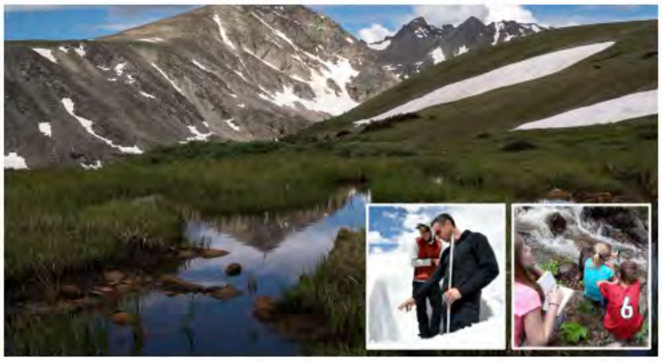

Fig. 1. For over 42 years, the NWT LTER has developed research, education, and outreach programs that emphasize understanding ecological change in the high-elevation, complex terrain of Niwot Ridge and the Green Lakes Valley. *Photo credits:* W. Bowman, A. Rose, J. Papasso

Mountain regions represent 10% of the Earth's land surface, support a third of terrestrial species diversity, and supply clean water to half of the global human population (Immerzeel et al., 2020). High topographic relief dictates how the wind redistributes falling snow, where solar radiation warms and cold air pools, and how water flows through the landscape (Badger et al., 2021; Moser et al., 2019; Musselman et al., 2015; Rey et al., 2021; Scherrer and Körner, 2011; Zhang et al., 2018). This complexity makes it difficult to anticipate how mountain systems will respond to climate change, leading to seemingly conflicting predictions that they will both track (Grabherr et al., 2010; Panetta et al., 2018; Steinbauer et al., 2018) and lag behind (Alexander et al., 2018; Körner and Hiltbrunner, 2021; Suggitt et al., 2018) changing climate (Graae et al., 2018; Seastedt and Oldfather, 2021). Here, we argue that the debate around the ecological consequences of climate change in mountain systems can be reconciled by focusing on the mechanisms that regulate the *rates of response to climate change* (Bueno de Mesquita et al., 2018; Gendron et al., 2019; Graae et al., 2018; Knowles et al., 2019; Suggitt et al., 2018). Long-term records and recent studies have documented substantial variation in how quickly different organisms and ecosystem processes are responding to rising air temperature at NWT, motivating our intent to explain the drivers of variable rates of response to climate change in NWT VIII.

The overarching goal of NWT LTER VIII is to identify and describe the interacting abiotic and biotic mechanisms that cause differential rates of ecological response to climate change. We focus on how responses to *rising air temperature* – a climate driver at Niwot Ridge that has shown directional change over the past 70 years – are mediated by abiotic factors that have not changed in step with air temperature (e.g., precipitation, climatological growing season length, nutrients) and biotic processes (life history strategies, community dynamics, ecosystem legacies). Informed by 40+ years of long-term observations, experiments, and models, we propose to test five hypotheses to explain variation in the rates at which different organisms, communities, and ecosystem processes respond to climate change (**Fig. 2**). The topographically complex landscape of Niwot Ridge and the Green Lakes Valley provides a particularly powerful context for testing these hypotheses, allowing for broad conceptual advances in ecological science while improving specific understanding of alpine and subalpine ecosystems. At the same time, we will continue to provide high-quality outreach and education activities to our community, grow our efforts to recruit and support participants from underrepresented groups in science, and deepen our relationships with local organizations that share a common interest in understanding, conserving, and managing our local mountains and the critical services they provide.

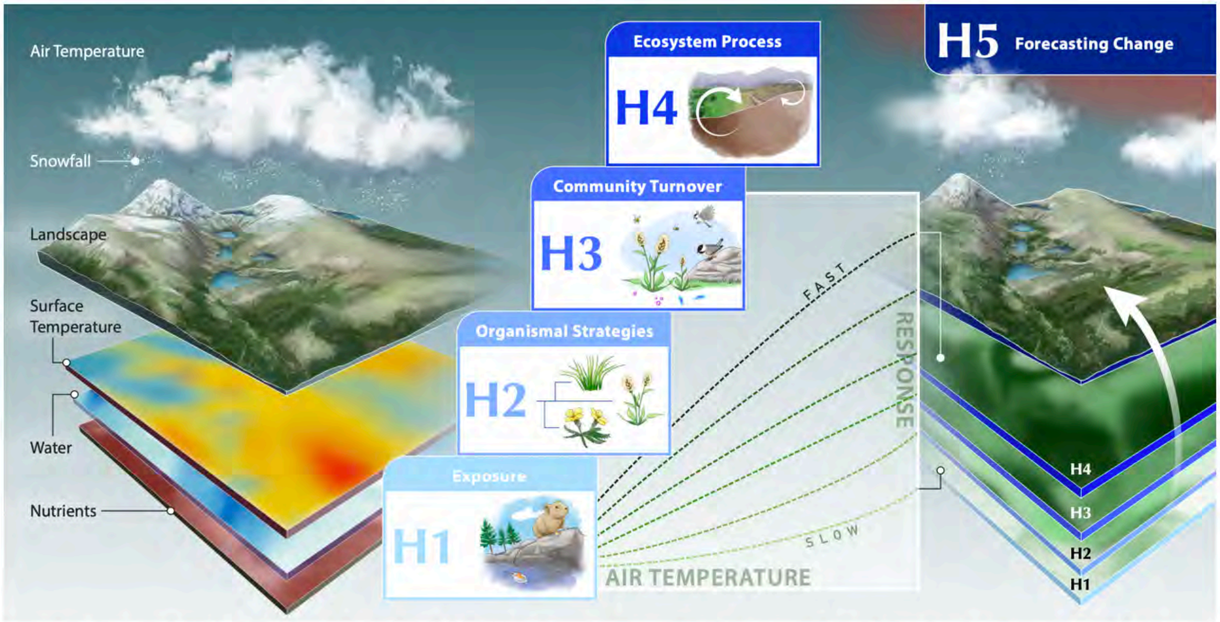

Fig. 2. Conceptual framework for NWT VIII. New and continued research builds upon the focus of LTER II-VII to understand the mechanisms that govern differential rates of ecological response to climate change. We structure our hypotheses around four mechanisms and their integration. **(H1)** Topographic heterogeneity mediates the extent to which organisms are exposed to changing climate (microclimate, *surface temperature heatmap*) and other limiting factors (*water*, *nutrients*) that can accelerate or attenuate their responses. (**H2**) Species characteristics – particularly climate niches, resource use strategies, and phenotypic plasticity – cause variation among organisms in how quickly fitness and population growth respond to changing climate. (**H3**) The rates of species turnover in communities will be influenced by the nature and specificity of species interactions. (**H4**) Legacies in soil attributes and biota will drive variation in the rates of biogeochemical responses to climate change. Each of these mechanisms can result in a range of slow to fast responses (*dotted lines*) across terrain. We then investigate how the integration of the rates of ecological change (*light to dark green*, *H1-H4 layers on right*) can improve forecasts of future change **(H5)**. *Illustration credit:* E. Hartley

1.1. ECOLOGICAL CONTEXT: HIGH-ELEVATION, HETEROGENEOUS TERRAIN. Mountain environments in temperate regions are defined by high elevations, rugged terrain, and extreme climate. Short growing seasons provide brief interludes from long, cold winters, when strong winds and intense snowstorms generate some of the harshest conditions inhabited by living organisms on the planet (Körner, 2021). Topographic heterogeneity mediates solar radiation and shapes how wind redistributes snow (Essery and Pomeroy, 2004), generating complex spatial variation in abiotic conditions that influence community structure and ecosystem processes (Litaor et al., 2008; Walker et al., 1993). In the alpine tundra, microtopographic variation in soil depth, moisture, nutrients, and growing season length drives plant species turnover over short distances (**Fig. 3**; Suding et al., 2015). In high-elevation aquatic systems, morphometry and stream geomorphology determine water residence times, water temperatures, light availability, and nutrient export (Poff and Ward, 1990), causing fine-scale variation in community structure (Hotaling et al., 2019).

There is growing evidence that climate change is amplified in mountains, with air temperatures rising faster than in their lowland counterparts (Gao et al., 2021; Pepin et al., 2015; Rangwala and Miller, 2012) at an average rate of 0.3°C ± 0.3°C /decade in many mountain regions (including Western North America), outpacing the global warming rate of 0.2 ± 0.1°C / decade (Hock et al., 2019). At Niwot Ridge, maximum annual air temperatures have increased even faster, at an average rate of 0.5°C /decade (see **2.1**). Rising air temperatures reduce snowpack volume (Mote et al., 2018, 2005), cause earlier, prolonged snowmelt seasons (Musselman et al., 2017), lead to wetter, heavier snow that is less easily redistributed by wind (Badger et al., 2021), and yield longer ice-free seasons in alpine lakes (Christianson et al., 2021). Here, we tackle how these broad macroclimate changes drive ecological responses across microtopographic heterogeneity.

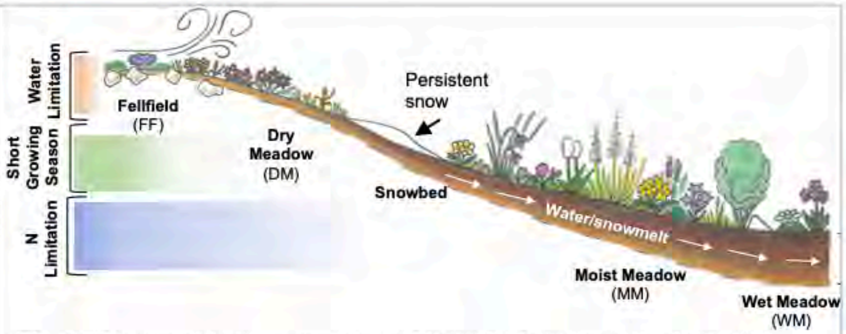

Fig. 3. Topographic heterogeneity at Niwot Ridge generates fine-scale spatial (microsite) variation in microclimate and other physical factors, including water availability, growing season length, nitrogen limitation, and soil depth. We broadly refer to the spatial distribution of these factors as the *hillslope gradient.* This variation occurs at finer spatial scales (e.g., 10-100m) than macroclimate variation (e.g., along elevation gradients). Our premise in NWT VIII is that these microsites generate variation in species composition, functional traits, and ecosystem processes that influence ecological rates of response to climate change.

1.2. CONCEPTUAL FRAMEWORK AND OVERARCHING QUESTIONS. As the complex impacts of climate change on natural systems unfold, a focus on understanding the drivers of variation in ecological *rates of response* provides a conceptual framework centered on the speed of ecological response to changing climate drivers (**Fig. 2**) (Blonder et al., 2015; Smith et al., 2009; Williams et al., 2021). For example, while some species may respond quickly to climate change, with changes in growth or reproduction that closely track the rate of climate change, the response of an entire community may be slower due to lags in the rate species are lost and new species colonize (Bardgett and Caruso, 2020; Shoemaker et al., 2022). A relatively slow rate of species turnover may affect ecosystem responses such as productivity that are influenced by community composition (Farrer et al., 2015). While variability in climate responsiveness is expected across ecological levels of organization as well as ecological context, the mechanisms that cause these differences are poorly understood (Ackerly et al., 2020; Trisos et al., 2020; Williams et al., 2021).

Explanations for variation in response rates can be broadly grouped into abiotic and biotic mechanisms. Abiotic mechanisms include landscape features that decouple the microclimate experienced by organisms from atmospheric changes and determine the distribution of other limiting factors (Ackerly et al., 2020; Dobrowski, 2011; Oldfather et al., 2020). Biotic controls include a broad range of physiological (Buckley et al., 2015), ecological (Adler et al., 2012), and evolutionary processes (Nadeau et al., 2017) that influence the extent to which organisms can respond to changes in the environment. The variety of potential abiotic and biotic circumstances for any organism generate a diversity of potential climate responses among components (individuals, populations, communities) within an ecosystem (Svenning and Sandel, 2013). To date, tests of these mechanisms are largely constrained to paleoclimate comparisons (Davis & Shaw 2001; Blonder *et al.* 2018a; Ordonez & Svenning 2020), and are rarely investigated across biological levels of organization in the same ecological context. Consequently, we currently know little about how the mechanisms operating at one biological scale (e.g., within individuals) influence processes at other biological scales (e.g., communities), and how heterogeneous rates of response aggregate to drive changes in ecosystem function at landscape scales.

In NWT VIII, we will leverage the natural heterogeneity of high-elevation mountain terrain to disentangle the abiotic and biotic drivers of ecological response rates across multiple levels of biological organization (**Fig. 2**). We propose to accomplish this goal by addressing the following questions:

Q1: EXPOSURE – How do terrain-related differences in climate exposure and other physical factors affect ecological response? Heterogeneous terrain provides a fixed physical template that mediates the microclimate that organisms experience and other potentially limiting factors, including moisture, growing season length, and nutrient availability (Hoylman et al., 2018; Körner and Hiltbrunner, 2021;

Morelli et al., 2020). We hypothesize **(H1): Ecological change will be fastest in microsites where organisms are most exposed to rising air temperatures and less limited by other abiotic factors.**

Q2: ORGANISMAL STRATEGIES – Which species attributes predict how quickly individuals and populations respond to changing climate? Species exhibit a wide range of responses to the same climate drivers due to their different strategies for responding to changing resources and unique evolutionary histories (Carscadden et al., 2020; Holt, 2009; Jackson et al., 2009; Nadeau et al., 2017). Considering these sources of organismal variation, we hypothesize **(H2): Differences in species thermal niches, resource use strategies, and potential for phenotypic plasticity will explain variation among species in the rates at which they respond to warming.**

Q3: COMMUNITY TURNOVER – What community attributes predict how quickly species composition changes in response to changing climate? Rates of change in communities are determined by the rates of species colonization, loss, and shifts in relative abundance, all of which are mediated by interactions among species (Alexander et al., 2015; Gilman et al., 2010; Olsen et al., 2016). We hypothesize **(H3): The rate at which communities respond to climate change will vary with differences in the nature and specificity of biotic interactions across microsites.**

Q4: ECOSYSTEM FUNCTION – How do soil attributes and community composition influence the rates at which ecosystem processes respond to a changing climate? The rates at which ecosystem processes change are mediated by the starting physical and chemical properties of the soil and plant and microbial community composition (Monger et al., 2015; Polussa et al., 2021; Strickland et al., 2015). Thus, we hypothesize **(H4): Legacies in soil attributes and plant and microbial communities will slow the rate at which ecosystem processes respond to rising air temperatures.**

Q5: FORECASTING CHANGE – Does including climate exposure and rates of biological responses across a heterogeneous landscape improve model forecasts of ecological change? Integrated ecological forecasts are complicated by the mechanisms that influence the rate at which ecological change occurs with shifting climate drivers (**H1-H4**). Ideally, forecasts integrate across both space (where rates of response vary among microsites; Ackerly *et al.* 2020) and levels of biological organization (e.g., individuals vs. communities; Smith et al., 2009). We hypothesize **(H5): Including heterogeneous response rates across space and among ecological systems in ecosystem models improves our ability to forecast landscape-scale changes in function with climate change.**

1.3. LONG-TERM RATIONALE. NWT is particularly well positioned to examine the abiotic and biotic mechanisms that determine the rates at which organisms, communities, and ecosystems respond to rising temperatures due to climate change, and the consequences of this variation in forecasting ecosystem function at landscape scales. 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, which remains the longest high-elevation continuous climate record in the US (McGuire et al., 2012) (**Fig. 4; Table 1A**). Since becoming an LTER site with the first cohort in 1980, NWT researchers have studied the biophysical drivers of change (NWT III-V), how these drivers change spatial heterogeneity and connectivity (NWT VI), and most recently, when and where changing climate drivers cause ecological responsiveness across complex terrain (NWT VII).

In NWT VIII, we build on our prior research that has documented variation in rates of response across ecological levels of organization and microtopography to understand the consequences of rapid changes in climate that are unfolding at Niwot Ridge and high-elevation systems worldwide. Experiments and observations confirm the influence of microclimate, species traits, biotic interactions, and soil properties in determining responses to climate variation in general (Farrer *et al.* 2015a; Gasarch & Seastedt 2015; Winkler *et al.* 2016; Yang *et al.* 2020; Huxley & Spasojevic 2021). However, we do not yet understand how these, and other processes, interact to cause variation in the *rates* at which ecological systems respond to increasing air temperature. **We are now poised to evaluate how complex abiotic and biotic processes drive variation in the rates at which organisms, communities, and ecosystem processes respond to rising air temperature at NWT.**

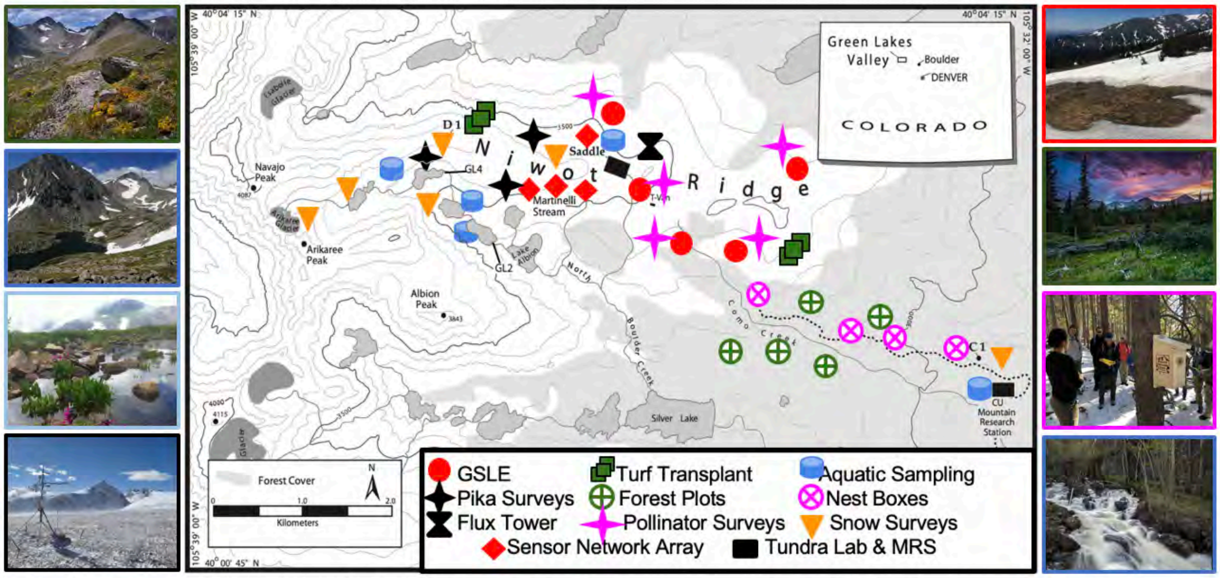

Fig. 4. The NWT LTER site includes Niwot Ridge and adjacent Green Lakes Valley. Long-term observations and experiments (subset indicated by symbols) are located from just east of the Continental Divide (3800m) to subalpine forest (2800m; light gray shading). Map shows 100m contours. NWT research includes (*clockwise from upper right*): an ongoing Growing Season Length Experiment; subalpine forest plots; Chickadee nest boxes; high-elevation streams; the highest flux tower in North America; alpine ponds; Green Lake 4 (looking towards Arikaree Glacier); the high alpine D1 site. GLSE = Growing Season Length Experiment; MRS = Mountain Research Station (of the Univesity of Colorado Boulder).

2. RESULTS OF PRIOR SUPPORT. *Niwot Ridge - Green Lakes Valley (NWT) LTER Program, 2016-2022*. $6,762,000. During LTER VII, NWT scientists authored 175 publications and 125 publicly available datasets. NWT publications included site-based, cross-site, and network-level contributions in both discipline-specific and high-impact journals. We trained over 120 undergraduate and graduate students as well as 18 postdoctoral researchers, and engaged with approximately 300 K-12 students annually. Our new website (launched in 2019) averaged 27,000 visits per year. Below we highlight progress in specific areas, including **10 selected publications** (**<u>in bold underlined text</u>** the first time they are cited in the following sections) that represent the breadth of outcomes from LTER VII.

Data Availability. NWT has published a total of 324 datasets that span 1940-2022; 38% include data that were collected during NWT VII. Datasets that have motivated the proposed work and will be used or expanded to test the hypotheses of NWT VIII are summarized in **Tables 1 and 2**, while a comprehensive list of NWT datasets is provided in **Tables S1A and B.** We reference the NWT datasets used to generate figures in this proposal by providing the Environmental Data Initiative (EDI) knb-lter-nwt package ID in captions. Our protocols for the collection, publication, and curation of these datasets, including timelines for data publication, are summarized in our **Data Management Plan.**

Table 1. NWT's long-term datasets that characterize the climate drivers and geophysical responses that motivate the proposed research and will be used to test **H1-H5.** See **Fig. 4** for sampling locations. MRS = CU Boulder Mountain Research Station; GLV = Green Lakes Valley.

Dataset	Locations	Measurement Details
A. Climate	C1, D1, Saddle	<u>1952-ongoing(C1, D1); 1982-ongoing (Saddle)</u>: Climate measures collected on chart recorders and data loggers.
B. Snow depth, snow water equivalent (SWE)	Saddle grid, GLV between D1 and Arikaree	<u>1992-ongoing</u>: Saddle grid plots (88 plots, measured bi-weekly), with periodic measurements of snow density at select locations; annual intensive snow survey in GLV at peak SWE.

C. Stream, lake, snow chemistry	Various GLV sites	1982-ongoing: Major cations and anions, pH, conductance, reactive silicate (Si), SO$_4$, dissolved organic nutrients (DOC, DON, DOP).
D. Streamflow	Various GLV sites	1981-ongoing: Daily streamflow discharge records.
E. Lake ice cover	Various GLV sites	1981-ongoing: Measurements of ice cover thickness and ocular estimates of ice cover (spring, fall); used to calculate ice-free duration.

Table 2. Long-term ecological observations and experiments from the NWT LTER that have motivated the proposed research and will be used to test **H1-H5.** We prioritize data sets that encompass multiple spatial locations for **H1**, species that vary in specific characteristics for **H2**, species pairs or multispecies communities in **H3**, responses with links between composition and function in **H4**, and parameters for the models we propose in **H5**. See **Fig. 4** for sampling locations. MRS = CU Boulder Mountain Research Station; GLV = Green Lakes Valley; GSLE = Growing Season Length Experiment.

Dataset *(location)*	**Hyp**	**Ecological Responses**	**Measurement Details**
A. Tundra vegetation *(Saddle; alpine)*	**H1** **H2** **H3** **H4** **H5**	Aboveground biomass, plant species composition	1989-ongoing: Annual surveys of 88 1m^2 plots, spaced at 50m intervals, point quadrat species cover. Adjacent 0.25m^2 plots harvested for aboveground biomass. 2006-ongoing: Experimental warming x snow x nitrogen manipulations in moist meadow. *New in NWT VIII:* install surface and subsurface (5cm) temperature sensors in each plot, expand functional trait measurements.
B. Subalpine forest *(C1 to treeline)*	**H1** **H2** **H3**	Survival, stand production, radial growth, seedling recruitment	1982-ongoing: 12 stands (>100 years old) distributed across a moisture gradient (xeric to hydric),~400 trees (>4cm DBH) per stand; 9 stands mapped and monitored 9 times in the last 40 years; 3 new permanent plots installed near treeline in 2016. 2015-ongoing: Monitoring soil moisture, seed production, germination, and seedling establishment annually; mortality and ingrowth every 3 years in 7 plots. 2020-ongoing: annual monitoring of diameter growth using dendrometer bands in 5 plots.
C. Pika population *(West Knoll near Saddle)*	**H1**	Habitat occupancy, population persistence, individual survival	1980-1990, 2004-ongoing: Representative population sampling. 2016-ongoing: occupancy survey. *New in NWT VIII:* increase spatial resolution of subsurface temperature and humidity sensors in talus.
D. Zoo-plankton and Primary Production *(Green Lakes)*	**H1** **H2** **H3**	Community composition, traits, chl-a	2012-ongoing: Weekly sampling with conical net from deepest location during ice-free season; zooplankton identified to species and classified as by developmental stage; body length measured for 50-100 individuals/taxon/sample.
E. Flux towers *(near Saddle)*	**H5**	Ecosystem carbon dioxide, water vapor, energy	2007-ongoing: Alpine eddy covariance flux towers.
F. Sensor Network Array *(Saddle, Saddle Catchment)*	**H1** **H2** **H3** **H4** **H5**	Soil moisture, soil and air temperature, snow depth, nutrient cycling, plant composition, phenology	2017-ongoing: 16 nodes distributed throughout Saddle Catchment; each node is instrumented with sensors that measure soil moisture and temperature at 2 depths (5cm, 30cm) in 3 subplots, co-located with snow depth and air temperature, and vegetation plots. Time lapse cameras (phenocams) capture images every 30 min. during the growing season. *New in NWT VIII*: annual surveys of pollinator attraction traits; ingrowth cores to assess belowground NPP; soil NO$_3^-$ and NH$_4^+$, total C and N, enzyme activity, microbial biomass.

G. Growing Season Length Experiment (GSLE) *(alpine)*	**H1** **H2** **H3** **H4** **H5**	Plant community composition, productivity, soil moisture and temperature, snow depth	2018-ongoing: 5 experimental sites, two 10 x 40m plots/site, one control and one with snowmelt accelerated by applying chemically inert black sand; 3 $1m^2$ experimental warming (OTC) chambers/plot measure interactive effects of snowmelt timing and warming; soil temperature and moisture, NDVI, vegetation, and pollinator visitation data collected in multiple subplots per plot.
H. Chickadee Nest Boxes (*subalpine forest)*	**H1** **H2** **H3**	Lay date, hatch date, chick quality, fledging success, DNA	2018-ongoing: 150 nest boxes distributed across an elevational transect from the subalpine forest to the MRS. Breeding, fledging, and genetic data collected annually. *New in NWT VIII:* install temperature sensors in all nest boxes.
I. Pollinators (*Saddle, GSLE sites)*	**H1** **H2** **H3**	Pollinator species abundance, richness, diversity, traits	*New in NWT VIII:* 2 vane traps and 5 bee bowls triplets (red/blue/white) on 50m transects at 5m intervals in 6 sites; sampled 3x/summer; air and soil temperature sensors to be installed along transects. *Sampling methods piloted in 2021.*
J. Pond and stream macro-invertebrates (*GLV, Saddle, MRS)*	**H1** **H2** **H3** **H4**	Macro-invertebrates	*New in NWT VIII:* collect on benthos and in water column using a D-frame kick net (250 um mesh, 30cm opening, $0.09m^2$ sample area); co-located measures of water temperature, pond bathymetry/stream geomorphology, depth, temperature, DO, conductivity, and pH. *Sampling methods piloted in 2021.*

2.1. CHANGING CLIMATE AT HIGH ELEVATION. NWT exhibits a strong temporal trend of warming, (Bueno de Mesquita et al., 2021; McGuire et al., 2012) with an annual maximum temperature increase of ~0.5°C/decade over the past 70 years in both subalpine (C1) and alpine (D1) environments (**Fig. 5A; Table 1A).** Over the same time period, precipitation (75% of which falls as snow at NWT) shows high interannual variability, with no overall trend in the subalpine. In the alpine, a step increased occurred in the 1980s, reflecting a decadal shift in atmospheric circulation 1980s (Kittel et al., 2015) (**Fig. 5B**). After taking this step change into account, we detect no significant trends in precipitation in either the alpine or the subalpine at NWT during the time period covered by LTER observations.

Prior to 2000, warming at NWT was coupled with longer, drier growing seasons, spurring our focus on extended summers in NWT VII. Updated analyses using recent climate records show a decoupling between summer temperature and the length of the frost-free season (**Bueno de Mesquita et al., 2021**), with temperatures continuing to rise without changes in season length. Consequently, **in NWT VIII we focus on rising air temperatures as a key driver of changing climate in this system.** We leverage the decoupling between temperature (increasing through time, **Fig. 5A**) and snowfall (no directional change through time, **Fig. 5B**) to explore the interacting effects of climate controls across heterogeneous terrain.

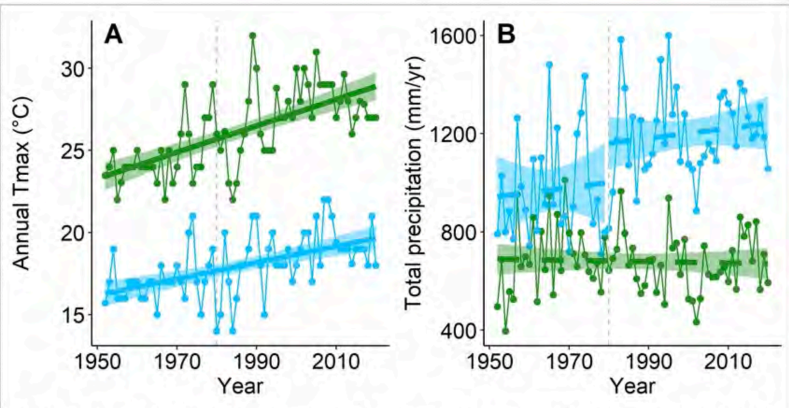

Fig 5. (A) The maximum annual temperature (T_{max}) has increased (solid lines) in both alpine (D1) and subalpine (C1) sites at NWT. **(B)** Total annual precipitation is highly variable in both time and space, with no detectable change (dashed lines) in alpine or subalpine (accounting for a decadal oscillation step change in the alpine in the 80s). Data sources: 184.5, 185.2, 186.3, 187.2, 411.13, 412.11, 414.13, 415.14

2.2. SNOWMELT AND ICE-OFF. In snow-dominated systems such as NWT, climate determines the onset and development of snow cover (snowfall), the conditions responsible for its ablation (solar radiation, air temperature), and its redistribution across the heterogeneous terrain (wind)(Jennings et al., 2018; Jennings and Molotch, 2020; Sexstone et al., 2018). Higher temperatures have increased snowmelt before maximum snowpack in the winter, consistent with regional patterns (Musselman et al., 2021), causing streams to begin flowing earlier in warmer springs (**Fig. 6A; Table 1D**). Rising temperatures have substantially increased the length of the ice-free period in NWT lakes: since 1983, the ice-free period in the Green Lake Valley has grown an average of 0.5 days/year (**Christianson et al., 2021**) (**Fig. 6B**; **Table 1E**). This decline in the duration of ice cover– which is ~50% faster than Northern Hemisphere lakes on average – is correlated with increased water residence times, thermal stratification, ion concentrations, dissolved nitrogen, pH, and chlorophyll-a, leading to shifts in overall lake functioning (Preston et al., 2016).

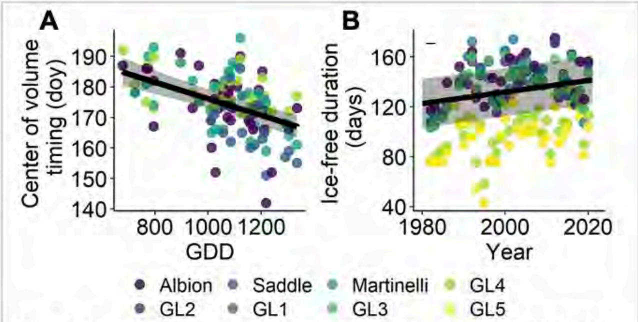

Fig 6. Seasonal changes in physical conditions at NWT are associated with warming temperatures. **(A)** Stream discharge occurs earlier in warmer years. Points show center of volume timing (day of year at which 50% of the annual streamflow has passed for each water year) against total growing degree days (GDD) at the Saddle climate station over the same periods; different colors represent different stream gauges. Here, and throughout the proposal, GDD is calculated as the annual sum of daily mean temperatures above 0°C **(B)** The length of the ice-free period is increasing over time in the alpine lakes of the Green Lakes Valley. Data sources: 78.3, 102.16, 103.14; 105.14, 106.4, 108.12, & 405.5

2.3. BIOGEOCHEMICAL AND HYDROLOGICAL CHANGES. In NWT VII, we made substantial progress quantifying the spatial distribution of soil moisture, inorganic nitrogen transformations and hydrologic connectivity across the heterogeneous terrain at NWT, providing a critical foundation for exploring how these processes mediate ecological change with rising temperatures. We quantified spatial variation in the temporal dynamics of soil moisture, with wind-scoured areas drying early in the growing season while areas with snowbanks retain moisture for most of the summer (**Hermes et al., 2020**). Wetter locations are hydrologically connected to the primary stream channel, while dry patches are disconnected year-round (Hermes et al., 2020). This patchiness causes spatial variation in the rates of nitrogen mineralization, microbial biomass, and primary production (Chen et al., 2020; Schmidt et al., 2015) (**Fig. 7A**).

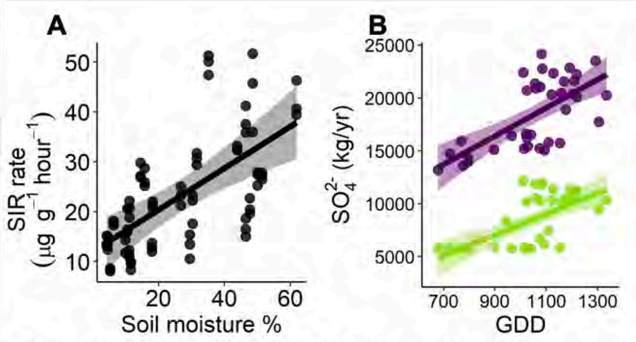

Fig 7. Processes at Niwot Ridge depend on hydrological dynamics that are sensitive to rising air temperatures at multiple spatial scales. **(A)** Across microsites in the Saddle catchment, substrate-induced respiration (SIR, an indicator of potential microbial activity and biomass) is higher in areas with greater gravimetric soil moisture. Points show SIR micrograms C-CO_2/g dry soil/hour. **(B)** In the Green Lakes Valley, annual sulfate flux, likely indicative of weathering, from the outlets of Lake Albion (purple) and Green Lake 4 (green) is higher in warm years. Points show flow-normalized flux by water year from two year-round streams against total growing degree days (base 0) at the Saddle climate station. Data sources: 78.3, 102.16, 103.14; 105.14, 108.12, 204.1 & 405.5

Recent work at NWT reinforces that the effects of warming on biogeochemical processes and primary productivity will be contingent on corresponding patterns of snowmelt, soil moisture, and nutrient deposition, and thus vary with topography (Chai et al., 2019; Hermes et al., 2020). During NWT VII, a modeling study found that gross primary production (GPP) in dry meadow plant communities is limited by air temperature early in the growing season, N availability mid-season, and soil moisture late in the season (Fan et al., 2016). Follow-up work using the Community Land Model (CLM; see **3.5.2**) found that productivity in wetter and drier tundra plant communities at NWT respond differently to warming and changes in growing season length (**Wieder et al., 2017**). The effects of nutrient addition on productivity also vary with topography, with wetter locations exhibiting stronger nitrogen and phosphorus limitation (Bowman, 1994; Bowman et al., 2012). The majority of base cations and nitrogen atmospheric deposition occurs during the snow season, and the redistribution of snow by wind can lead to large differences in nutrient inputs across the landscape (Heindel et al., 2020; Litaor et al., 2018) with strong cumulative effects on nutrient stocks (Bowman et al., 2018). Moving into NWT VIII, we know that atmospheric nitrate and sulfate deposition at NWT – once eight times background levels – have declined, while atmospheric ammonium deposition related to agricultural emissions is increasing (**Crawford et al., 2020**).

As predicted in NWT VII, rising temperatures are having increasingly detectable effects on geophysical processes at Niwot Ridge and throughout the Green Lakes Valley. Higher temperatures are associated with increased weathering and thawing of patchily-distributed permafrost and rock glaciers throughout the valley and across the ridge (Crawford et al., 2019; Leopold et al., 2015) (**Fig. 7B; Table 1C,D**). The Arikaree Glacier (**Fig. 4**) is shrinking and projected to disappear within two decades (Leopold et al., 2015). Thawing events create new subsurface flow paths in areas that may not often receive flushing from snowmelt water, enhancing sulfate and ammonium export in surface waters over time (Crawford et al., 2019; Williams et al., 2015) while depleting the ice sources that provide valuable hydrological buffers in drought years (Leopold et al., 2015). Thawing may also contribute to net ecosystem carbon loss by stimulating soil respiration **(Knowles et al., 2019)**.

2.4. POPULATION, COMMUNITY AND ECOSYSTEM RESPONSES TO WARMING. We find that temperature is a key structuring factor for many ecological processes at high elevation, including phenology (**Collins et al., 2021**; Jabis et al., 2020), alpine plant and subalpine tree mortality (**Andrus et al., 2021**; Nomoto and Alexander, 2021), tundra plant compositional turnover (Elmendorf et al., 2012; Myers-Smith et al., 2015), and aquatic production (Oleksy et al., 2020; Preston et al., 2020). Yet, at NWT, we observe substantial variation in the rates at which organisms and processes have changed with warming: as illustrated in the following 5 case studies, some organisms, communities, and processes have responded quickly to changing temperatures, others have shown more attenuated responses, and still others have shown no detectable response to date. These varied responses align with general observations that rates of response to climate change are be mediated by microclimate variation and other abiotic and biotic drivers (Bjorkman et al., 2018a; Körner and Hiltbrunner, 2021; McLaughlin et al., 2017).

2.4.1. Rapid responses to warming in pikas. The American pika (*Ochotona princeps*) is considered a sentinel of climate change, largely due to its sensitivity to warm temperatures. Occupancy rates of pika talus habitats are projected to decline near NWT (Schwalm et al., 2016) and across the Western US (Ray et al., 2012), and pika recruitment (juvenile:adult ratio) at NWT has declined with warmer temperatures since 1980 (**Fig. 8A; Table 2C**). Temporal variation in stress hormones also appears to be driven in part by subsurface talus temperatures (**Whipple et al., 2020**), which recent analyses suggest may be rising even faster than air temperature; on one north-facing slope at NWT, recent subsurface temperatures (measured at 1.5 m deep) have been up to 12°C higher than they were in 1964, while air temperature has increased by 7°C (Monk and Ray, *in review*). These patterns suggest that the pika's rapid response to warming may be at least partially driven by amplified thermal changes in its subsurface refugia.

2.4.2. Variable responses in tundra plant communities. The rates at which plant community composition changes with warming varies among community types in NWT tundra vegetation (**Fig. 8B; Table 2A**) (Spasojevic et al., 2013; Suding et al., 2015; Yang et al., 2020). Over the last 30 years, compositional turnover with warming has been fastest in the communities that experience the most extreme abiotic conditions: wet meadow and snowbed, which experience the most persistent snowpack, shortest growing seasons, and highest soil moisture during the summer; and fellfields, which experience the least snow and longest, driest growing season (**Fig. 3**). In contrast, dry and moist meadows show no significant turnover with warming. However, even where turnover is minimal, we see notable changes in species abundance: species whose geographic ranges span temperatures that are, on average, warmer than NWT are becoming more abundant in moist meadow, wet meadow, and snowbed communities, while species whose ranges span temperatures that are, on average, cooler than NWT are becoming increasingly common in the dry meadow (see **3.2.2**). The increase in "cooler-than-NWT" species in drier habitats may reflect an increasing benefit of drought-tolerant traits, some of which can also increase cold tolerance (Šímová et al., 2017), and is consistent with a shift toward more conservative, stress-tolerant traits including lower specific leaf area (SLA) and increased water use efficiency (Huxley and Spasojevic, 2021) in alpine tundra vegetation.

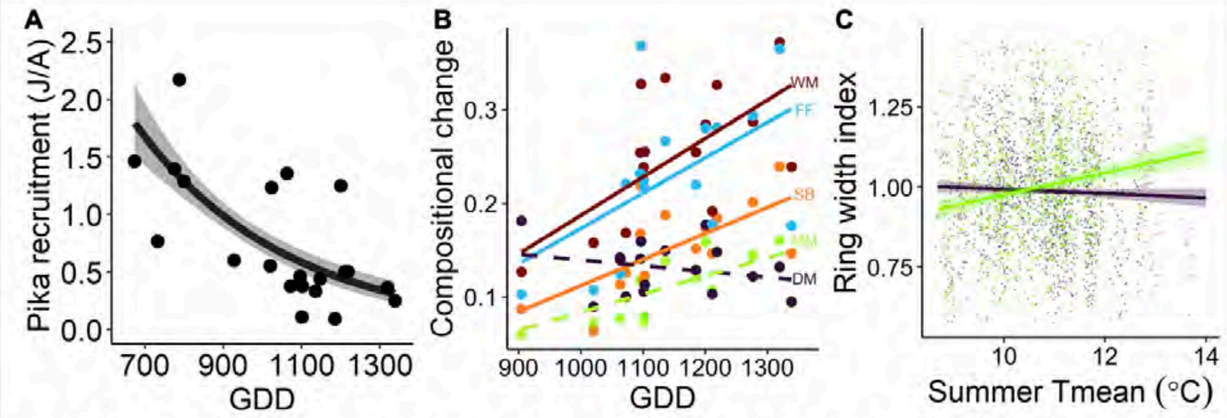

Fig 8. NWT long-term records show substantial variability in species responses to warming. **(A)** Pika recruitment over time varies inversely with growing degree days (GDD). **(B)** Compositional turnover with increasing GDD varies across plant community types in the alpine tundra (DM = dry meadow, MM = moist meadow, WM = wet meadow, SB = snowbed, FF = fellfield). **(C)** Tree growth (ring width index) response to summertime temperature conditions varies with site-level moisture conditions, with hydric (green) sites showing a stronger positive response than xeric (purple) sites. Data sources: 8.4, 43.4, 78.3, 93.5, 185.2, 405.5, 413.11; Villalba *et al.* 1994 (noaa-tree-35293, 35294, & 35295), R. Chai, thesis *in prep*

2.4.3. Soil moisture-mediated responses in tree populations. In the subalpine forest, warmer climate conditions have been broadly associated with decreased seedling establishment (Andrus et al., 2018) and increased tree mortality (Andrus et al., 2021). However, these responses are contingent upon temporal variation in the degree of aridity: since 1982, seedling recruitment events have been episodic, only occurring in cool, wet summers (Andrus et al., 2018) and moisture largely compensates for the negative effects of warming on establishment above treeline (Conlisk et al., 2018). Moreover, topographically-mediated moisture availability and stand age were shown to predict aboveground live tree biomass production in NWT permanent plots over a 35-year time period (Chai et al., 2019; 1982-2016, **Table 2B**; Villalba et al., 1994), with radial growth increasing with higher summer temperature in hydric sites, but not xeric sites (**Fig. 8C**). Collectively, these results indicate that the rate at which forest stands respond to warming via recruitment, mortality, and above-ground biomass production at Niwot will hinge on water availability, which varies among years and across the subalpine terrain.

2.4.4. Rapid range expansion in shrubs. Consistent with global patterns (Elmendorf et al., 2012), shrubs (predominantly *Salix* species.) have rapidly expanded into alpine tundra at NWT (Bueno de Mesquita et al., 2018; Formica et al., 2014; Scharnagl et al., 2019). Bueno de Mesquita (2018) calculated that shrub cover in the alpine at NWT has increased by nearly 8% per decade between 1972 and 2008. This encroachment is correlated with warming trends at NWT and linked to rising temperatures by experimental work (Formica et al., 2014). Shrubs change fine-scale patterns of snow accumulation and microclimate, plant community composition, and the nature of species interactions under their canopy (L. Brigham, thesis *in prep*).

2.4.5. Variable zooplankton responses to extended ice-free seasons. Rising temperatures over time are associated with longer ice-free seasons in the alpine lakes of the Green Lakes Valley (Christianson et al., 2021). The two dominant zooplankton species in these lakes – *Daphnia pulicaria* and *Hesperodiaptomus shoshone* – respond to longer ice-free seasons at different rates, with *Daphnia* showing stronger, faster increases in biomass while *Hesperodiaptomus* exhibits no significant response (**Loria et al., 2020**). These responses likely reflect the different life histories of the species (see **3.2.2**).

2.5. BROADER IMPACTS. Outreach and Education. In NWT VII, the goals of our Education and Outreach program were to improve the professional development of our graduate students, develop new outreach and education initiatives and partnerships, and broaden participation from underrepresented groups across all of our activities. To support **graduate student professional development**, we offered an annual 1-credit graduate seminar (EBIO 6100: *Science Communication and Outreach*) where students learned science communication skills, developed outreach materials that reflected their personal goals and interests, and shared their materials with public audiences in libraries, schools, and museums. Graduate students then participated in many **new K-12 outreach initiatives** that we developed in partnership with community organizations to broaden the diversity of the audiences we could reach in our region. Most notably, we worked with: (1) the Winter Wildlands Alliance (WWA) to bring several hundred students from low-income local schools to join us on snowshoes for a day of "Snow School" to learn about their watershed, snow science, and winter ecology; (2) Nature Kids Lafayette/Jóvenes Naturaleza to transform our long-running Mountain Research Experience course to specifically recruit first-generation college students, low-income, and Latino youth to participate in this week-long residential field science course at the MRS and Niwot Ridge each summer (14 students per summer); (3) the Boulder Creek CZO to produce an exhibit on the Boulder Creek Watershed for the Museum of Boulder and bring >150 elementary school students to meet NWT scientists; and (4) the CU Mountain Research Station (MRS) to create a series of self-guided interpretive trails in the subalpine, highlighting the work of NWT researchers. We also developed a new curriculum kit, *Adaptation and Variation in Colorado Mammals*, that was adopted by the Boulder Valley School District and used in over 80 classrooms.

To **broaden participation** at the undergraduate level, we began partnering with a Research Experience for Community College Students (RECCS) at CU Boulder in 2018 to recruit and support community college students for our REU positions. All REU students recruited through this program have been first-generation college students and/or people of color. Finally, to recruit and retain diversity within NWT, we established a graduate fellowship to recruit students from groups inadequately represented in the NWT community. We also conducted an internal community climate survey, developed priorities and implemented measures for improving inclusivity and equity at NWT, formalized a DEI plan and made it available on our website, and improved reporting mechanisms to ensure the safety and well-being of all individuals that participate in, or interact with, the NWT LTER.

2.6. RESPONSE TO MID-TERM SITE REVIEW. The August 2019 NWT VII mid-term site review team was enthusiastic about the research, training, outreach, and data management activities of the NWT LTER. The review concluded that NWT's focus "on heterogeneity and multi-scale sensitivity to biotic and abiotic drivers is providing a coherent pathway for integration across disparate research areas." The review team provided three primary suggestions that have guided our activities since the review and our preparation of this proposal:

Aligning research priorities with team expertise. The review team noted that an imbalance in aquatic and terrestrial expertise on our team was compromising our ability to effectively apply our conceptual framework equally across aquatic and terrestrial ecosystems. They encouraged us to reduce the emphasis of aquatic processes in NWT VIII while simultaneously working to strengthen our aquatic research program by recruiting new faculty with appropriate expertise. Since the review, we have facilitated the involvement of two aquatic ecologists – Dr. Daniel Preston (Colorado State University) and Dr. Kurt Anderson (UC Riverside) – who began preliminary work at the site in 2021. Additionally, our home unit at CU Boulder (INSTAAR) received permission to initiate a search for a tenure track position in aquatic ecology/aquatic biogeochemistry that is currently underway. We are optimistic that these efforts will increase our aquatic expertise over the next several years and allow us to extend our long history of excellence in aquatic alpine science. Until these scientists become established at NWT, we center our proposed research for NWT VIII on the terrestrial systems of Niwot Ridge, but still identify relevant datasets and developing projects in the aquatic systems that clearly align with our conceptual framework.

Broadening participation. The review team encouraged NWT to increase the participation rate of early-career scientists from underrepresented groups. In addition to strengthening our efforts to engage and support scientists from diverse groups (see **Results of Prior Support: Broader Impacts)**, we have supported several new faculty in establishing research projects at NWT that align with our LTER goals, which has increased diversity within our senior leadership (see **Project Management Plan**).

Preventing and reporting harassment. Finally, the team recommended that we formalize our training materials on preventing, reporting, and handling harassment, particularly in the field setting, into protocols and documents that are readily available to all participants. The NWT DEI committee has implemented this advice by integrating this information into our Code of Conduct, which is easily accessible on our website and discussed at length in our annual all-NWT training orientation program.

3. PROPOSED RESEARCH FOR LTER VIII. We propose a research program that integrates long-term monitoring, experimentation, and modeling to examine how ecological rates of response to increasing air temperature are shaped by climate, topographic complexity, and biological processes. By addressing the questions below within our proposed conceptual framework (**Fig. 2**), we will (1) continue to characterize how high-elevation mountain systems are responding to climate change, (2) test hypothesized mechanisms that explain variation in the rate at which ecological responses track rising air temperature, and (3) explore how the aggregated effects of variable rates of response to rising air temperature alter forecasts of future ecosystem function in mountain environments.

Integration. Our focus on understanding variation in *rates of response* provides a flexible metric – change per degree of warming – that allows us to ask a shared set of questions across the diversity of organisms, processes, and datasets we aim to integrate in NWT VIII (**Tables 1, 2**). While the specific responses of interest necessarily vary, the focus on understanding why some organisms and processes respond quickly to change in a common driver (rising air temperature), while others show more attenuated responses, provides a **conceptually integrated** approach for linking patterns in NWT long-term datasets, results of short-term experiments, and predictions in models for landscape-level changes in ecosystem function (**Fig. 2**). The five questions we address are fundamentally linked, with responses at each level of biological organization influencing, and being influenced by, responses at other levels. Consequently, our results will inform conceptual models that strive to predict how rates of response vary across levels of ecological organization (e.g., organismal responses will be faster than community responses, which will be faster than ecosystem responses; Smith et al., 2009). In NWT VIII, we expect a range of response rates at each biological scale given the range of organisms (fast-cycling soil microbes to long-lived subalpine trees) and processes (phenotypic plasticity, community turnover, carbon cycling). Considering multiple scales within a common conceptual framework (**Fig. 2**) allows us to explicitly investigate how they interact to drive long-term ecological change and future ecosystem function.

NWT VIII will draw upon shared experimental approaches, co-located observational datasets, and modeling to ensure that our work is **empirically and methodologically integrated**, including a new turf transplant experiment that will evaluate our first four hypotheses and inform the models that will test our fifth hypothesis (**Box 1**). We will also expand measurements in our Sensor Network Array (**Table 2F**) to generate observational data relevant to each hypothesis. Our final hypothesis, **H5**, will provide **integration by modeling,** both guiding and using the data collected in **H1-H4** to forecast how variable rates of response alter projected changes in ecosystem function.

BOX 1. Integrative Experiment: Turf Transplant across a Temperature Gradient

In NWT VIII, we propose a turf transplant experiment that will integrate across the hypotheses in our conceptual framework by measuring population, community, and ecosystem-level responses to warming (**Fig. 2**). This experiment will complement our *in situ* temperature manipulations (~1°C increases using open top chambers (OTCs); **Table 2A,G**) by providing a larger temperature increase than we can achieve with OTCs and incorporating novel interactions that will occur when low-elevation species migrate to higher elevations and interact with higher-elevation communities.

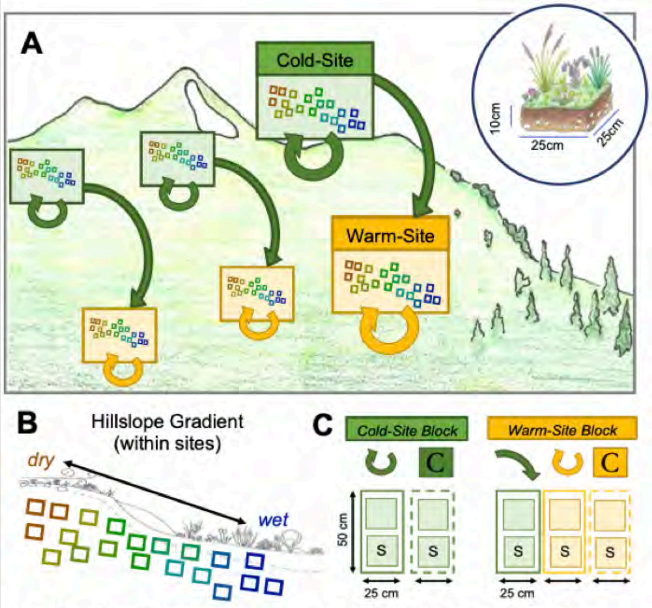

Fig. 9. A turf transplant experiment will complement our long-term observations and *in situ* warming experiments in NWT VIII. **(A)** Turfs will be transplanted from 3 high-elevation (cold) sites into paired low-elevation (warm) sites and locally replanted within sites by excavating 25cm x 25cm subplots (inset), with 5cm edge buffers, to the maximum rooting depth (5-10cm, Webber and May 1997). **(B)** Turfs will be transplanted into microsites across hillslope gradients that are similar to their original location. **(C)** Within each block, transplants will be assembled as pairs into 25cm x 50cm plots (solid borders) alongside unmanipulated controls (dashed borders). Half of of each plot (one turf) will be destructively sampled (squares labeled with "S"). Additional turf transplants will be established on the leeward sides of shrubs in one cold-warm site pair (not shown) to explore biogenic effects of shrubs (see **3.3.4**).

Experimental design: Our design is modeled after turf transplant experiments conducted in alpine tundra around the world (Alexander et al., 2015; Bay and Ebersole, 2006; Klanderud et al., 2015). We will manipulate *macroclimate* by transplanting tundra turfs (plots of intact plants and soil) from three high-elevation "cold" sites into paired low-elevation "warm" sites (**Fig. 9A**). The cold and warm sites represent the upper and lower elevational limits of the alpine tundra plant community at NWT, respectively, and differ by ~2°C in annual air temperature. Transplants will be placed in blocks arrayed across naturally occurring *hillslope gradients* (**Fig. 3**), with each turf transplanted into a microsite that is similar to its location in its original site (i.e., dry meadow turfs will be transplanted into dry meadows, and moist meadow into moist meadow; **Fig. 9B**). We will also locally replant turfs and establish unmanipulated controls (**Fig .9C**) at all sites. There will be 20 blocks distributed across hillslope gradients at each site, for a total of 60 blocks / elevation.

Response variables: We will measure response variables that effectively test each hypothesis (**section 3**), enable integration across hypotheses, and inform our models that forecast changes in landscape-scale ecosystem function in **H5.** For example, in **H2** (organismal strategies) we will measure plant responses in terms of individual fitness and population growth rates, which will directly influence changes in plant community composition (**H3**) and ecosystem legacies (**H4**). We will also prioritize measurements of plant traits, community patterns, and ecosystem responses used in **H5.**

Hypothesis testing: The majority of our predictions for **H1-H4** involve testing for interactions between transplant destination (the macroclimate treatment) and microclimate and abiotic variables associated with hillslope location (**H1**), species characteristics (**H2**), community composition (**H3**), or ecosystem processes (**H4**). To assess how multiple covarying characteristics contribute to responses, we will use multiple regression approaches with AIC model selection, acknowledging that in some cases strong covariation may limit inference. We will characterize how rates of responses change across levels of ecological organization (e.g., the hierarchical-response framework, Smith et al., 2009) by comparing effect sizes (Arft et al., 1999; Elmendorf et al., 2012; Pold et al., 2021; Yang et al., 2010).

3.1. Q1: EXPOSURE – How do terrain-related differences in climate exposure and other physical factors affect ecological response?

3.1.1 Ecological theory and rationale. Our first hypothesis builds on a growing body of research showing that responses to climate warming are strongly mediated by local-scale microclimatic and topographic factors (Carnicer et al., 2021; De Frenne et al., 2021; Körner and Hiltbrunner, 2021;

Pincebourde and Woods, 2020; Zellweger et al., 2020). Across ecosystems, many studies have documented that microsite variation is more important than prevailing local or regional air temperature in explaining variation in physiology (De Frenne et al., 2021; Graham et al., 2012; Wundram et al., 2010), species distributions (Löffler and Pape, 2020), functional trait and community structure (Blonder *et al.* 2018a; Graae *et al.* 2018; Zellweger *et al.* 2020), microbial activity and composition (Delgado-Baquerizo et al., 2016; H. Zhang et al., 2020), and nutrient and carbon cycling (Fisk and Schmidt, 1995). Here we propose to evaluate how topographically-mediated spatial variation in microclimate and other abiotic factors influences variation in the rates at which organisms respond to rising air temperatures at NWT.

In rugged mountain terrain, microclimate variation may provide refugia that buffer the effects of climate change on biodiversity (Dobrowski, 2011; Gentili et al., 2015; McLaughlin et al., 2017; Morelli et al., 2020). In NWT VIII, our first hypothesis addresses two aspects of topographic heterogeneity that we expect to play a critical role in mediating biogeochemical and ecological rates of response to increasing air temperature (**Fig. 2**). First, we expect that complex terrain causes microsite variation in surface (and subsurface) temperature across hillslopes, thus mediating the extent to which organisms are exposed to warming conditions (Lembrechts et al., 2021). Second, we expect that hillslope position will determine the relationships among air temperature, microclimate, and other important abiotic variables – particularly water, growing season length, and nutrients (**Fig. 3**) – that regulate ecological and biogeochemical responses. We hypothesize **(H1): Ecological change will be fastest where organisms are most exposed to rising air temperatures and less limited by other abiotic factors.** We will evaluate **H1** in five different systems at NWT: alpine tundra plant communities, shrubs and herbaceous subalpine plants, subalpine forest, pika populations, and freshwater ponds and streams.

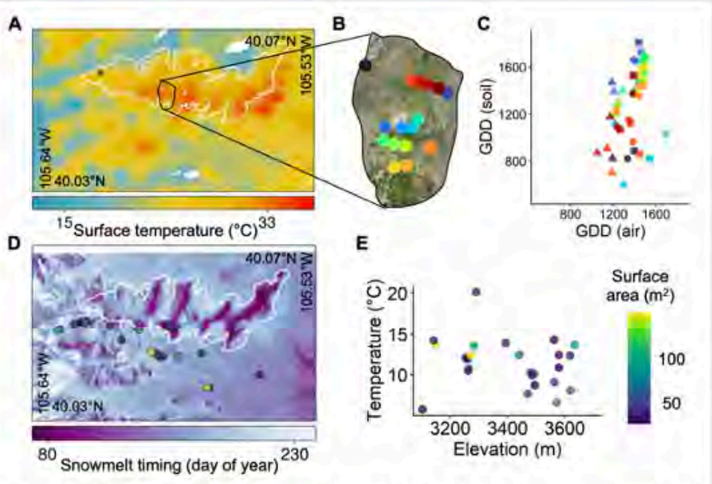

Fig. 10. Complex terrain creates substantial microsite variation in important abiotic controls that may influence how organisms respond to climate. **(A)** Spatial variation in summer land surface temperature over Niwot Ridge (ECOSTRESS satellite, average of all daytime cloud free July-August overpasses). Tundra on Niwot ridge is outlined in black. **(B)** an RGB image of the Saddle Catchment Sensor Node Array (grey outline in A) from mid-August, symbols indicate sensor nodes. **(C)** At fine scales, such as across the sensor node array in B, above- and below-ground air temperatures can become decoupled due to climate exposure, here shown as GDD calculated from above- and subsurface temperature sensors in 2018 (circles), 2019 (triangles) and 2020 (squares); colors denote different sensor nodes (as in B). **(D)** Average snow-free day of year also varies substantially with terrain. Pond locations are indicated by circles. **(E)** Temperatures across ponds at NWT (locations shown in subpanel D), also show substantial variation. Data sources: 67.1, 210.3, 292.1, 294.1, 919.1, Hook and Hulley 2019a, 2019b

3.1.2 Evidence from NWT. *A. Alpine tundra.* In alpine tundra, plant communities are distributed across environmental gradients that extend from wind-exposed ridges to more sheltered depressions (**Fig. 3**) (Billings and Mooney, 1968). While consistent increases in air temperature over the past several decades have been documented at NWT (**Fig. 5A**), surface temperatures vary enormously among topographic positions (**Fig. 10A**) (Körner, 2021; Scherrer and Körner, 2011). For example, across the Sensor Network Array (**Table 2F**), growing degree days calculated from soil temperatures (at 5cm depth) varied three-fold in 2020, with values both above and below co-located air temperature measurements (**Fig. 10 B,C**). The specific ecological consequences of this variation in temperature exposure on alpine tundra plants are not yet clear. Biophysical models of plant photosynthesis suggest that temperature responses are primarily controlled by leaf temperatures, which are higher (and closer to the optimum temperature for photosynthesis) in dry meadows (Wentz et al., 2019). In contrast, simulations using the Community Land Model (see **3.5**) predict that wet meadow vegetation could show faster responses to warming if higher temperatures generate a temporal disconnect between soil water availability and plant water demand (Wieder et al., 2017). These contrasting model predictions emphasize the importance of evaluating variation in climate exposure alongside other physical factors that covary across the hillslope gradient (**Fig. 3**).

B. Shrubs and subalpine herbaceous plants. Although microclimate refugia for mountain biodiversity are usually considered to be the result of abiotic features (e.g., topography), biogenic microclimates created by habitat-modifying species can also create large differences in climate exposure (Cáceres et al., 2015; Sweet et al., 2015). At NWT, shrubs buffer temperatures and facilitate the growth of resource-acquisitive alpine plants (L. Brigham, thesis *in prep*), suggesting that shrubs offer a protected microclimate that could buffer alpine communities from the same global change drivers that are driving shrub expansion (Bueno de Mesquita et al., 2018). With experimental plantings, we find that shrubs may act as “stepping-stones” for subalpine plants that are shifting uphill to track their climatic niche, largely due to reductions in freezing degree days and increases in soil moisture (L. Brigham, thesis *in prep*).

C. Subalpine forest. Contrary to the common perception that tree growth in subalpine forests is constrained by temperature, dendrochronological analyses from the 1990’s demonstrate that the radial growth response of trees to summer temperatures at NWT depends upon moisture availability, which can vary with topography over relatively short distances (<500 m) (**Table 2B**; Villalba et al., 1994). In the decades since these patterns were first reported, subalpine summer (June/July/August) air temperature at NWT has significantly increased, leading to higher rates of tree mortality when warm years were accompanied by dry conditions (Andrus et al., 2021). Preliminary analyses updated through 2015 indicate that radial growth of Engelmann spruce (*Picea engelmanii*) has increased with rising temperatures at hydric, but not xeric sites (**Fig. 8C**). Together, these patterns underscore the pivotal role of water availability in determining the rates at which tree mortality and growth change with rising air temperature.

D. Pikas and talus. While we find a strong signal of warming on pika decline at NWT (**Fig. 8A**; **Table 2C**) and other locations across the Western US (Smith et al., 2019), microclimate variation and pika behavior have the potential to buffer this signal. Pikas persist more often in talus slopes that create suitable subsurface microclimates (Millar and Westfall, 2010), and adjust their behavior to spend more time in deep (1m below surface) areas of the talus when locations closer to the surface provide less refuge from warm surface temperatures (Benedict et al., 2020). Nonetheless, a range retraction in the pika population associated with a the loss of suitable microclimates has been documented at our long-term West Knoll study site (Hill, 2021), as maximum talus temperatures have increased even faster than air temperature over the past 60 years (Monk and Ray, *in review*).

E. Ponds and streams. Small ponds, springs, and streams dot the alpine landscape and connect melting snow to the alpine lakes of the Green Lakes Valley (**Fig. 3**). Our preliminary sampling of ponds across Niwot Ridge and through the Green Lakes Valley shows that midday water temperature can differ by as much as 4-11°C among ponds at similar elevations (**Fig. 10E**). These differences are driven by complex terrain, with topography determining pond size, depth, and exposure to solar radiation, and driving the distribution of insulating snowpack and the transport patterns of cold water from upslope locations and melting glaciers. Temperature fluctuations in ponds and streams are expected to have large effects on biogeochemical and ecological process rates, as well as aquatic community structure at NWT (Fields and Dethier, 2019; Huber, 2021), with water bodies that are cooled by glacial meltwater inputs potentially providing refugia for alpine specialist aquatic taxa (Brighenti et al., 2021).

3.1.3 Predictions related to H1. Based on theory and evidence from our past work (above), we predict:

1A. Exposure. Landscape position (topography) influences the extent to which organisms are exposed to rising air temperatures. For example, organisms that occupy exposed ridges and south-facing slopes will experience greater exposure to changing air temperatures, and thus respond more rapidly, than organisms that occupy more thermally buffered microsites.

1B. Other abiotic constraints. Variation in ecological responses to changes in air temperature will be constrained by other abiotic factors that are not changing, changing more slowly, or changing in different directions relative to air temperature. For example, temperature responses will be reduced in sites where water, nutrients, or other abiotic factors limit growth, recruitment, or biogeochemical cycling rates.

3.1.4 Experiments and observations to test H1. To test these predictions related to **H1**, we take a series of approaches, including extending several of our long-term observational datasets, installing sensors to monitor microsite temperature in recently-established observational studies, continuing two experiments that disentangle the effects of temperature from snowmelt timing and/or nutrients on plant community dynamics, and conducting a new turf transplant experiment (**Box 1).**

A. Continued long-term monitoring. In NWT VIII, we will continue to collect long-term datasets that have been critical for documenting increasing temperatures, variable precipitation, and the associated trends in physical and biotic processes and patterns over the last 4 decades (**Table 1A-E, Table 2A-F**). We will analyze these data to test for the effects of temperature exposure (e.g., surface or subsurface temperature, water temperature) and other abiotic factors (snow-off/ice-off date, soil moisture) in determining the rates at which populations (pikas, subalpine trees, zooplankton), communities (tundra plant community), and ecosystem processes (NPP, chlorophyll-a) respond to changes in air temperature.

B. New observation campaigns. In preparing for NWT VIII, we have pursued new observational campaigns in three systems that have historically not been part of our long-term monitoring program. These systems are particularly well-aligned with our conceptual framework (**Fig. 2**) and the expertise of new LTER investigators (see **Project Management Plan**): insect pollinators, freshwater stream and pond communities, and soil biogeochemical processes. We expect these systems to be particularly sensitive to increasing temperature and exhibit variable rates of response due to spatial variation in microclimate and other abiotic factors, particularly snowmelt date (pollinators), water input sources (ponds and streams), and soil moisture dynamics (nutrient cycling). Measurements in these systems are also important for evaluating the mechanisms explored in **H2-H4** and forecasting ecosystem responses in **H5**. Over the next funding cycle, we will continue pollinator surveys that we piloted in 2021 **(Table 2I)** and refine and implement a long-term sampling plan for macroinvertebrates, periphyton, and habitat characteristics in streams and ponds across Niwot Ridge and throughout the Green Lakes Valley (**Table 2J**). Finally, we will extend our measurements of soil processes in the Sensor Network Array (**Table 2F**).

C. Continue ongoing experiments. We will continue the Growing Season Length Experiment (GLSE, **Table 2G**, currently in its 5th year), where we extend the growing season by applying a thin layer of black sand to reduce snow albedo and enhance melt rates without concurrently affecting snowpack depth (after Blankinship et al., 2014). This experiment allows us to measure how plant responses to warming are mediated by snowmelt timing and associated changes in nutrient availability and soil moisture. While we are beginning to detect responses in plant phenology (Forrester, 2021), plant-pollinator interactions (A. Rose-Pearson, thesis *in prep*), and plant community composition (J. Huxley-Anderson, thesis *in prep*), extending the experiment for 3 more years will allow us to better characterize slower responses that have been slower to develop. We will also continue an experiment that investigates warming in combination with augmented snowpack and nitrogen availability in moist meadows (**Table 2A,** currently in its 16th year) (Collins et al., *in review*; Farrer et al., 2015; Smith et al., 2012).

D. Turf transplant experiment. We will test our predictions for **H1** in the turf transplant experiment (**Box 1**), by comparing the responses of individual plants, plant communities, microbial communities, and ecosystem processes in alpine turf transplants *across warming macroclimate* (**Fig. 9A**) and *across the hillslope gradient* (**Fig. 3, 9B**). TMS (Tomst® TMS-4) dataloggers in each block will characterize microsite variation in soil moisture, soil temperature (5cm deep), surface temperature, and air temperature. We will quantify biological responses to macroclimate (cold-to-warm vs. warm-to-warm) and the mediating effects of other abiotic factors (microsite conditions) by measuring a variety of response variables. For individual plants, we will measure survival, growth, reproductive output, and phenology for ~10 focal species that will be marked and monitored in the turf transplants (more information on focal taxa and sample sizes is provided in **3.2**). At the plant community scale, we will measure community composition at peak productivity using the same point-quadrat methods that we use for other NWT vegetation datasets (**Table 2A,F,G**). Microbial community responses will be measured in years 2 and 4 by extracting DNA from bulk soil and root samples collected from the subplots designated for destructive sampling (**Box 1, Fig. 9C**). Bacterial 16S rRNA marker genes will be amplified using PCR and sequenced on an Illumina MiSeq instrument using paired-end (2x250 bp) chemistry to a minimum depth of 25,000 sequences per sample. We will use a similar approach for fungal analyses, targeting the ITS1 region of the rRNA gene as described in Brigham *et al.* (2022). Finally, in years 2 and 4 of the experiment, we will characterize ecosystem processes by measuring total soil C and N content, soil enzyme activity, microbial biomass, soil respiration, and plant productivity (aboveground biomass) in the subplots set aside for destructive soil sampling using our standard protocols (**Table 2A,F,G**).

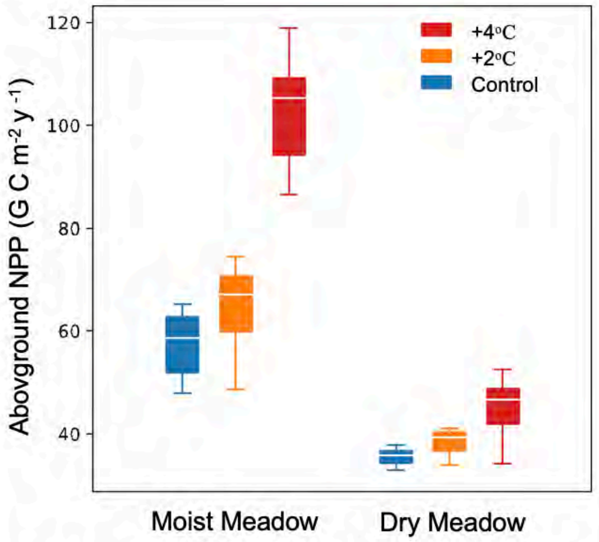

Fig. 11. Annual aboveground plant productivity in moist and dry meadow communities simulated by CLM5 using an idealized configuration of hillslope hydrology in the Saddle. Control simulations were forced with meteorological input from the NWT eddy covariance towers and Saddle from 2008-2020 (**Table 1,2E**). Warming simulations are designed to replicate turf transplant experiments experiencing +2°C air temperature warming. Data sources: 16.5 31.18, 57.5, 191.3, 210.3 416.11, Knowles 2021a, 2021b

For each variable described above, we will evaluate our predictions by testing for interactions between the macroclimate treatment and the microsite conditions associated with the location of each plot along the hillslope gradient. For example, *prediction 1A* will be supported if cold-site turfs transplanted in the warmest microsites of the warm-sites show larger responses to the increase in macroclimate (i.e., cold-to-warm transplantation) than those in cooler microsites (i.e., a significant microsite effect associated with surface temperature variation). *Prediction 1B* will be supported if responses to macroclimate are mediated by other plot-level environmental covariates, particularly soil moisture or nutrient availability (**Fig. 3**). Preliminary analyses of this prediction at the community scale using the Community Land Model (CLM; see **3.5**) suggest moist meadow communities will show faster and larger responses to rising temperatures (consistent with *prediction 1B*), as persistent water limitation is likely to constrain responses in the dry meadow (**Fig. 11**). The contributions of biotic processes in shaping these responses (as illustrated in **Fig. 2**) will be further investigated in **H2-H4.**

3.2. Q2: ORGANISMAL STRATEGIES – Which species attributes predict how quickly individuals and populations respond to changing climate?

3.2.1 Ecological theory and rationale. A major challenge in ecology is identifying quantitative predictor variables (e.g., niches, traits, plasticity, and phylogeny) that can effectively explain the variation we observe among organisms in their direct responses to changing climate (Buckley et al., 2015; Huey et al., 2012; Lynn et al., 2021; Nadeau et al., 2017). Interspecific variation in climate responses reflects the unique physiological, developmental, morphological, and behavioral traits that have evolved in each lineage in response to past climates (Carscadden et al., 2020; Jackson et al., 2009; Nadeau et al., 2017). As a result, measurements that capture species' adaptations to climates past, in addition to their ability to tolerate stress and take advantage of resources when they become available, provide strong candidates for predictors of species-level responses to current and future climate change.

Recent studies have demonstrated that incorporating climate niche information, typically estimated as the climate conditions encompassed within a species geographic range, can help explain different temperature responses among species within communities (Lynn et al., 2021), biomes (Blonder et al., 2015), and geographic regions (Peng et al., 2021). These studies predict that species at that are near the extremes of their thermal niches (i.e., near their thermal limits) will respond more rapidly to changing temperatures, with species at the "cold" limit of their niches showing the fastest positive responses to warming, and those at their "warm" limits experiencing the most rapid declines (Lynn et al. 2021). In functional ecology, species with resource-acquisitive traits (i.e., traits that allow them to rapidly acquire and process resources) often respond faster to environmental change than species with more conservative resource use strategies (Soudzilovskaia et al., 2013). Similarly, variation in phenotypic plasticity – the ability of organisms to adjust their phenotypes in response to changes in their environment – will also cause differences among species in the rate at which they respond to environmental change (B. Zhang et al., 2020). Species that are adapted to habitats where change has historically been preceded by reliable cues (e.g., areas with temporal autocorrelation in temperature or moisture) are expected to show more phenotypic plasticity than those adapted to randomly fluctuating environments (Brown and Venable, 1986; Cohen, 1966; Leung et al., 2020). Further, in comparisons among taxa, phylogenetic relationships can explain some similarities and differences among species by accounting for patterns of shared ancestry (Holt and Gaines, 1992; Wiens et al., 2010).

In NWT VIII, we aim to explain interspecific variation in the rates at which organisms respond to increasing temperature by simultaneously considering how climate niches, traits, and phenotypic plasticity shape species' abilities to sense and respond to environmental change. Based on this rationale, we hypothesize **(H2): Differences in species thermal niches, resource use strategies, and potential for phenotypic plasticity will explain variation among species in the rates at which they respond to warming.** Below we describe patterns in our long-term data of tundra plants and subalpine trees, as well as some preliminary pairwise comparisons in zooplankton and chickadees, that have motivated this hypothesis in NWT VIII.

3.2.2 Evidence from NWT research. *A. Tundra plants.* Preliminary analyses of our long-term tundra plant community composition data from the Saddle (**Table 2A**) indicate that climate niche and functional trait variation can help predict differences in the rates at which plants respond to warming growing seasons. We observe variation among community types (**Fig. 3**) in the relationship between species' climate niches and their trajectory through time; for example, we see early evidence of thermophilization (an increase in warm-adapted species) in snowbed, wet meadow, and moist meadow communities, reverse thermophilization (an increase in cold-adapted species) in the dry meadow, and no trend in the fellfield community (**Fig. 12A**). The functional composition of alpine tundra plant communities at NWT and across the Rocky Mountains has shifted toward more conservative, stress-tolerant traits, including lower specific leaf area (SLA) and increased water use efficiency (Huxley and Spasojevic, 2021). Early analyses of the co-located vegetation monitoring plots and air temperature sensors in the Sensor Network Array suggest that NWT tundra species associate with different patterns of temporal variability in air temperature (**Fig. 12B**) and show substantial variation in their climate niches and traits that likely influence thermal tolerances (**Fig. 12C**), though NWT is a relatively "cool" site for most taxa relative to the temperatures they experience elsewhere in their geographic ranges.

B. Subalpine forests. Consistent with the expectation that warmer temperatures should drive greater mortality of cooler-adapted species than warmer-adapted species, data from NWT suggest that Engelmann spruce (*Picea engelmannii)* and subalpine fir (*Abies lasiocarpa*) experience greater mortality and lower recruitment in response to warming than limber pine (*Pinus flexilis*), which occupies a warmer climate niche than the other species (**Table 2C;** Kueppers *et al.* 2017; Andrus *et al.* 2018, 2021).

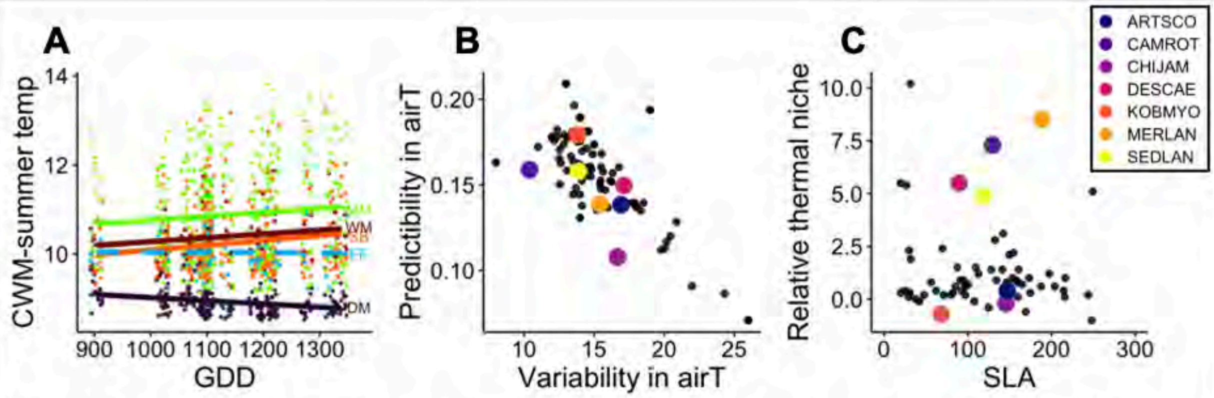

Fig. 12. NWT tundra plants response to warming may be governed by species traits as well as microsite habitat. **(A)** Different plant community types (abbreviations in **Fig. 3**) show contrasting thermal niche responses to the temporal increase in growing degree-days (0°C base). The community-weighted climate niche, based on the average summer temperature niches of the constituent species, was calculated annually for each of the 88 plots of our long-term alpine vegetation (**Table 2A**) and weighted by species abundance. **(B)** Tundra plant species in the SNA (**Table 2F**) show different associations with temperature variation (the number of times daily mean temperature crosses 0°C each season) and predictability (the strength of the average daily autocorrelation in air temperature over a season). **(C)** Species also vary in climate-related functional traits and thermal niches. A subset of the focal species used to evaluate **H1** and **H2** are highlighted with large colored points (abbrev, first 3 letters genus and species). Data sources: 78.3, 93.5, 191.3, 210.3, 413.11, 405.5, 500.2, Abatzoglou et a. 2018, Derived dataset GBIF.org https://doi.org/10.15468/dd.pjnrvf

C. Soil microbial communities. In a cross-site study that included NWT, Oliverio *et al.* (2017) identified a core group of soil bacteria that shift in relative abundance with elevated soil temperatures in both laboratory incubations and across natural gradients in the field. Temperature-sensitive taxa spanned a wide range of lineages, and the directions of their temperature responses could not be predicted from phylogeny alone. We expect that these broader patterns also apply across the heterogeneous terrain at NWT, with taxa showing variation in both the rate and direction of their responses to temperature, given the high turnover in microbial communities we observe along environmental gradients (Farrer et al., 2019; Porazinska et al., 2018; Zausig et al., 1993) and across experimental manipulations (Brigham et al., 2022).

D. Pairwise comparisons in zooplankton and chickadees. While datasets of multiple species (tundra plants, subalpine forest, microbes) provide the strongest way to identify the species attributes that correlate with climate change response rates, pairwise comparisons among a few specific taxa at NWT further underscore the potential to test **H2** with broader sampling and longer time series. For example, different life history strategies of the two dominant zooplankton taxa in NWT alpine lakes - the clonal *Daphnia pulicaria* and sexually-reproducing *Hesperodiaptomus shoshone* - likely explains the more rapid density response by *Daphnia* to warmer, longer ice-free seasons (**Fig. 13**) and higher sensitivity to within-season variation (Loria et al., 2020) and experimentally manipulated water temperature (Preston et al., 2020). Recent data from the new chickadee nest box network (**Table 2H**) indicates that Black-capped chickadees (*Poecile atricapillus*), which typically occur at lower elevations than mountain chickadees (*Poecile gambeli*), are more likely to experience egg and nestling mortality during late spring snowstorms than mountain chickadees,

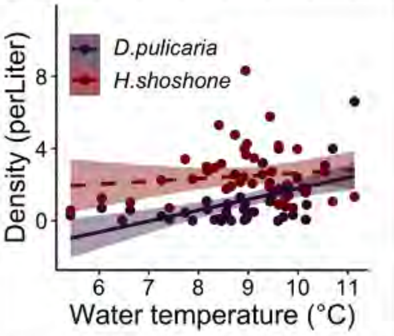

Fig. 13. The densities of two abundant zooplankton species in Green Lake 4 respond to increasing temperature at different rates, with *H. shoshone* responding less strongly than *D. pulicaria*. Solid line indicates a significant relationship. Data sources: 157.6, 161.3

potentially due to differences in physiology or nest construction between the two species (A. Theodosopoulos, thesis *in prep*).

3.2.3 Predictions related to H2. Based on theory and evidence from our past work (above), we predict that the following attributes can explain interspecific variation in the rates at which organisms respond to rising air temperature:

- *2A. Thermal niches.* Organisms that are near the extremes of their thermal niches at NWT will respond more rapidly to temperature variation than organisms that are experiencing conditions similar to their mean thermal niche.
- *2B. Functional traits.* Organisms with resource-acquisitive strategies will respond more rapidly to warming than organisms with more conservative strategies, particularly in places where warming enhances resource availability.
- *2C. Phenotypic plasticity.* Organisms with higher phenotypic plasticity, as inferred from patterns of intraspecific trait variation, will respond faster to increasing temperatures than those with relatively fixed phenotypes.

3.2.4 Observations and experiments to test H2. We will test our predictions for **H2** by extending our collection of several long-term datasets, expanding our trait databases, characterizing thermal responses of microbial taxa, and testing our predictions in the turf transplant experiment (**Box 1**).

A. Continued long-term monitoring: In NWT VIII, we will continue to collect long-term datasets that document the individual and population-level responses of different species to temperature variation at Niwot Ridge and in the Green Lakes Valley, including the Saddle tundra plant communities, subalpine trees, and lake zooplankton (**Table 2A,C,D**). Our ongoing data collection in the Sensor Network Array (**Table 2F**) will allow us to characterize fine-scale spatial and temporal variation in tundra plant species' responses to changing air temperature, snow persistence, and soil moisture, and compare the predictive power of relatively coarse, range-wide estimates of climate niches to those estimated using high-resolution, ground-level sensor data (Löffler and Pape, 2020).

B. Expand climate niche and trait datasets for NWT taxa. We will extend our measurements of functional traits for NWT tundra and subalpine plants (e.g., foliar C:N, δ^{13}C, SLA, plant height; Spasojevic, 2010; Spasojevic et al. 2013) to include more species, climate niche data, better estimates of intraspecific trait variation, and additional traits that we expect to influence changes in plant fitness and population growth rates in response to warming (Soudzilovskaia et al., 2013), including root (belowground carbon content and allocation), seed (mass, length, surface area), and physiological responses (photosynthetic rate, photosynthetic efficiency, stomatal conductance). These data will also be used to parameterize CLM-FATES (**H5**, section 3.5). We will calculate climate niche estimates for taxa with sufficient regional occurrence records to test *prediction 2A* (Ackerly et al., 2020; Lynn et al., 2021), and our new monitoring efforts in aquatic communities, pollinators, and chickadees (**Table 2H-J**) will expand the taxa and traits we can use to test *predictions 2A-C*. Finally, we will use our temperature and soil moisture measurements in the Sensor Network Array (**Table 2F**) and subalpine forest (**Table 2B**), as well as measurements from additional temperature sensors we plan to deploy across multiple systems (**Table 2**) to test if interspecific variation in climate responses can be explained by the patterns of temperature variability that species experience (Nadeau et al., 2017) and the extent of intraspecific trait variation they exhibit in the field (as one indicator of plasticity; Violle *et al.* 2012; Henn *et al.* 2018) (*prediction 2C*).

C. Assessment of temperature optima of microbial taxa. While it is not feasible to characterize microbial climate niches using distributional data due to challenges in accurately characterizing their geographic distributions, we can characterize their thermal responses under controlled laboratory conditions (Crowther and Bradford, 2013; Oliverio et al., 2017). To describe variation in plasticity and thermal adaptation across microbial taxa, we will collect soils across the hillslope gradient in the SNA and incubate them in the laboratory at different temperature and moisture levels. We will measure respiration following Bradford *et al.* (2010) and quantify fungal and bacterial community composition and biomass, as well as soil enzymes and mineral N, following Brigham et al (2021). Data from these incubations will be used to parameterize growth rates, growth efficiency, and their sensitivities to temperature and moisture for the winter and summer microbial communities that are simulated by the CLM-MIMICS soil biogeochemical model (**H5**, section 3.5).

D. Turf transplant experiment. We will evaluate the role of species' thermal niches, resource use strategies, and phenotypic plasticity in explaining interspecific variation in climate change response rates in 10 common tundra plant species that span the range of thermal niche, functional trait, microhabitat variability, and phylogenetic diversity that exists within the NWT tundra plant community (**Fig. 12**). We have preselected seven species that meet these criteria (**Fig. 12B,C**), show contrasting abundance trends in our long-term data, are common in the turf experiment sites, and have been successfully transplanted in prior experiments (e.g., Bueno de Mesquita *et al.* 2020) and our own pilot studies. An additional three taxa will be selected based on their abundance in the turf transplants and potential to represent under-sampled parameter space in our predictor variables. We will individually mark 30-50 individuals of each species in turf transplants and unmanipulated controls at each site, including a range of sizes and adding seedlings as they emerge each year. All marked individuals will be monitored for survival and fecundity to estimate fitness components (Bemmels & Anderson 2019) and long-term demographic growth rates (Angert, 2009; DeMarche et al., 2021; Oldfather and Ackerly, 2019), and measured for functional traits that may influence the effects of warming on tundra plant fitness and population growth rates (SLA, LDMC) (Bjorkman et al., 2018a; Niittynen et al., 2020). We will evaluate the extent to which thermal niche estimates (*prediction 2A*), resource use traits (*prediction 2B*; estimated from datasets in **3.2.4B**), and phenotypic plasticity (i.e. phenotypic variance among sites; Valladares *et al.* 2006) (*prediction 2C*) explain differences among species in the rates and directions of fitness and demographic responses to warming (species predictor x macroclimate treatment interaction), and if this response varies with the locations of the focal taxa along the hillslope gradient (species predictor x microsite interactions).

3.3. Q3: COMMUNITY TURNOVER – Which community attributes predict how quickly species composition changes in response to changing climate?

3.3.1 Ecological theory and rationale. As climate changes, species can colonize sites that become newly suitable to them, be lost from sites that become unsuitable, or persist and re-order in abundance (Alexander et al., 2015; Olsen et al., 2016). Species will differ in their rates of response (**H2**), with delays in colonization (e.g., due to dispersal ability), local extinction (e.g., due to life history), and shifts in relative abundance (e.g., due to competitive ability). Importantly, varied rates of species responses within a community change the nature and intensity of species interactions (Gravel et al., 2019; Mathiasson and Rehan, 2020; Tylianakis and Morris, 2017) particularly at the leading (where species colonize new communities) and trailing edges (where transient resident species interact with new colonizing species) of a species range (Bueno de Mesquita et al., 2016; le Roux et al., 2013). These interactions can amplify or buffer organismal responses to a changing climate (Aschehoug et al., 2016; Germain et al., 2018; Gilman et al., 2010), particularly for species that depend on facilitation or resource partitioning for persistence (Alexander et al., 2015; Olsen et al., 2016).

We draw upon several frameworks to investigate how biotic interactions, beyond individual organismal responses (**H2**), shape varied rates of community turnover in response to climate change (HilleRisLambers et al., 2013). First, habitat-forming species can create microclimates that buffer warming effects (Bimler et al., 2018), which can both facilitate the establishment of new species (as stepping stones) and reduce extinction risk of persisting species (as microrefugia) (Anthelme et al., 2014; Bulleri et al., 2016; Lenoir et al., 2017). Second, warming is expected to exacerbate moisture stress in some areas and not in others (le Roux and McGeoch, 2010; Schuchardt et al., 2021), mediating predicted shifts in species interactions. The stress-gradient hypothesis predicts that facilitative interactions will increase in importance in microsites with increased moisture stress (Anthelme et al., 2014), while warming in mesic microsites could intensify neighbor competitive effects through the combination of increased biomass production, shifts in community composition to more resource-acquisitive strategies (greater leaf area, height), and increased abundance of the dominant species (Alexander et al., 2018; Olsen et al., 2016; Yang et al., 2020). Lastly, we expect that climate-mediated shifts can have particularly large impacts on interactions when the species involved specialize on a subset of available interaction partners that respond to warming at different rates.

In NWT VIII, we leverage the differences in microsite community attributes and biotic interactions occurring over relatively fine spatial scales (~10 m) across hillslope gradients (**Fig. 3**). We hypothesize **(H3): The rate at which communities respond to climate change will vary with differences in the nature and specificity of biotic interactions across microsites.** Below we develop predictions based on three aspects of communities that will influence interactions: A) facilitative effects of habitat formers, B) neighborhood competitive effects and shifts in dominant species abundance, and C) dependency on specialized interactions in plant-pollinator and plant-microbial interactions.

3.3.2 Evidence from NWT research. *A. Facilitative effects of habitat-forming species*. In the tundra, shrubs act as habitat-forming species, changing the temperature, moisture and light conditions experienced by neighbors (Callaway et al., 2002; Cavieres et al., 2014; J. Chen et al., 2019; Myers-Smith et al., 2011). At NWT habitat-forming shrubs (*Salix spp*), are rapidly increasing in both the xeric and mesic microsites of the tundra, showing an exponential increase since the mid-1940s (Formica et al., 2014). Shrubs buffer temperature extremes, increasing minimum temperatures (via snow accumulation) and decreasing maximum temperatures (via shading) (L. Brigham, thesis *in prep*; Myers-Smith et al., 2011). These biogenic microclimate effects influence community composition, supporting a community of species with more resource acquisitive traits than adjacent areas without biogenic effects (L. Brigham, thesis *in prep*). In microsites directly influenced by these biogenic buffering effects, we expect slower species turnover due to a decoupling from warming air temperature trends, particularly in areas where warming intensifies abiotic moisture stress (Schuchardt et al., 2021).

B. Intensifying competitive effects. We expect warming to intensify competitive interactions in densely vegetated alpine meadows with deeper organic soil and higher water-holding capacity. We focus on two community attributes as indicators of this intensification: changes in the effect traits (Suding et al., 2008) of the community and abundance shifts in the dominant plant species (Collins et al., *in review*; Farrer et al., 2015; le Roux et al., 2012) (**Fig**. **14**). First, the ability of a species to colonize a new area is influenced by its interactions with the resident community. We expect the functional trait composition of communities that are more competitive to be more likely to exclude new arrivals (Meineri et al., 2020), beyond simple biomass effects. The exclusion of new species will slow turnover relative to less intrinsically competitive communities. Second, the responses of the dominant (most abundant) species to warming can be a strong determinant of community structure (Avolio et al., 2019). If the dominant species increases with warming, we expect a faster rate of species loss and therefore faster rate of species turnover (Collins et al., *in review*). In contrast, if the dominant decreases with warming, we expect competitive release to slow the rate of species turnover (Kulonen et al., 2018).

At NWT, we can address these ideas in tundra plants as well extend them to datasets where we are monitoring pairs of interacting species: chickadees, zooplankton, and aquatic macroinvertebrates. We are just beginning to learn about these dynamics (e.g., Loria et al., 2020; **Fig. 13**), and as such, our initial predictions are based on observed range shifts and density dependence. For instance, the dominant Black-capped chickadee (*P. atricapillus*) appears to be migrating to higher

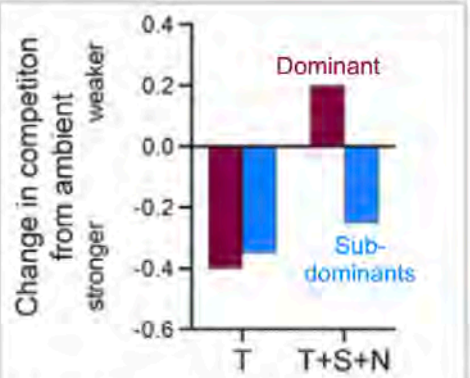

Fig. 14. Species interactions can buffer and accelerate response to climate change. Using a Bayesian hierarchical approach (gjamTime; Clark et al. 2020) to infer interactions from long-term data, we find that 16 years of warming manipulation (T) increases competitive interactions for the dominant species, *Deschampsia caespitosa (red)*, as well as the less abundant sub-dominant species (blue), in moist meadow. However, under warmed conditions with added snow and nitrogen (T+S+N), competitive interactions decrease in intensity for *Deschampsia* while staying strong for the subdominant species. Data sources: 13.4; 405.5; 31.17

elevations with warming temperatures, increasing competition with the resident Mountain chickadee (*P. gambeli*) (A. Theodosopoulos, thesis *in prep*). In lakes, warmer temperatures may cause smaller-bodied taxa to outcompete larger-bodied taxa, potentially leading to algal blooms and cascading ecosystem effects (Redmond, 2018).

C. Dependence on specialist interactions. While plant-plant interactions are usually assumed to be generalized, other interactions vary in the degree of specialization of the interacting species pair. We expect that species that depend on specialized mutualisms will be more limited by the rate of response of their partners than those that engage in more generalized interactions. Based on recent patterns documented in subalpine meadows near NWT (Resasco et al., 2021), we expect generalized plant-pollinator interactions to be more common in warmer sites than colder ones. As a result, we expect relatively fast rates of species loss and greater turnover in communities in colder locations (e.g., high alpine), and overall less disruption in communities with higher rates of generalized interactions.

3.3.3 Predictions related to H3. Based on theoretical expectations and our prior work, we make the following predictions for the rates at which tundra plant communities (*predictions 3A* and *3B*) and trophic interactions (*prediction 3C*) will respond to rising air temperature:

- *3A. Biogenic effects*: Habitat forming species (shrubs) will slow species turnover in more stressful (xeric, wind-blown) microsites through facilitative microrefugia effects. In less stressful microsites, biogenic effects will facilitate the colonization of new species, acting as stepping stones for leading-edge colonization.
- *3B. Competitive effects:* In areas without biogenic effects of habitat-forming species, we expect warming to intensify plant-plant competitive interactions. Competitive interactions will increase most strongly in mesic tundra microsites, specifically due to shifts in functional effect traits, greater biomass, and increased abundance of dominant species. This intensification will result in slowed rates of colonization by new species and more rapid loss of resident species with less resource acquisitive traits.
- *3C. Specialist-generalist effects:* Warming will disrupt specialized species interactions and increase the importance of generalized interactions, resulting in loss of specialized species and increased abundance of species benefiting from generalized mutualist interactions.

3.3.4. Experiments and observations to test H3. Measuring interactions is challenging, particularly in diverse communities dominated by long-lived, slow-growing species like alpine tundra. Consequently, we aim test our predictions for **H3** using a series of complementary approaches: developing modeling approaches to infer species interactions from long-term observational data, continuing experimental warming experiments (**Table 2A**), expanding ecological observations to encompass plant-pollinator interactions and microbial root colonization, and including tests of interaction strengths in the turf transplant experiment (**Fig. 9**).

A. Development of modeling approaches to infer species interactions. Various statistical approaches have been proposed to assess species interactions using observational data (e.g., Legendre & Gauthier 2014; Ovaskainen *et al.* 2017b, 2019), yet limitations of these approaches – including challenges in distinguishing among processes that are expected to drive similar co-occurrence patterns (Barner et al., 2018) – have made application to long-term multi-species datasets rare. In NWT VIII, we propose to refine a method (Weiss-Lehman et al., 2022) that implements Bayesian variable selection via sparsity-inducing priors to specifically examine how species deviate in their interaction strength, and how variation in environmental conditions (such as air temperature) alter species' density-independent growth rates and the strength of species interactions (as in **Fig. 14**). We will first apply this approach to existing long-term plant community datasets that span hillslope gradients, and then will modify the method to include newer datasets on other interactions as they mature (e.g., pollinators, pond and stream macroinvertebrates; **Table 2I,J**), as well as data from ongoing experimental manipulations (**Table 2A,G**) (Collins et al., *in review*; Farrer et al., 2015).

B. Expansion of ecological observations to encompass plant-pollinator interactions. While purely associational, long-term, co-located observations are essential to relate ecological responsiveness in process rate (e.g., compositional turnover, survival) to species interactions. In NWT VIII, we propose to characterize how plant-pollinator interactions change with warming by measuring floral attractive traits in the existing vegetation plots across the Sensor Network Array (**Table 2F**), and continuing to survey pollinator communities (**Table 2I**) at the five sites where we have plant community composition and phenology data (Forrester, 2021) from the Growing Season Length Experiment (**Table 2G**).

C. Turf transplant experiment. The tundra turf transplant experiment (**Box 1**) will allow us to test *predictions 3B* and *3C* by comparing rates of community turnover between cold-turfs and locally replanted warm-turfs across hillslope gradients in warm (low-elevation) sites. While our general expectation is that the composition of cold-turf communities will eventually converge to become similar to warm-turf communities due to warming, we expect the rate of convergence to vary based on: (1) community-level functional traits, where communities with resource-acquisitive traits (e.g., high SLA and height) will be more effective at excluding new recruits than those with less competitive traits; (2) the response of the dominant species to warming, with faster rates of species loss in communities where the dominant species shows the greatest change in abundance with increasing temperature; and (3) the frequency of pollinator specialization, where plant species that rely on a narrower subset of the pollinator community for pollinator services will decline faster, and show stronger phenological mismatches with the surrounding plant community, than those that engage in more generalized interactions.

D. Transplants to shrub microsites. To test *prediction 3A,* we will expand the turf transplant experiment at one warm site (**Box 1**) to evaluate the effects of shrubs in determining the rate at which tundra plant community composition changes with warming. Specifically, for one cold-warm site pair (**Fig. 9A**), we will transplant an additional set of turfs (n=20) to the leeward side of shrubs across the hillslope gradient. We expect that shrubs will slow the rates of community turnover in drier microsites by creating microclimates that reduce moisture stress. In contrast, we expect shrubs to increase the rate of turnover in wetter microsites (which do not experience increased water limitation with warming) by facilitating the colonization of warm-site species.

3.4. Q4: ECOSYSTEM FUNCTION: How do soil attributes and community composition influence the rates at which ecosystem processes respond to a changing climate?

3.4.1. Ecological theory and rationale. Soil microbial communities determine the rates of ecosystem processes like heterotrophic respiration, nutrient cycling, and organic matter transformations. Microbial processes are mediated by the physical and chemical attributes of soil, including organic matter content, nutrient availability, texture, pH, and the accessibility of substrates to microbes (Cusack et al., 2010; Davidson and Janssens, 2006; Lehmann et al., 2020). While substrate limitation can partially explain diminishing soil respiration rates with warming, changes in microbial physiology and community composition likely are key contributors to ecosystem responses (e.g., carbon storage and nutrient transformation) to warming over longer time periods (Melillo et al., 2017; Pold et al., 2017; Romero-Olivares et al., 2017, p.). Recent work suggests that initial community composition can affect contemporary microbial responses to climate change by constraining the physiological capacity of the local microbial community (Glassman et al., 2018; Hawkes and Keitt, 2015; Keiser et al., 2011; Matulich and Martiny, 2015; Mills et al., 2014). For example, Strickland *et al.* (2015) demonstrated that biotic legacies of a decomposer community (i.e., initial composition) were as important a determinant of litter decomposition rates as temperature and moisture.

Like microbial communities, plant composition can generate legacy effects on ecosystem C and N cycling through litter, root, and resource use traits (Chen et al., 2019; Cusack et al., 2018; Freschet et al., 2021; Smith et al., 2019). Plant species adapted to different temperatures, with different functional traits, can have contrasting effects on soil biogeochemical function through the quantity and chemical quality of substrates supplied to soil microbes and contrasting ecosystem nutrient economies (Faucon et al., 2017; Hobbie, 2015; Phillips et al., 2013; Reich, 2014). These biotic effects can influence ecosystem response to climate change. For instance, in the Swiss Alps, Walker *et al.* (2021) found that warming alone had negligible effects on soil carbon loss, but the combination of warming and the migration of warm-range plants increased soil C loss by 50%, likely via increased rates of root exudation and microbial respiration.

Based on this rationale, we posit **H4: Legacies in soil attributes and plant and microbial communities across microsites will influence the rates at which ecosystem processes respond to rising air temperatures.**

3.4.2. Evidence in support of H4. *A. Soil physical and chemical attributes.* Across the NWT landscape, particularly in wetter microsites, we see evidence of non-steady-state carbon cycling. Microbial respiration of old carbon, perhaps related to permafrost degradation, results in areas of the tundra that are net annual carbon sources to the atmosphere (Knowles et al., 2019). Even in areas without a known history of permafrost, low density soil carbon fractions turn over on decadal time scales, and denser, mineral-associated fractions turn over on multidecadal to millennial time scales (Cusack et al., 2011; Neff et al., 2002). As climate warms, we expect these physical and chemical properties of soils will slow the rate at which ecosystem processes respond in some sites (Bradford et al., 2021).

B. Microbial community control. Microbial communities at NWT vary in composition of temperature sensitive taxa (Oliverio et al., 2017) as well as patterns in community turnover over seasonal cycles (Schmidt et al., 2015) across hillslope terrain. Prior work at NWT suggests that alpine microbial communities respond rapidly to seasonal transitions, with a shift in microbial composition between winter and summer that is most strongly linked to C limitation (Lipson et al., 2000; Schmidt et al., 2015). Heterogeneity in the physical template generates spatial variation in rates of soil freezing and thawing, depth of freeze, and C availability, all of which can have large effects on microorganism communities through cold winters (Lipson et al., 1999; Sorensen et al., 2020).

C. Plant community control. Plant traits such as leaf area, foliar nitrogen concentration, and height are key characteristics contributing to production at NWT (Liu et al., 2018; Migliavacca et al., 2021; Spasojevic and Suding, 2012). Similarly, we find that plant tissue and litter chemistry influence nutrient transformations through effects on microbial processes (Brigham et al., 2022; Steltzer and Bowman, 1998; Suding et al., 2008). Compositional shifts due to shrub expansion also affect function, as shrubs are associated with large differences in N and C cycling relative to herbaceous vegetation (Chen et al., 2020; Myers-Smith et al., 2015; Sweet et al., 2015). As a result, we find that environmental changes can indirectly affect ecosystem processes through changes in plant composition (Farrer et al., 2015).

3.4.3. Predictions related to H4. Based on theory and evidence from our past work (above), we predict:

4A. Abiotic constraints. Physical and chemical attributes of soil influence the response of heterotrophic respiration to warming, with microsites that have higher organic matter concentrations responding more rapidly to warming than soils with lower soil organic matter concentrations.

4B. Microbial composition. The composition of microbial communities will influence the processing rates of soil organic matter and nutrients. Specifically, we expect that heterotrophic respiration rates of wintertime microbial communities will have higher temperature sensitivity than summertime microbial communities, particularly in microsites with greater winter thermal insulation due to persistent snowpack.

4C. Plant composition. Plant species compositional shifts will mediate warming effects on NPP and soil organic matter dynamics. Specifically, we expect plant communities with resource-acquisitive traits (e.g., in wetter microsites and in warm-range species from lower elevations) to shift more quickly and have higher NPP compared to areas with more resource conservative plant species.

3.4.4. Experiments and observations to test H4. To test these predictions, we propose to take a three-pronged approach that includes a) long-term observations and experiments, b) laboratory soil incubations, and c) turf transplant experimental analyses that relate rates of soil microbial and plant community responses to ecosystem-level processes.

A. Continued long-term observations and experiments. Associational, co-located observations are essential to characterize the physical, chemical, and biological controls on ecosystem responsiveness (soil organic matter characterization, nutrient dynamics and primary production) (*prediction 4A*). We are continuing to build these datasets for terrestrial tundra systems through the Sensor Network Array (**Table 2F**) and experimental manipulations (using OTC's in the GSLE and Snow x N x Temperature experiments, **Table 2A,G**). We will also explore the connections between composition and function in stream and pond ecosystems as these datasets mature (**Table 2J**). We are developing quantitative methods for inference of direct climate and indirect effects via composition (*predictions 4B* and *4C*), similar to our work inferring effects of species interactions (Kimmel et al., 2021). These datasets are critical for capturing patterns of abiotic and biotic properties across space and relating our findings from the laboratory incubations (below) to the alpine landscape.

B. Laboratory incubations. We will use the microbial incubations (**3.2.4*C***) to evaluate microbial community effects on ecosystem processes by combining the compositional assessments with measures of microbial response (soil respiration rates, enzyme activity, microbial biomass, and net N transformation rates, as in **3.1.4*D*** and **3.2.4*C***). We expect soils that have higher initial organic matter content (e.g., moist and wet meadows) to be dominated by higher particulate organic matter concentrations (free light fraction) that have a lower chemical quality (higher C:N ratio) than less productive sites with lower soil organic matter content. Therefore, based on *prediction 4A*, we expect soils from moist and wet meadows to show faster and larger microbial responses to warming than dry meadows during summer. Based on *prediction 4B*, we also expect to see higher temperature sensitivity in heterotrophic respiration by wintertime microbial communities from these microsites.

C. Turf transplant experiment. The turf transplant experiment (**Box 1**) will allow us to test if the rates of compositional shifts in the microbial community correspond to rates of change in soil function (e.g., soil respiration) and substrate quality when communities are subjected to warmer conditions (i.e., cold-to-warm transplants). Destructive measurements will be collected from the designated turfs (**Fig. 9C)** in years 2 and 4 of the experiment. We will measure soil respiration, microbial biomass, and soil enzyme activity to assess microbial responses. In treatments that show significant changes in soil respiration and microbial measures, we will also assess changes in soil organic matter pools using density fractionation, and assess the biomolecular composition of the fractions using ^{13}C nuclear magnetic resonance spectroscopy following Cusack *et al.* (2018). We expect that turfs from (and transplanted to) wetter microsites along the hillslope gradient will show faster responses to warming than those in drier microsites because the soils have physical and chemical properties that do not restrict their response (*prediction 4A*). Given biotic legacies (*prediction 4B*), we expect to see slower rates of change in microbial community composition and ecosystem process rates in cold-site transplants compared to those measured in locally replanted turfs at each site. Similar analyses can be done to assess plant compositional change relative to production, with the expectation that cold-to-warm site convergence of plant functional traits will lead to more rapid responses, while divergence or sustained differences will produce slower responses (*prediction 4C*).

3.5. Q5: FORECASTING CHANGE – Does including climate exposure and rates of biological responses across a heterogeneous landscape improve model forecasts of ecological change?

3.5.1. Ecological theory and rationale. An understanding of the abiotic and biotic mechanisms that drive variable ecological responses to climate change (**H1-4**) should improve the accuracy of projections for how ecosystem-level functions will change in the coming century (Buotte et al., 2021; Koven et al., 2020; Lombardozzi et al., 2015; Moorcroft et al., 2001). In NWT VIII, we will use our long-term data and results from our experiments in **H1-H4** to integrate across space (where different landscape patches may vary in their rates of response; Ackerly *et al.* 2020) and across types of ecological change (where rates of response may vary in magnitude; Smith *et al.* 2009) to predict climate-driven effects on ecosystem function. Thus, we hypothesize **(H5): Including heterogeneous response rates across space and**

among ecological systems in ecosystem models improves our ability to forecast landscape-scale changes in function with climate change.

3.5.2. Evidence in support of H5. *A. Forecasting ecosystem change using CLM.* The established Community Land Model (CLM; Lawrence *et al.* 2019) provides an internally consistent modeling platform that offers a numerically tractable approach to capture important landscape ecohydrological features in mountainous regions (Swenson et al., 2019; Wieder et al., 2017). Previous NWT modeling efforts using CLM demonstrated that long-term measurements from the alpine eddy covariance towers and plot surveys across the Saddle grid can be used to parameterize, validate, and project changes in ecosystem carbon, water, and energy fluxes across vegetation communities at NWT (Wieder *et al.* 2017; **Fig. 11**). This work highlighted potential vulnerabilities of wet meadow vegetation productivity to simulated warming due to higher surface soil temperatures and accelerated snowmelt generating a temporal disconnect between soil water availability and periods of plant water demand.

B. Incorporating relevant organismal traits. Previous land models used for climate change projections have historically lacked sophisticated representations of terrestrial ecology, but progress in recent years seeks to address this gap (Bonan and Doney, 2018; Fisher and Koven, 2020). For example, the default parameterization for NWT models is a single C3 Arctic grass, which vastly oversimplifies the diversity of plant functional traits that occur in the NWT tundra and limits our ability to accurately predict potential changes across vegetation communities. Using new features available in CLM (version 5.1), we will more accurately represent functional traits at NWT, including: 1) foliar characteristics that reflect measured differences in plant traits (specific leaf area and foliar C:N ratios); 2) phenology parameters to simulate the short growing seasons of alpine communities; 3) plant hydraulic strategies that represent more conservative growth strategies that can better withstand hot, dry conditions (Spasojevic et al., 2013; Wentz et al., 2019); and 4) explicit consideration of microbial traits and functional diversity (Wieder et al., 2019). The data we will use to represent these traits will be collected in the process of testing **H1-H4.**

C. Representing abiotic heterogeneity. Historically, land models crudely approximated subgrid heterogeneity, but new model features in CLM represent abiotic heterogeneity that is generated by the physical template (Swenson et al., 2019). Using a model that considers variation in snow and soil water availability that are observed across complex terrain improves our ability to predict changes in ecosystem carbon, water, and energy fluxes across vegetation communities at NWT (Wieder et al., 2017). These simulations capture patterns and dynamics that are likely to cause variation in the rates at which individuals, populations, and communities track rising air temperatures (**H1-H4**). For example, preliminary simulations demonstrate that: 1) dry meadow soil moisture is highly dependent on episodic rain events that occur during the growing season, as opposed to winter snow, which drives differences in soil moisture among landscape locations during the growing season; 2) moist meadow aboveground productivity is limited by the timing of snowmelt and length of the snow-free period, potentially limiting the extent to which tundra communities are exposed to rising temperatures; and 3) wet meadow communities receive growing season water subsidies from moist meadow patches that help maintain high soil moisture conditions. These findings are consistent with our theoretical understanding of factors limiting productivity and hydrologic connectivity at NWT (**Fig. 3**). Moving forward, we are particularly interested in investigating how growing season length, the predictability of soil moisture variation, and hydrologic connectivity may shift with continued warming in alpine ecosystems.

3.5.3. Predictions related to H5. Based on theory and evidence from our past work (above), we predict:

- *5A. Spatial integration.* Rising temperatures will alter spatial and temporal patterns of hydrologic connectivity that, in turn, affect forecasts of biogeochemical activity and ecosystem productivity across the alpine landscape.
- *5B. Biotic integration.* Biotic interactions, shifts in community traits, and variable rates of responses will moderate forecasts of biogeochemical cycling and ecosystem productivity across the alpine landscape.

3.5.4. Approach to test H5. To disentangle the biogeophysical and biogeochemical complexity of co-occurring changes across alpine ecosystems, we will leverage new capabilities in CLM 5.1 to investigate how interactions among abiotic conditions and variable rates of biotic responsiveness will alter patterns of ecosystem productivity and water fluxes at the landscape scale (**Fig. 15**). First, we will use the representative *hillslope hydrology model* (**CLM-HH**; Swenson *et al.* 2019) to investigate how abiotic changes in air temperature, soil temperatures and the timing of snowmelt affect hydrologic connectivity for different vegetation patches under climate change scenarios. Second, we will modify the *Microbial-Mineral Carbon Stabilization soil biogeochemical model* (**MIMICS-cn**; Kyker-Snowman et al., 2020; Wieder et al., 2015) to explore how changes in snowmelt and soil temperature influence the seasonal dynamics of microbial activity and nitrogen availability across a heterogeneous alpine landscape. Finally, we will use the *Functionally Assembled Terrestrial Ecosystem Simulator* (**FATES**; Fisher et al., 2015; Koven et al., 2020) to investigate how changes in plant community composition – which may emerge from warming and associated changes in hydrology and microbial activity – influence plant productivity across the Saddle and Saddle Catchment with rising air temperature.

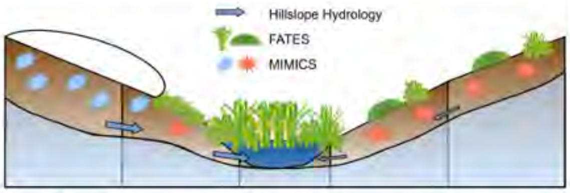

Fig. 15. Schematic of the model proposed to test **H5**, which integrates CLM v.5.1 with the hillslope hydrology model (allowing for connectivity between microsites having different rates of response), the MIMICS soil biochemistry model (allowing for different microbial functional groups), and the FATES model (allowing for different plant traits) to predict ecosystem functional responses to climate drivers.

A. Forecasting changes in abiotic conditions: the role of spatial integration. We aim to characterize abiotic changes that are likely to occur with continued air temperature increases across the heterogeneous physical template of Niwot Ridge (testing *prediction 5A*). Our forecasting experiments will leverage the latest generation of climate projections (CMIP6; Eyring *et al.* 2016), focusing on a subset of high-resolution climate models (HighResMIP; Haarsma *et al.* 2016) to emphasize the importance of higher resolution in capturing processes in topographically-complex regions like NWT. Climate trajectories capturing a range of warm vs. cool and wet vs. dry scenarios will be downscaled to alpine (Saddle and D1) and subalpine (C1) sites, following the approach of Livneh and Badger (2020) and constraining climate projections to preserve multivariate relationships (Bhowmik et al., 2017) among temperature, precipitation, and solar radiation to ensure realistic snow dynamics across sites. We will also quantify potential changes to the timing and magnitude of water subsidies and how changes in soil moisture may influence soil temperature and the balance of latent and sensible heat fluxes within and among vegetated patches across different landscape positions (Livneh and Hoerling, 2016). Subsequently, we will explore changes in productivity under warming scenarios in landscape patches where the rates of hydrologic and thermal change are potentially decoupled from each other.

B. Forecasting biotic changes: soil microbial communities and tundra plants. We aim to identify functional traits of soil microbial communities that shift seasonally, and forecast how changing abiotic conditions may alter microbial community composition and ecosystem function (*prediction 5B*). The MIMICS-cn model explicitly represents the physiology and activity of two microbial functional groups – fast (copiotrophic) and slow (oligotrophic) growth strategies (Wieder et al., 2014) – and their influence on soil organic matter turnover and persistence (Kyker-Snowman et al., 2020; Wieder et al., 2019, 2015), providing an opportunity to incorporate the seasonal turnover between winter and summer season microbial communities (Lipson *et al.* 2002; Schadt *et al.* 2003; Sorensen *et al.* 2020) and its ramifications for ecosystem N cycling and retention (Brooks et al., 2005, 1998, 1996; Lipson et al., 2009, 2002, 2000, 1999; Monson et al., 2006; Schadt et al., 2003; Sorensen et al., 2020). Model experiments will quantify how rates of change in microbial community composition and function (as examined in **H4**) influence plant N availability and inorganic N export across the heterogeneous physical template under historical and future climate scenarios.

Parallel to our analyses of soil microbial community function, we will also investigate how variation in alpine plant functional traits will mediate changes in ecosystem function in response to rising air temperatures. We will incorporate community differences in functional trait tradeoffs (e.g., leaf economic spectrum for foliar C:N, SLA), allocation (root:shoot ratios), and demographic parameters (e.g., mortality as a function of frost or heat exposure) using previous (Spasojevic et al., 2013), ongoing, and new (**H2**) functional trait measurements of NWT vegetation. Our first series of simulations will include a sensitivity test that uses a prescribed distribution of vegetation and associated plant traits. This approach will allow us to calibrate parameters of functional traits for individual vegetation communities. We will then conduct simulation experiments holding vegetation composition and plant traits constant vs. changing over time to reflect shifts due to plasticity (**H2**) and community composition (**H3-4**) that may occur in the turf transplant experiment and under climate change scenarios. These experiments will allow us to establish a range of potential outcomes that depends on the rate and extent of biotic response to experimentally imposed and projected warming. Our second series of simulations will use CLM-FATES to simulate prognostic shifts in biota and potential shifts in their mean functional trait distributions (**H2, H3**). Using this model, we will conduct hindcasts to simulate the selection of community traits based on characteristics of the physical template. For *prediction 5B*, we expect that the hindcast accuracy (as validated against measurements of ANPP across the Saddle) will improve with simulations that allow for environment-trait relationships to shift with exposure to warming summer temperatures. Subsequently, we will quantify the potential rate of change that alpine ecosystems may experience as communities shift in response to future warming.

C. Forecasting changes: the role of variation in response rates. Given uncertainties in the rates of biological responses to warming, we will use model sensitivity tests to explore the ecosystem implications of varying the rate and magnitude of biotic responses to expected warming (*prediction 5B*). For example, how do patterns of plant productivity shift across the Saddle when the functional traits of particular communities respond quickly to warming, whereas other communities do not? How do rates of inorganic nitrogen transformations and export change if the phenology and turnover of soil microbial communities tracks warming soils? How may this be amplified if the phenology of vegetation responds more slowly due to slow compositional turnover or photoperiod constraints? Addressing these questions requires developing a stronger quantitative understanding of the biotic traits, their potential plasticity (**H2**), the nature of species interactions (**H3**) and the rate of potential lagged responses across a heterogeneous physical template (**H1-H4**) of alpine ecosystems.

We acknowledge that our initial tests will not account for the full range of biodiversity and ecological responses we evaluate in **H1-H4**. We start tests of **H5** with components that have well-documented linkages between composition and function, as well as components that we are able to include in our model framework. In the future, we hope to expand these links to include more ecological responses as well as predictions of future biodiversity.

3.6. SYNTHESIS. In NWT LTER VIII, we will integrate observations, experiments, and modeling to understand the mechanisms that explain variable rates of response to rising air temperatures and evaluate the consequences of this variation for forecasting the landscape-scale consequences of climate change (**Fig. 2**). Amplified rates of warming (Gao et al., 2021; Pepin et al., 2015; Rangwala et al., 2013), sharp physical gradients over small spatial scales (Isard, 1986; Litaor et al., 2008; Oldfather et al., 2020), and well-established links between microclimate, species interactions, and ecosystem functions make mountain systems a particularly powerful context for identifying the mechanisms behind differences in the rates at which organisms respond to climate change, and how variation in response rates scales across levels of ecological organization. Each of our five hypotheses builds on and informs the work in every other hypothesis (**Fig. 2**), ensuring that NWT VIII will continue its tradition of highly integrated research that leverages the collective expertise of our interdisciplinary team and provides ecological insights across biological scales of organization. Finally, our overall question – ***when and where will ecological systems keep up with climate change?*** – is immediately relevant to conservation, resource management, and the well-being of society. Consequently, this research provides a strong platform for advancing general ecological theory, cooperating with stakeholders in alpine science and conservation, sharing safe and synthetic science with diverse groups, and engaging with people of all ages and backgrounds in our efforts to address the global problem of warming in mountain ecosystems.

3.6.1 Related research projects. Many complementary projects at NWT support research related to LTER or provide insight into mechanisms that underlie long-term changes in the structure and function of high-elevation systems (**Fig. 16**). None, however, are essential to the research proposed here. The Boulder Creek Critical Zone Collaborative Network (CZ Net) 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_2 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.

3.6.2 Cross-site synthesis and contributions to Network-level Science. NWT investigators are PIs for two of the NCO-sponsored synthesis groups. Suding co-led the “Synthesizing population and community synchrony to understand drivers of ecological stability across LTER sites” group (Luo et al., 2021; Shoemaker et al., 2022; Walter et al., 2021; Zhao et al., 2020). Wieder co-leads the “Advancing soil organic matter research: Synthesizing multi-scale observations, manipulations & models” group (Billings et al., 2021; Wieder et al., 2021). NWT has also contributed to 4 cross-site tundra synthesis projects since the mid-term site review; two of these are part of a special issue in Arctic Science (Prevéy et al., 2021; Rixen et al., 2022). A fourth cross-site project, led by NWT postdoctoral scientist Courtney Collins, evaluated tundra plant phenological sensitivity to experimental warming (Collins et al., 2021). NWT scientists have also co-led several tundra-wide syntheses of ITEX experiments (Bjorkman et al., 2018a, 2018b; Thomas et al., 2020, 2019), as well as a cross-LTER review that focused on showing the importance of long-term data collection and experiments for addressing the hardest questions in ecology (Iwaniec et al., 2021). Finally, data on NWT functional plant traits were included in the update to the TRY plant trait database (Kattge et al., 2020).

4. BROADER IMPACTS

Building on the successes of NWT VII, we will continue to provide professional development in science communication and outreach for our graduate students and foster opportunities to improve data literacy and engage with diverse audiences. In addition, NWT VIII will feature two new activities that will significantly extend the broader impacts of this project. First, we will play a pivotal role in an NSF-funded research study at CU Boulder that is testing whether an immersive, field-based graduate orientation program can reduce barriers in graduate school for students from historically excluded groups. Second, we will lead a consortium focused on science co-production and communication with stakeholders that share a common goal of understanding the impacts of climate change in our local mountains (**Fig. 16**). We will assess these efforts through pre and post surveys using audience-specific survey devices, modifying them as appropriate to best achieve our goals of engagement, data literacy, self-efficacy, and retention.

4.1. Improving STEM Educator Development: Graduate Student Training. In NWT VIII, we propose to continue to offer our one-credit seminar in Science Communication and Outreach to our graduate students and, following the course, opportunities to practice those skills through organized outreach and education events (see **2.5**). Based on feedback from graduate students, we will also develop a structured program for continued student outreach activities following the required one-year course.

4.2. Increased Public Scientific Literacy and Public Engagement with Science through Schoolyard Programming. During the COVID-19 pandemic, we partnered with the nearby Cal-Wood Environmental Education Center for our one-week residential high school field science course, the **Mountain Research Experience** (see **2.5**). While we have typically held this program at the MRS, Cal-Wood facilities were aligned with public safety requirements during the pandemic, allowing us to continue this program while campus facilities were under restricted access. This partnership yielded many additional benefits, including an increase the number of students we were able to serve, better recruitment of students with limited outdoor experience, and more effective connections with underrepresented and underserved students. Given the opportunities for our program to grow with this partnership, we will continue to host the residential camp at Cal-Wood in NWT VIII. Our new programming emphasizes "constructive hope" and integrates art into the curriculum alongside field trips to Niwot Ridge and interactions with NWT scientists. The Cal-Wood property, which experienced a 10,000-acre wildfire in 2020, provides a particularly poignant context for engaging students in activities that focus on hope and creativity. We will also continue our partnerships with the Wild Bear Ecology Center and Winter Wildlands Alliance to offer summer enrichment opportunities and Snow School through the NWT VIII Schoolyard Program (see **2.5**).

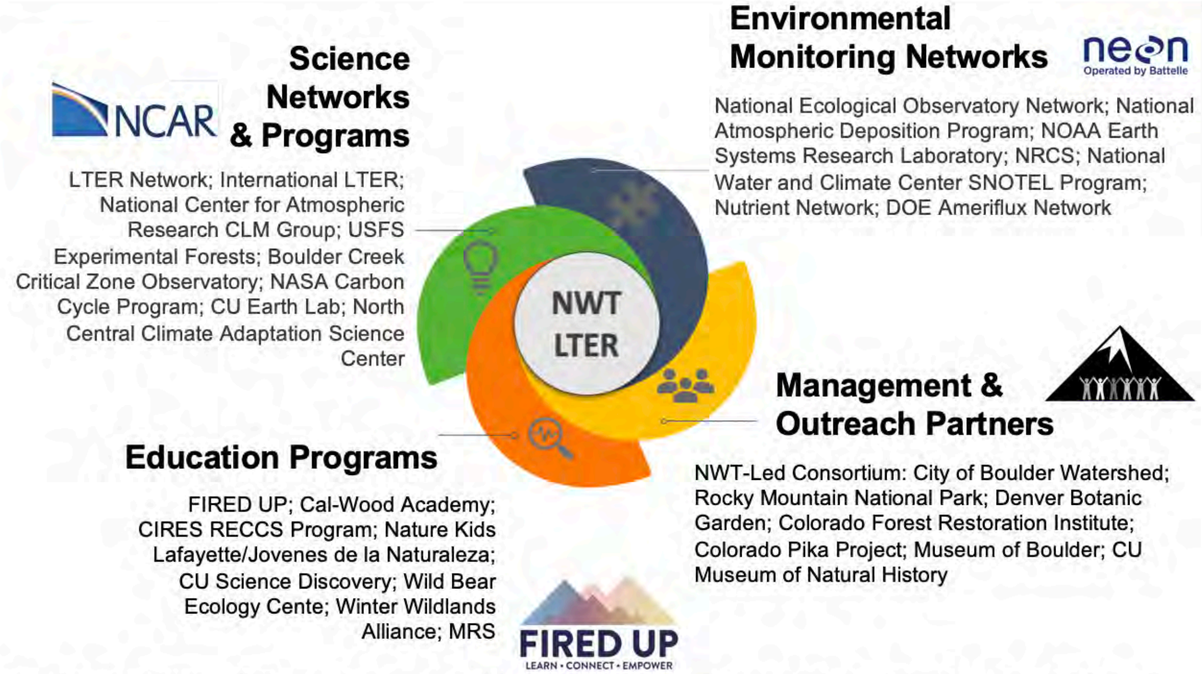

Fig. 16. The NWT LTER program is strongly linked with other science research networks and activities, education programs, environmental monitoring networks, and management and outreach partners. The LTER program provides a platform that attracts broad interest, encourages new studies and programs, and leverages research funding and outreach activities.

In addition to continuing to invest and expand our successful outreach activities, we will develop two new outreach programs – *Chronolog* and *Tempestry* – to bring NWT science to students in their communities and classrooms. *Chronolog* is a cross-site community science initiative that provides standardized photos, taken from reference locations, to teachers and students who can then remotely monitor phenology at Niwot Ridge. *Tempestry* is a data visualization project in which participants create and display tapestries that reflect real-life temperature records using standardized colors of yarn. Working with the artists who developed *Tempestry*, NWT Outreach Coordinator Dr. Alex Rose is adapting the program to engage K-12 and public audiences with NWT's long-term data on temperature and other trends. We will display the products of these fiber art projects throughout the community, at the CU Museum of Natural History, and at the Mountain Research Station.

We use formative and summative assessment in all outreach and education activities. We are particularly interested in measuring if our programming is promoting STEM learning activation in participants: are we increasing participants' fascination with science and changing their values about the natural world, their belief in their own competency as scientists, and their comfort with learning and trying new things? We use survey instruments developed by organizations such as the Learning Activation Lab and the STEM Learning and Research Center (STELAR) as well as non-survey methods that work well in informal science learning contexts (Friedman, 2008; National Research Council, 2015).

4.3. Broadening Participation in Science. NWT VIII will play a key role in a new NSF-funded research project at CU Boulder called **FIRED UP** (*Field-Intensive Research Emphasizing Diversity UP in the Alpine*) that will test the efficacy of an immersive field experience, early training in large-scale science, and cohort-building as a cohesive intervention program to increase the retention and science identity of PEER (persons excluded due to ethnicity or race) students in field-based sciences (see letter of collaboration from project PI, Dr. Valerie McKenzie). Barriers to recruiting and retaining PEER students include feelings of not belonging, which can in part be overcome through shared experiences in field environments (Leaper and Starr, 2019; O'Brien et al., 2021; Pickrell, 2020; Zavaleta et al., 2020). Co-PI's on the FIRED UP award (NSF IGE 2021) include several NWT Scientists (Emery, Taylor, and Resasco) and Dr. Lisa Corwin, a discipline-based education researcher who is leading data collection and analysis for the study. Each year, NWT scientists and staff will train the incoming student cohort in fundamental skills in field biology while collecting NWT long-term datasets. In the fall, NWT scientists, including IM Elmendorf, will co-teach a "Data Discovery" course that teaches these students fundamental data management, manipulation, and analytical skills using NWT datasets. The goal of these experiences is to demystify the methods of field and "big data" science, provide students with exposure to a wide range of tools for dissertation research, and get student feedback (through formal assessments) on how to facilitate learning and skill development in these areas. Results of this study will be published, are broadly applicable to other STEM disciplines, and will be used to refine the program. Informed by the results of the initial 2.5-year program, NWT will work with CU Boulder and the MRS to extend it to other field-based disciplines and a broader range of departments at CU Boulder.

NWT VIII will also continue several ongoing efforts to recruit and support incoming graduate students from groups that are inadequately represented in our community, including PEER students, members from the LBGTQ+ community, students with disabilities, and first-generation college students. We will continue our partnership with the CIRES RECCS program (see **2.5**) to recruit community college students for REU positions each summer, which has successfully diversified our REU participants to include more people of color and first-generation college students. Our new partnership with Cal-Wood allows our Mountain Research Experience program to connect with diverse and underserved groups, particularly Latinx families, in our community.

In addition to broadening participation through graduate training opportunities, NWT will continue to recruit and support early-career scientists from underrepresented groups to become involved in our community (see **Project Management Plan**). Our DEI committee has developed a plan to improve the culture of our community, improve mechanisms for reporting inappropriate behavior, expand our bystander and field safety trainings, and host diverse speakers in our monthly meetings.

4.4. Increased Partnerships Between Academic and Non-Academic Organizations. NWT has long engaged with non-academic stakeholders, including local agencies and non-profit organizations, to support conservation, management and education about mountain systems and the important societal services they provide. In NWT VIII, we will work with a formal consortium of agencies that share common interests and goals with respect to mountain systems: Rocky Mountain National Park, the Denver Botanic Gardens, City of Boulder Water, and the Colorado Forest Restoration Institute (see Letters of Collaboration). NWT scientists have already developed regular interaction with these entities. For example, during NWT VII, we offered science team briefings to City of Boulder Water and collaborated on habitat surveys with Rocky Mountain National Park. To further increase the involvement of consortium members in NWT research, we co-developed three primary ways to work together: (1) consortium members will have regular opportunities to share research needs and priorities with NWT researchers; (2) annual presentations by NWT graduate students will feature topics and data requested by consortium members; (3) with consortium input, NWT researchers will develop a recurring *State of the Mountain* report including NWT datasets and trend analyses will be broadly distributed throughout the Colorado Rocky Mountain region. We anticipate that these efforts will lead to greater use of NWT data for local natural resource decision-making and broaden NWT's reach within the public sphere.

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DATA MANAGEMENT PLAN

The primary goal of the NWT Information Management (IM) program is to facilitate scientific discovery by ensuring the quality, security, integrity, and timely availability of data collected through the NWT LTER program. All IM procedures at NWT are consistent with the LTER Network data access policy and follow guidance as laid out in DataOne's data management best practices hub. NWT's primary repository is the Environmental Data Initiative (EDI). An overview of the NWT data workflow is shown in **Fig. S1**.

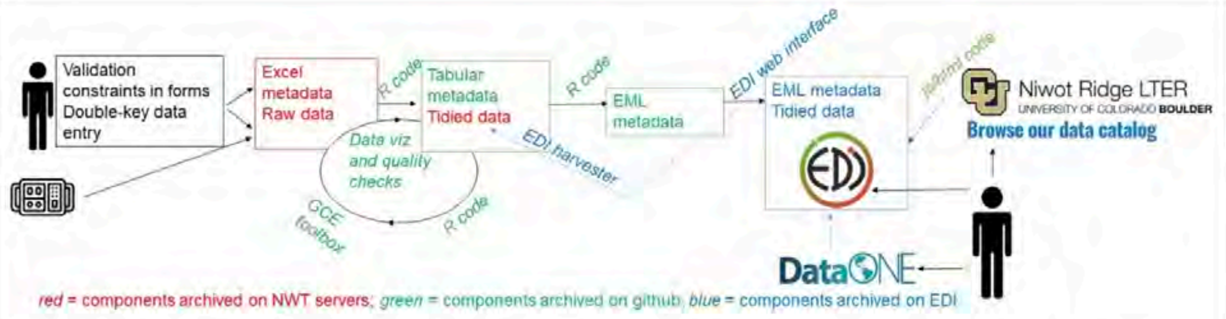

Fig. S1. End-to-end workflow for NWT LTER data collection and management, from field to portal. Data are entered into spreadsheets or collected by loggers, and both raw data and metadata are backed up on NWT's server. R/Matlab code (GCE toolbox) are used to perform quality control checks on the data in an iterative process, consulting the original data providers and raw data sheets as necessary. Finally, R code is used to create the tidied data and EML metadata that are submitted to EDI. EDI harvests data directly from the NWT server and provides public access to citable, versioned datasets, including DOIs. EDI is a DataOne member node, so the same data are also available via DataOne. The Niwot Ridge LTER data catalog (nwt.lternet.edu/data-catalog) uses customized .js and html code to provide an additional point of entry to the data archived on EDI. Thus, the same data and metadata are discoverable through any of the 3 portals (EDI, NWT, and DataOne).

NWT VII ACCOMPLISHMENTS. During NWT VII, we completely revamped our information management system to better leverage network-wide resources available from EDI. Specifically, we have migrated all published datasets formerly hosted only on Niwot Ridge's local website into EDI, eliminating the need to maintain two separate systems and ensuring that the most up-to-date versions of all datasets are always available on EDI. Simultaneously, we updated our website from a local content-management system to Squarespace, which provides a more modern and accessible interface than our previous platform. The new NWT website continues to provide a local data catalog for search and discovery of NWT data datasets. Under the improved architecture, data searches on our local catalog provide only one of several means to discover the NWT datasets on EDI. In response to suggestions we received in our mid-term review, we have added interactive plots of research locations to our website and improved graduate/postdoc training in data management.

RESOURCES. The NWT data management team is led by information manager (hereafter IM) Dr. Sarah Elmendorf. With a Ph.D. in ecology and career experience with informatics & biostatistics, Elmendorf participates in all aspects of the NWT data life cycle, starting with experimental and sampling design, extending through data processing/validation/curation, and culminating in the publication of well-documented, open access data in public repositories. Elmendorf has led and participated in many data synthesis projects that rely on public datasets and is therefore very familiar with the practices that ensure that metadata contents (e.g. methods) are sufficient for reuse and adhere to community-wide standards for publication. Her breadth of training scientific training has enabled her to develop and run quality control routines across a diversity of datasets and iterate with individual data providers to improve data quality. Furthermore, as a member of the NWT steering committee, Elmendorf is fully integrated into the science team and regularly participates in NWT research and publications. The 80% FTE for the NWT IM position is additionally supported by (1) an Institute of Arctic and Alpine Research (INSTAAR) system administrator, who is responsible for IT tasks such as server hardware updates, maintenance and security, and (2) hourly graduate, recently graduated, or advanced undergraduate students who assist with routine tasks in preparing metadata or data quality control (QC), supervised by Dr. Elmendorf.

DATA LIFE CYCLE

Plan: NWT's data management plan encompasses a comprehensive data storage system, a workflow for identifying datasets that will be collected with NWT funds, and a strategy to ensure each dataset is properly backed up, documented, and archived using reproducible pipelines (**Fig. 1**). **We archive all data collected with NWT funds to public repositories that follow Findable, Accessible, Interoperable, Reusable (FAIR) principles** (Wilkinson et al., 2016). Data are shared under a CC-BY license in a timely fashion in accordance with the LTER Network Data Access policy (LTER Science Council, 2017). The vast majority of NWT's data are "Type I" (data released within 2 years from collection and no later than the publication of the main findings from the dataset), although we make exceptions for data that are the subject of graduate student theses ("Type II"). For Type I data, **typical data latency from collection to publication is <1 year**; for graduate student data the default data latency is 2 years from collection, but individual graduate students may request that their data be published on a later schedule if they are still working toward publications using those data at the 2 year mark. The NWT IM also works with PI's from NWT-affiliated projects to archive data in NWT's collection on EDI as requested for individual projects.

The IM tracks all NWT-funded datasets from the initial planning stage through publication. For NWT VIII, we plan to continue to produce the core long-term "signature datasets" that we rely on to discern long-term trends, listed in **Supplemental Table S1A,** as well as any new datasets described in the proposal (e.g., see **Table 2** and **Box 1**). We also plan to continue the majority of the 'ongoing' datasets listed in **Supplemental Table S1B.** The IM meets individually with lead staff members responsible for climate, vegetation, and aquatic components of the program to generate a plan and timeline for each year's additions to core/ongoing datasets. In addition, individual researchers requesting NWT support are required to submit a list of datasets that will be collected, a timeline for delivery to the NWT IM, and a timeline for public release of the data. The IM coordinates with co-PI Taylor (the Director of the Mountain Research Station) for the research permit submission process each spring to maintain an up-to-date map of research locations for all research (including non-LTER projects) at the site. Research permits are used to identify the geolocations of new studies on Niwot Ridge, which are added to the interactive and downloadable map of research locations on the NWT website.

Collect, Process & Validate: NWT's signature, long-term datasets (**Supplementary Table S1A**) are generally collected by NWT staff. This ensures consistently high quality in our long-term records and provides data continuity that is not possible with graduate students or other short-term researchers. Datasets produced by the NWT LTER generally fall into 4 categories: (1) electronically provided data collected by equipment and transferred via wireless network; (2) electronically provided data that are manually downloaded in the field; (3) data recorded on hard-copy field forms or charts; and (4) results from laboratory analyses. Other ("non-signature") datasets include short-term datasets collected by graduate students and/or NWT-affiliated researchers (**Supplementary Table S1B**).

We recognize that errors or questionable data values are best addressed as early in the data workflow as possible, when simple human mistakes such as mis-labeling or transcription errors can be easily corrected and instruments can be promptly recalibrated and repaired. Therefore, for each signature dataset, the IM uses customized R scripts to run basic quality control scripts and visualization (e.g., plotting of all numeric variables, checks for missing and duplicate values, correcting misspelled taxonomic names) *before public archiving* (**Fig. S1**). When quality issues are identified, she iterates with the designated point-of-contact for each dataset to resolve any issues before archiving. This process can involve double-checking raw data (e.g., reviewing questionable records in scanned paper datasheets,or field records on sensor maintenance, rechecking labels, re-running lab samples). The same scripts are used to generate 'Tidy data' (long-form, ascii-files; one variable per column, one table per type of observational unit, with consistent naming conventions and date formatting) (Wickham, 2014). We archive all code used to QC and process the data on GitHub to ensure that all data post-processing is traceable (Borer et al., 2009). While we have invested extensive effort in developing individualized QC routines for our signature datasets, we also run a subset of shared quality checks for non-signature data. We also leverage the QC routines developed by the Environmental Data Initiative, particularly the EML Congruence Checker, which provides a standardized series of checks for metadata completeness and congruence between metadata and data attributes for each submitted dataset (Clarke, 2018).

In addition to the final checks before submission outlined above, the following workflows are used by staff or researchers responsible for particular areas of the program:

Signature datasets from electronic sensors: Sensor-derived datasets collected by NWT climate technicians are processed using the GCE Toolbox (Sheldon, 2019), a MATLAB program developed by the GCE LTER that provides automated quality checks, flagging potential problems or errors, and (in some cases) aggregation to larger timesteps. In addition to the automated quality checks, NWT staff do a visual check of the data each year, manually flagging data as needed and checking any instrument errors prior to making annual updates to the archived, quality-controlled data on EDI.

Signature datasets collected using paper datasheets: We have developed standardized Excel data templates that match field sheets to facilitate straightforward and accurate data entry. Data templates include internal cell-level validation/dropdown menus as appropriate. Datasets are double-entered by NWT technicians to catch and correct typographical errors. Raw data sheets are scanned and archived on the NWT server for internal use and re-referencing as necessary.

Signature datasets from laboratory analyses: Laboratory-generated data are reviewed by the lab manager and re-run as needed following standardized lab protocols. After final QC checks, sample remnants are discarded; NWT LTER does not at this time maintain a physical sample archive for environmental samples. However, because Niwot Ridge is also a NEON site, sample archives of biological, genomic, and environmental materials from the site are accessible for current and future researchers through the NEON Bioarchive. Zooplankton and pollinator specimens from the LTER program are archived at the University of Colorado's Museum of Natural History.

Curate: NWT maintains a 4 disk, RAID 6, ReadyNAS server housed in the INSTAAR building on the CU campus that is used to store (1) raw data (electronic copies and scans of paper data sheets), (2) data in the processing queue, and (3) local copies of published versions of NWT datasets. The RAID 6 setup ensures that the system can recover from the loss of two disks. Following best practices recommendations for data backup from DataOne (DataOne, 2016), these data are, in-turn, automatically backed up to 2 additional locations, including an off-site backup. Rsync scripts run nightly to back up the contents of the ReadyNAS to an external hard drive and the Petalibrary maintained by Research Computing at CU Boulder (ZFS raidz2 in a separate campus location).

Raw data are uploaded to the server by one of three routes: (1) Where possible, data are transferred via wireless network and downloaded automatically onto NWT's server using Campbell Scientific LoggerNet software. (2) For sensors not connected to the wireless network, data are downloaded manually when visited by NWT climate technicians (typically once/month) and then uploaded to the NWT server. (3) Remaining datasets (e.g., signature datasets collected on paper datasheets, data from our analytical chemistry lab, and data collected by NWT-funded graduate students or short-term researchers) are manually transferred to the NWT server for backup. Scanned datasheets are also backed up for all staff-collected datasets where paper datasheets are used for field-collected data.

Publish: NWT uses the Environmental Data Initiative (EDI) as its primary data repository (**Fig. S1**). EDI provides a comprehensive risk-management system, including mirrored storage offsite and in the cloud. This ensures that all data collected with NWT funds are preserved in perpetuity and provides further assurance against data loss in addition to NWT's own backups described above.

Metadata are submitted to EDI alongside data in EML (Ecological Metadata Language) format – a machine-readable structured metadata format (Jones et al., 2019). Individual researchers and/or staff are primarily responsible for providing the information used to populate the EML. Specifically, the point of contact (the staff or researcher that is primarily responsible for the collection of the data for each package) completes an Excel-based metadata form that is available on the NWT website. The contents are checked by the IM, edited for accuracy and clarity if needed, and then converted via R code into EML. Finally, EML files are submitted to EDI for publication (**Fig. S1**). EDI harvests data directly from the QC'd versions stored on the NWT server, ensuring that the two systems remain synchronized.

EDI is a general ecological repository, but we recognize that there are certain cases where a strong community of practice has developed around access, discovery, processing and/or aggregation of select types of data NWT collects through portals other than EDI. For this reason, we also rely on three non-EDI repositories (Ameriflux, NADP, and NCBI). For these specialized repositories, datasets are typically submitted directly by the scientists responsible for the collection of the data, in coordination with the IM.

Discover: NWT facilitates data discovery through several pathways. During NWT-VII, we revamped the NWT website, migrating from a local Content Management System (CMS) to a commercially hosted platform (Squarespace). The new website provides a clean interface that is easy to edit and maintain, while still aligning with the core requirements of LTER websites (LTER Science Council, 2018). The new NWT website includes enhanced dynamic content such as the ability to "explore the ridge" via real-time weather graphs and embedded ArcGIS Online interactive maps of research locations and our user-driven tundracam. It also provides information on publications, personnel, education & outreach as well as news & events and is linked to our social media accounts.

NWT also hosts a local data catalog on our website. Our local data catalog uses embedded javascript and html code to directly query NWT metadata stored on EDI via the PASTA REST API, providing links to download data and metadata directly from EDI. This setup solves the challenge of maintaining multiple search interfaces for the same data while ensuring that the parallel systems do not become desynchronized. EDI also provides access to NWT data via its own search page. Finally, because EDI is a DataONE member node, NWT data are discoverable through the DataONE search interface. Data archived outside of EDI are not duplicated on EDI, but we maintain linkages to facilitate search and discovery of these data via (1) dataset inventory tables archived in EDI (Gries et al., 2021), or (2) the "Other Niwot Datasets" page on our website, which links to NWT's Ameriflux and NADP data, as well as data collected by other (non-LTER) researchers at Niwot Ridge (**Fig. S1**).

ADDITIONAL IM ACTIVITIES

Network Participation: The IM attends monthly LTER network-wide information meetings to track best-practices and new developments in data management tools and standards. In NWT VII, Elmendorf co-authored documents describing best practices for archiving for non-tabular data (e.g., drone and next-generation sequencing data; Gries et al. 2021), which will guide our procedures for archiving these types of datasets included in the current proposal.

Stakeholder responsiveness: While EDI provides a stable repository for long-term data access and an excellent suite of tools for reproducible scientific research, it does not necessarily meet the needs of all audiences (e.g., resource managers and conservation practitioners). For example, to complement our annual meteorological data uploads to EDI (which undergo an annual manual quality check in addition to the automated flagging procedure prior to archiving), we provide real-time meteorological data graphically on our website and via ASCII files on an ftp site. This addition was made in response to a request by the National Weather Service Staff at the NWS office in Boulder Colorado to support real-time decision-making. NWT meteorological data are harvested by the NWS in real time and then fed into NCEP's publicly available Meteorological Assimilation Data Ingest System (MADIS) and the University of Utah's MesoWest databases. NWT data are used by NWS staff in hour-by-hour forecasting and warning operations to assess conditions above treeline and the potential for damaging winds to descend to lower elevations, inform the public of the severity of the conditions, and support hourly gridded weather analyses (RTMA/URMA, NCEP Internet Services Team, 2017). Real-time meteorological data collected by NWT are also used on a daily basis by forecasters for the Colorado Avalanche Information Center.

Going forward, we aim to retain the ability to respond in an agile fashion to partner organizations who are not easily served by static archives.

Education & Training: Each year, the IM provides an overview of NWT data policy & procedures to the entire NWT research community during the spring all-NWT Field Orientation meeting. She also provides individual support to researchers for metadata preparation and data submission to EDI, and offers short courses to the NWT community (including students, post-docs, and staff) on reproducible research (e.g., git workshops). She also supports data science courses and training at CU (e.g., co-instructing a graduate seminar in Ecological Forecasting), and provides statistical advice and one-on-one consulting to postdocs and graduate students.

GOALS FOR NNWT VIII. In NWT VIII, we plan to continue the timely **archiving** of high-quality data in EDI, leverage new tools as they are developed across the network (e.g., the Data Explorer tool, currently in development at EDI), and improve our data quality checks on an iterative basis. **New initiatives in NWT VIII include:**

(1) Developing **enhanced data summary products** for our consortium partners and research scientists. Following best practices for stakeholder engagement (Bamzai-Dodson et al., 2021), we anticipate this will be an iterative process beginning with listening sessions and collaborative design that focuses on the needs and goals of the intended audiences.

(2) Investing additional IM resources in the **education and outreach** initiatives outlined in the main proposal. The IM will provide training on reproducible research and data management best practices to incoming graduates as part of the FIRED-up program, supporting broader project goals of a diverse community of researchers with the skills to analyze the datasets provided by the LTER.

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PROJECT MANAGEMENT PLAN

The NWT LTER Program is based at the University of Colorado Boulder within the Institute of Arctic and Alpine Research (INSTAAR). INSTAAR is an interdisciplinary, research-focused unit at CU Boulder that has oversight of the Mountain Research Station, providing an appropriate and effective administrative home for the NWT LTER.

Project Management for NWT LTER VIII strives to (1) ensure an inclusive, collaborative environment that facilitates interdisciplinary approaches to reaching the stated goals of the NWT LTER, (2) implement a model of distributed leadership that supports new investigators and ideas while maintaining the integrity of our long-term monitoring programs, (3) provide transparency in communication and decision-making, and (4) uphold a culture that embraces diverse perspectives and backgrounds and is firmly committed to safe, equitable, and inclusive practices.

LEADERSHIP STRUCTURE. *Nancy Emery* will rotate into the PI role for NWT VIII, replacing *Katharine Suding*, who served as NWT PI since 2014. Suding will remain in a co-lead position to ensure a smooth transition of leadership and until a new co-lead is identified who will, in turn, be mentored by Emery to be the next PI. As PI of NWT VIII, Emery will be responsible for overall scientific leadership, coordination of NWT activities, fiscal oversight, timely reporting to NSF, communication with the LTER Network, and the preparation of the NWT IX renewal proposal.

Emery will work closely with a **Core Leadership Team** comprised of the four signatory co-PIs – *Katie Suding, Eve Hinckley, Will Wieder,* and *Scott Taylor* (**Fig. S2**). The Core Leadership Team shares responsibility for decisions that have significant implications for NWT resources, personnel, and research programming. The team meets each fall to approve the budget for the upcoming calendar year, and each spring to allocate funding for summer graduate student support. Co-PI Taylor, in his role as the Director of the CU Mountain Research Station, provides oversight to ensure that NWT research plans align with permit requirements and are coordinated with other activities on Niwot Ridge.

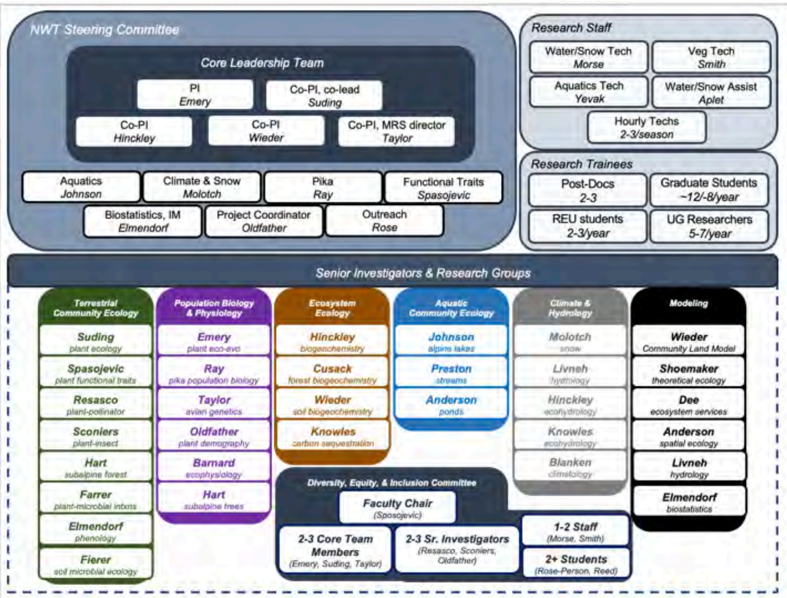

Fig. S2. The NWT LTER is led by a Core Leadership Team that consists of the PI and signatory co-PI's. Major LTER activities are coordinated by this team and additional personnel on the NWT Steering Committee. Senior investigators span 6 research areas that collectively address the 5 hypotheses in NWT VIII and include multiple individuals from groups that are underrepresented in STEM fields. Research Staff and Trainees are supervised by the Core Leadership Team and individual senior investigators. The DEI committee includes representation from all of these groups. Participation in the DEI committee is open to all NWT members (2022-23 members shown here).

The **NWT Steering Committee** consists of the Executive Committee plus other key scientific personnel with important scientific expertise for NWT VIII: *Chris Ray* (pikas), *Noah Molotch* (snow), *Piet Johnson* (lakes), and *Marko Spasojevic* (functional traits), as well as *Alexandra Rose* (Outreach Coordinator), *Sarah Elmendorf* (IM lead), and *Meagan Oldfather* (Project Coordinator) (**Fig. S2**). Each member of the Steering Committee is responsible for supervising the ongoing collection, quality assurance, and curation of data sets that align with their scientific expertise. Steering Committee members also contribute to annual reports, co-organize the mid-term review, attend LTER Science Council meetings, participate in synthesis projects, and submit research proposals that leverage and complement NWT LTER research.

The **NWT DEI Committee** consists of a chair from the Steering Committee (rotated every two years) and a minimum of 2-3 members of the Core Leadership Team, 2-3 additional Senior Investigators, two staff, and two students. Membership is open to all NWT members (**Fig. S2**). The committee meets monthly to address priorities that are established at the beginning of each year based on the results of an annual community climate survey. The committee is responsible for conducting community culture surveys every three years, annual post-season surveys to monitor NWT participants' experiences, organizing speakers and program-wide DEI trainings for three all-NWT meetings/year, and updating our orientation, harassment and field safety, code of conduct, and diversity plan materials each year.

The **External Scientific Advisory Board** provides feedback and guidance on NWT research activities while facilitating synthesis and integration with other programs and organizations. The board consists of nine members whose expertise aligns with key areas in NWT VIII: *David Ackerly* (UC Berkeley), *Jake Alexander* (ETH Zürich), *Lauren Buckley* (University of Washington), *Sharon Collinge* (CU Boulder), *Jim Elser* (University of Montana), *Rosie Fisher* (Center for International Climate Research, Norway), *Jesse Nippert* (Kansas State University), *Melany Fisk* (Miami University Ohio), and *Vigdis Vandvik* (University of Bergen). We expect to meet with the board on a biannual basis.

CONTINUITY AND SUCCESSION. The NWT community recognizes the value of distributing and rotating leadership to share the responsibilities of running a successful program and bring new perspectives to NWT science. We also recognize that the steep learning curve involved in transitioning leadership can create a loss of continuity and disrupt developing collaborations. To facilitate smooth leadership transitions, we have adopted a "co-lead" model where a current PI is either mentored by the prior PI or a mentor for an upcoming PI. In 2019, Emery stepped into a co-lead role in anticipation of serving as the PI for NWT VIII, and Suding will serve as a co-lead with Emery until a new co-lead is ready to begin preparing for a future PI role. We have found this model creates important redundancy in leadership that minimizes disruptions during an LTER cycle (e.g., when a PI takes sabbatical), and that sharing administrative responsibilities makes LTER leadership more sustainable.

LTER VIII brings several new faculty members into leadership roles while ensuring continuity. Emery, Suding, and Hinckley were PI or Co-PIs, and Wieder and Taylor were active participants, in NWT VII.

WELCOMING NEW INVESTIGATORS. NWT VIII will continue to welcome and engage new investigators to the LTER. The activities proposed for NWT VIII leverages the expertise of several new investigators that are developing research programs at Niwot Ridge and in the surrounding region, including *Julian Resasco* (pollination ecology, CU Boulder), *Warren Sconiers* (entomology, CU Boulder), *Laura Dee* (statistical modeling, CU Boulder), *Sarah Hart* (forest ecology, Colorado State University), *Dan Preston* (stream ecology, Colorado State University), *Lauren Shoemaker* (community ecology and modeling, University of Wyoming), *John Knowles* (ecosystem science, California State University Chico), *Daniela Cusack* (biogeochemistry and ecohydrology, Colorado State University), and *Emily Farrer* (plant-soil interactions, Tulane University). In addition, LTER VIII includes participation from *Kurt Anderson* (UC Riverside) and *Dr. Holly Barnard* (CU Boulder) to extend our expertise in aquatic community ecology and plant ecophysiology, respectively. We will continue to encourage use of the NWT LTER site and datasets by a broad range of investigators (see **DATA MANAGEMENT PLAN**).

We have found that the flexible and open funding structure we developed over the last six years has encouraged the participation of new researchers and supported their success in getting research established at NWT. As a result, we have maintained continuity in the longstanding research programs of recent LTER retirees, built expertise in new areas (e.g., trophic interactions, evolutionary biology), strengthened our program in aquatic ecology, and increased the representation of scientists from historically under-represented groups in our community and disciplines. Although the majority of NWT investigators have traditionally been based at University of Colorado, 1/3 of the senior investigator team for NWT VIII come from other universities, including two other institutions from the Rocky Mountain Region (Colorado State and the University of Wyoming), and two Hispanic Serving Institutions in California (UC Riverside, CSU Chico). LTER supports the participation of these scientists and their students by providing logistical support, field assistance, data management support, and, when possible, modest research funding when research campaigns align with LTER goals.

RESEARCH PLANNING PROCESS. Every autumn the NWT Steering Committee will lead an all-NWT meeting to review the activities from the prior field season and coordinate research plans for the upcoming year, including priorities for sample processing, plans to present NWT research at conferences, and organizing participation in outreach activities. Our priorities will be to fulfill the objectives outlined in the LTER VIII proposal, encourage integration and synthesis across areas of research, and support the collection of data of shared interest across investigators. However, we always encourage investigators to bring new ideas to the Steering Committee and the NWT community, particularly those that are aligned with NWT priorities and engage new researchers.

PROJECT-WIDE COMMUNICATION. We encourage collaboration and promote scientific and programmatic interactions among NWT investigators. During the academic year, we hold monthly all-NWT meetings for all scientists, staff, and graduate students, with off-campus participants joining by Zoom. These meetings include research presentations, workshops, LTER planning, DEI training and events, and discussion of issues directly related to local or network-level LTER activities. Two all-NWT meetings are dedicated to graduate student research presentations each year. We also maintain a NWT-wide Slack workspace with dedicated channels for general announcements, specific collaborative projects, graduate students, staff, safety training and logistics, outreach, recent publications, and data management.

FIELD SAFETY TRAINING, LOGISTICS, AND COORDINATION. One all-NWT meeting is set aside for a NWT Field Orientation each spring that provides critical information about field safety, community expectations, and logistical coordination for the upcoming summer field season. At this meeting, we review the NWT Code of Conduct & Community Engagement Guidelines, outline expectations and workflows for data collection and submission, and coordinate with the MRS to provide a detailed field safety presentation that includes procedures for preventing, recognizing, and reporting harassment in the field. The information is compiled into a NWT orientation guide that is distributed to all participants and made available on our website. **All NWT LTER participants are required to attend the orientation each spring (or watch the video recording) and sign a document confirming that they have reviewed the information and agree to abide by the NWT Code of Conduct & Community Engagement Guidelines.** Participants are not allowed to use NWT resources (e.g., shuttles, field equipment, instrumentation) until they have completed this training and signed these forms each year.

Each spring, the MRS director (co-PI Taylor) solicits proposals for all activities to be conducted on Niwot Ridge/Green Lakes Valley/MRS properties. Taylor compiles these plans, coordinates with researchers if adjustments are needed to meet permit requirements, and coordinates with the US Forest Service and City of Boulder to formalize permission for fieldwork in the upcoming year.

BROADENING PARTICIPATION. LTER VIII includes researchers from all career stages and a diversity of backgrounds. We have increased the representation of early career investigators (i.e. assistant professor or equivalent) from 45% in NWT LTER VII to 54% in LTER VIII. We have increased the representation of women (from 9 to 12; = 50% of LTER VIII), doubled the representation of individuals from underrepresented groups (from 2 to 4; =17% of LTER VIII). Our team includes faculty who openly identify with the LBGTQ+ community and have veteran status. An ongoing search for an aquatic biogeochemist, which is expected to attract candidates interested in participating in the NWT LTER, has placed a high priority on recruiting candidates that will contribute to the university's mission to improve diversity, equity, and inclusion on campus. We engage in several activities to recruit and support graduate students and REU students from underrepresented groups, such as targeting first-generation college students for our REU program, playing a key role in a research study aimed to increase the retention of students from underrepresented groups in the field sciences (FIRED UP), and running a high school summer field program that targets underserved youth (see **BROADER IMPACTS**). While we are encouraged that our efforts are increasing diversity at all levels of our organization, we recognize that we are still far from equal and fair representation, and are committed to further investing in these and other efforts in NWT VIII.