

Overview:

The Arctic is rapidly warming. Some responses to this warming involve acceleration of processes common to other ecosystems around the world (e.g., shifts in plant species), whereas others are unique to the Arctic but with global consequences for society (e.g., carbon loss from permafrost thaw). The objectives of the Arctic Long-Term Ecological Research (ARC-LTER) project for 2023-2029 are to determine how and how fast trends in climate change and especially climate variability are changing arctic ecosystem structure and function. To understand these changes we will extend our use of the concepts of biogeochemical and community “openness” and “connectivity,” developed during our previous award, to understand the responses of arctic terrestrial and freshwater ecosystems. These objectives will be met through continued long-term monitoring of changes in undisturbed and disturbed ecosystems along the terrestrial to aquatic continuum in the vicinity of Toolik Lake, Alaska. In addition, we will measure the recovery of these ecosystems from natural or imposed disturbances, maintain existing long-term experiments, and initiate new experimental manipulations and observational studies to achieve the objectives. Based on the data generated, carbon and nutrient budgets and measures of species composition and abundance will be compiled for major components of the arctic landscape. Through a combination of data analysis and modeling we will assess how climate change and climate variability will affect biogeochemistry and community dynamics of ecosystems, and determine how ecosystem responses will propagate across the landscape.

Intellectual Merit:

Building on our ongoing focus of how ecosystem openness and connectivity affect the response of biogeochemical cycles and communities to climate change and disturbance, the proposed research is centered on the hypothesis that climate variability is a stronger driver of change in the Arctic than are the mean, long-term trends in climate. The research will answer three interconnected questions: (1) How does climate variability affect the openness and connectivity of arctic ecosystems? (2) How does climate variability affect key consumers and their influence on ecosystems? (3) How does climate variability affect carbon dynamics along the terrestrial-aquatic continuum? Natural climate and environmental variability will be analyzed or manipulated to examine how key consumers like fish and small mammals move on the landscape and influence system productivity, organism abundance, and species composition, and how key processes such as organic matter production and consumption along the terrestrial-aquatic continuum function to control carbon dynamics and balance of tundra ecosystems. The research will use synthesis of ongoing, long-term observations and experiments, and new activities combining observations, experiments, and modeling. These activities will answer the research questions about how trends in mean climate, climate variability, and disturbances all interact to control arctic ecosystem structure and function, now and in the future.

Broader impacts:

ARC-LTER research has broad impacts on science with over 68,000 citations of the 730 journal publications by our researchers and collaborators since 1975. The 145 publications since 2017 have been cited 2,660+ times. This impact will grow with new publications from ongoing long-term and proposed research. Associated researchers, postdocs, and students benefit from access to long-term data and the ability to conduct complementary studies in our monitoring and experimental sites. This approach will maintain a pipeline of support for the many excellent assistant and associate researchers now affiliated with the project. Education and outreach to non-scientists will be expanded, and a new ARC-DEI plan guides our efforts to broaden diversity and participation in all our activities. These activities include: (i) engagement of K-12 teachers in summer research programs via our Schoolyard program, Earth Camp, NSF RET, and NSF PolarTREC efforts, (ii) support, mentoring, and inclusion of undergraduates (including two REUs) and graduate students associated with ARC, (iii) briefings to Alaska State, North Slope Borough, and US government agencies overseeing environmental and natural resource programs, (iv) collaboration with the NSF SEARCH program co-producing knowledge with Indigenous experts for use in decision making, (v) engaging learners in analysis of ARC data by producing education modules, and (vi) graduate student participation in workshops, LTER all-scientist meetings, and in an open, annual ARC-LTER meeting.

I. Project Description

INTRODUCTION

For over 45 years scientists have studied the ecology of tundra, streams, and lakes (the terrestrial-aquatic continuum) near Toolik Lake, Alaska. In 1987 Toolik became the Arctic tundra site of the NSF LTER program (Fig. 1; Hobbie & Kling 2014). Based at the Toolik Field Station (TFS) in the northern foothills of the Brooks Range, the ARC-LTER studies model systems for advancing general ecological understanding, is the only terrestrial and freshwater Arctic LTER site, and thus it represents a major biome with great importance in the integrated Earth system.

The Arctic is also one of the most rapidly warming regions on Earth (Ballinger et al. 2020), and thawing of large stores of permafrost carbon (C) could amplify global warming (e.g., MacDougall et al. 2012, Schuur et al. 2015). Climate variability is also increasing, with more extreme weather events like heat waves, flooding, and storms (Karl et al. 1995, Thornton et al. 2014, Vonk et al. 2015, Bintanja et al. 2020). The effects of climate variability (temperature, precipitation) in the Arctic are often realized as increased disturbances, such as increased thermal erosion of permafrost and land-surface failures (“thermokarst;” Bowden et al. 2008), more frequent tundra wildfires (Mack et al. 2011, Hu et al. 2010, 2015), and a longer thaw season (Overeem & Syvitski 2010).

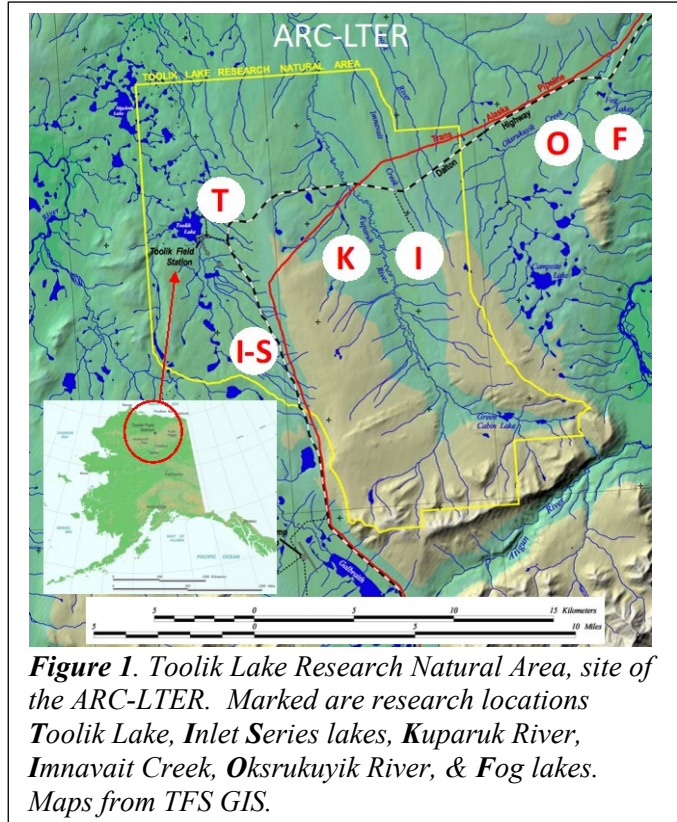


Figure 1. Toolik Lake Research Natural Area, site of the ARC-LTER. Marked are research locations Toolik Lake, Inlet Series lakes, Kuparuk River, Imnavait Creek, Oksrukuyik River, & Fog lakes. Maps from TFS GIS.

Arctic ecosystem responses to climate change and disturbance are variable in space and time. For example, Rocha et al. (2012) found recovery of tundra canopy greenness and function within a decade after fire, but Schuur et al. (2007) found changes in plant composition five decades after subsidence from thermokarst. Modeling indicates that although vegetation and surface soils can recover from disturbance in a few decades, deep soil recovery might require centuries (Pearce et al. 2015, Jiang et al. 2015, 2017). Connectivity among ecosystems means that this disturbance-recovery cycle can have important consequences for downslope streams and lakes. The ARC-LTER has shown how warming and increased climate variability increase hillslope connectivity and alter nutrient transport, especially during extreme events, thus impacting receiving aquatic communities (Bowden et al. 2008, Cory et al. 2013, Kendrick & Huryn 2015, Daniels et al. 2015). Even with disturbance there is strong resistance to new species entering terrestrial systems (Gough et al. 2016), and long lags before new species enter aquatic systems (e.g., fertilization, Slavik et al. 2004). However, in general open aquatic systems tend to respond and recover faster than closed terrestrial systems (Bowden et al. 2012, 2014, Luecke et al. 2014, Budy et al. 2021).

This proposal continues our long-term investigations and current focus on biogeochemical and community openness and connectivity among tundra ecosystems. As described in detail in the research sections below, as our research has progressed, we learned that many aspects of ecosystems including openness and connectivity might depend strongly on climate variability. For example, less frequent but more intense storms might change the transport of C and nutrients on the landscape even if the mean precipitation is unaltered, and storms redirect nutrient inputs in lakes and alter lake productivity. Climate variability can have analogous effects on the movement, reproduction, and trophic interactions of species on land

and in water. Therefore, to understand how ecosystem structure and function are related to disturbance, openness, and connectivity, key ecological themes important in all ecosystems, in this renewal we specifically add new research on the role of climate variability. Our approach includes continuation of long-term datasets and experiments, new syntheses of long-term data to determine links between climate variability and system response, and new experiments and modeling to address research questions on the ecological role of climate variability in ecosystems.

Project History: Research near Toolik began in 1975. In 1987 the site joined the LTER network. The overall goal of the ARC-LTER is to *understand ecological structure and function along the terrestrial-aquatic continuum*. The specific focus evolves with each renewal as our understanding grows and as discoveries generate new opportunities and questions:

ARC-LTER I (1987-1992): Descriptions of tundra, stream, and lake ecosystems; long-term change versus short-term controls on ecosystem components.

ARC-LTER II (1992-1998): Ecological variability and long-term change; top-down versus bottom-up controls on tundra, streams, and lakes.

ARC-LTER III (1998-2004): Prediction of the future characteristics of arctic ecosystems and landscapes; controls by physical, climatic, and biotic factors.

ARC-LTER IV (2004-2010): Understanding changes in the arctic system at catchment and landscape scales through knowledge of linkages and interactions among ecosystems.

ARC-LTER V (2011-2017): Understanding (i) direct effects of climate change on processes and linkages in ecosystems, and (ii) indirect effects of climate change through altered disturbance.

ARC-LTER VI (2017-2023): The role of biogeochemical and community openness in governing arctic ecosystem response to climate change and disturbance.

This proposed renewal will continue our recent LTER themes but add a new theme of the role of climate variability. Through ongoing research, synthesis of past data, and new activities, we will assess how increased variability in climate and disturbance interact with climate mean trends and biogeochemical and community openness and landscape connectivity to control ecosystem structure and function.

II. RESULTS FROM PRIOR RESEARCH

Publications and Other Products: LTER-related research at Toolik Lake has had significant *broader impacts* in ecology and ecosystem science, with over 68,000 citations of the 730 journal publications since 1975 that include contributions from ARC-LTER scientists and their collaborators. These publications are currently cited more than 5000 times per year with an overall h-index of 136 (Fig. 2). In addition, ARC-LTER scientists have produced 7 books, 97 book chapters, 43 PhD theses, and 70 Master's theses. Since the start of the current grant in 2017, ARC-LTER scientists and their collaborators have published 145 journal articles that have been cited 16,629 times. Recent major syntheses include a field guide (Huryn & Hobbie 2012) and a book based on ARC-LTER research (Hobbie & Kling 2014).

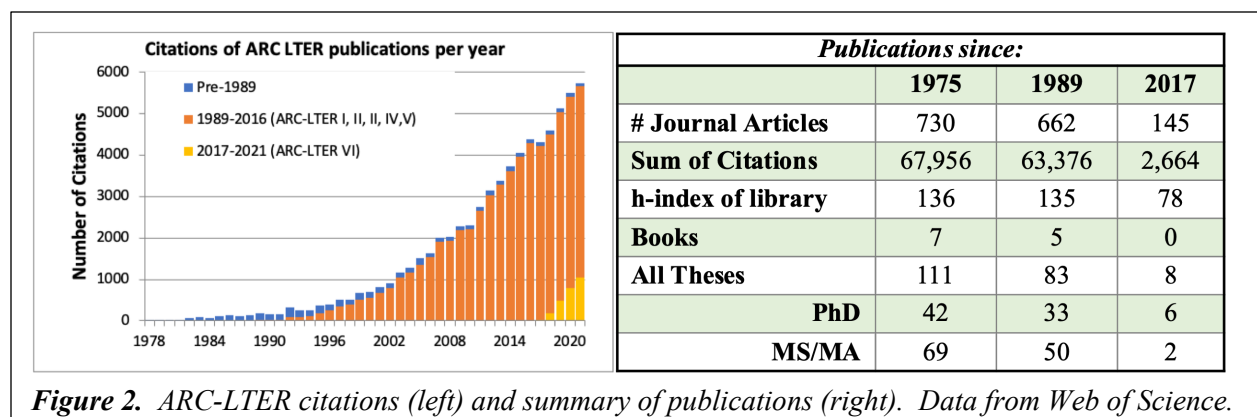


Figure 2. ARC-LTER citations (left) and summary of publications (right). Data from Web of Science.

Ten Significant Papers: Below we annotate ten key papers from ARC-LTER VI (2017-2023) that highlight our contributions and broader impacts in ecology. Nearly all of these papers result from long-term studies on our themes of biogeochemical and community openness and connectivity. *More detail on our long-term research is presented in the "Rationale and Background" sections below.*

(1) **Rastetter et al. (2021)** show how ecosystem response to disturbance depends on the openness of the nitrogen (N) cycle, N distribution between vegetation and soils, and the proportion of N losses that are in a refractory form. Openness, a high fraction of N in vegetation, and high refractory N losses exacerbate post-disturbance N losses but speed recovery as plant and soil processes are rebalanced.

(2) **Rastetter et al. (2022)** show how “explicitly representing grazers in models” vs. “having grazer effects implicitly aggregated with other biogeochemical processes” alters responses to elevated CO₂ and warming. The mechanism is that grazer-mediated processes and the processes with which they are aggregated respond differently to climate change. The aggregated approach underestimates the ecosystem response to climate change, and the magnitude of this underestimation increases with grazer density.

(3) **Klupar et al. (2021)** show that moist acidic tundra (MAT) responds to fire with greater canopy height and greenness, and greater soil nutrient availability. The plant community shift from tussock to shrub-dominated in previously-burned tundra also occurred in unburned tundra with N and phosphorus (P) added; there were no new plant species in the burned tundra 10 years after fire, but there was a shift in existing species dominance.

(4) **McLaren and Buckeridge (2019)** use long-term fertilization to demonstrate that dwarf birch becomes common in MAT when nutrient availability increases, but remains almost absent from moist non-acidic tundra (MNT) regardless of nutrient availability. MNT communities stabilized earlier, with increased graminoid dominance, suggesting different future trajectories for these two communities. Microbial biomass and function responded most strongly to P in MAT but to N in MNT.

(5) **Neilson et al. (2018)** show how surface microtopography creates “porpoising” of water between the land surface and soil, driving a rapid exchange of overland flow with shallow groundwater. Together with rapid leaching of soil organic matter, this explains high concentrations of dissolved C in soils and streams during both low and high flow conditions. The persistence of groundwater contributions in arctic watersheds will influence C export to rivers as permafrost thaw depth increases in a warmer climate.

(6) **Bowen et al. (2020a)** show that ancient dissolved organic matter (DOM, >4000 yrs old) draining permafrost soils is oxidized to CO₂ by even the less-energetic visible wavelengths, thereby settling a debate on photochemical reactivity of permafrost DOM. New knowledge of the mechanisms involved shows that photomineralization rates of permafrost DOM to CO₂ are double that of modern DOM, and thus current estimates of arctic amplification of global warming from permafrost C are too low by ~14%.

(7) **Budy et al. (2021)** use a 12-yr lake fertilization and 6-yr recovery period in deep lakes with fish and shallow fishless lakes to show that effects of fertilization were more pronounced in the deep than in the shallow lake. However, there was moderate resistance to changes in ecosystem function at all trophic levels. Eventual responses were often non-linear, and post-fertilization recovery was most rapid (2-4 years) at the base of the food web while higher trophic levels failed to recover after 6 years.

(8) **Pennock et al. (2021)** test the effects of food availability and temperature on fish growth, consumption, respiration, and nutrient excretion. Lower growth rates coincided with lower P excretion at higher temperature, suggesting that fish selectively retained P when food is low and temperature is high. Such climate effects will dictate whether fish can cope with warming and how food webs will respond.

(9) **Kendrick et al. (2018)** use long-term records in LTER rivers to show that significant temporal changes in alkalinity (+), NO₃ (+), dissolved organic C (DOC) (-), and total P (-) are consistent with local degradation of permafrost. The decrease in total P might suggest an interaction (binding) with mobile iron (Fe) released from thawing permafrost.

(10) **Shogren et al. (2021)** use high temporal-resolution measurements over broad spatial scales to show significant differences in concentration-discharge relationships in streams for DOC and NO₃ that could be attributed to season and landscape type. The analysis shows that variability in storm events might contribute disproportionately to export of dissolved C and N in arctic streams.

Together, these 10 papers highlight a consistent theme of how the function of arctic ecosystems is driven by climate and disturbance, and modified by ecosystem openness and landscape connectivity. This work also points to the importance of climate variability, which is the new theme of this renewal proposal.

Data availability: ARC-LTER data are archived in the Environmental Data Initiative (EDI) repository. Some collaborating investigators use the Arctic Data Center (ADC) or genomic repositories (see Data Management Plan and dataset list). As of March 2022, the ARC-LTER online database contained 631 datasets. From 2019-2021, 80,058 data files were downloaded from the EDI data repository and ARC website. (Effort was made to eliminate bot downloads by excluding downloads <5 seconds apart.)

Results from Broader Impacts: ARC-LTER supports a multifaceted education and outreach program with substantial broader impacts to scientists, students, and the public. Each component optimizes different education opportunities, and our strategy uses specific activities to reach a diverse audience including K-12, undergraduate and graduate students, the public, and government and science planning agencies. We support students, postdocs, and teachers to work at our sites (e.g., travel or user costs) and to have access to our labs, long-term experiments, and databases. Quarantine restrictions in 2020 and 2021 shifted many activities to a virtual format. We describe some of these activities below.

1. Our ***Schoolyard LTER program*** engages K-12 teachers in research activities because our site's remote location precludes interactions with local schools. Activities are supported by ARC-LTER Schoolyard funds, NSF PolarTREC, and private sources. Amanda Morrison, ARC Schoolyard Coordinator, collaborates with LTER educators and participates in network-wide education activities.

Our Schoolyard program has been substantially impacted by the pandemic, and in the last two years four teachers, including two from rural Alaska schools, were unable to travel to Toolik. However, we expect this to return to normal in 2023, where prior to 2020, 26 K-12 teachers from 6 states participated in two-week field-lab experiences at Toolik. Morrison develops a Professional Learning Community (PLC) with each teacher cohort prior to the trip to facilitate interactions and set expectations for being at Toolik, and for development of curricula following the field experience. We estimate that the curricula developed have reached at least 3300 K-12 students (likely a conservative estimate).

We shifted recruitment efforts to teachers and administrators in Alaska, specifically in Utqiagvik and Fairbanks, who work with Alaskan Indigenous and other students typically under-represented in STEM. We believe these connections with administrators will help maintain our recruitment pipeline, especially with the high teacher turnover in Alaska. Morrison also recruits by collaborating with the Palmer LTER to engage teachers in monthly professional development activities around polar literacy, and by serving on the LTER Education and Outreach Committee and co-leading the RET subcommittee, holding virtual summer workshops for all LTER site RETs in 2020 and 2021. Finally, Morrison is a Co-PI on a recently awarded BioRET grant that links RET's from HJA, SBC, and ARC-LTER sites.

2. We host ***PolarTREC K-12 Teachers***, with complementary goals to our Schoolyard program. Since 2013, co-PI Cory and collaborator Crump have hosted five K-12 teachers at Toolik (one in the last grant), and we continue to collaborate with these teachers. We helped teachers convert their science experience into STEM lesson plans and hands-on activities grounded in Next Generation Science Standards and inspired by an arctic environment few students can experience (lesson plans free at PolarTREC). Results include peer-reviewed curricula (e.g., Taterka & Cory 2016) and presentations at several conferences for educators and scientists (e.g., AGU Information for Teachers workshop in 2017). The K-12 teachers have taught 600+ high school students and 400+ K-12 teachers about climate change in the Arctic.

3. ***Arctic REUs and graduate students:*** Each year we support at least 2 REU students and 2-10 other

students in association with collaborator grants (because of COVID restrictions, in 2020 we did not support any REUs but in 2021 REU's worked at PI home institutions on ARC projects). REU's are mentored by a PI and present their independent research projects in a symposium at Toolik. Graduate students supported on collaborating grants make use of our long-term experiments and datasets, and we encourage foreign collaborators to send students. At Toolik our students are regular participants in a weekly seminar series that promotes interactions among all Toolik researchers. Graduate students and REUs attend our annual ARC meeting in Woods Hole to present their results and to participate in research planning.

4. Public outreach includes occasional talks by ARC-LTER scientists to Alaskan Indigenous communities at Anaktuvuk Pass, Kaktovik, and Utqiagvik (associated with the Barrow Arctic Science Consortium). ARC-LTER personnel reach out to their local communities, newspapers, magazines, and blogs or podcasts about science for public consumption. For example, in 2021, the Institute of the Arctic adapted one of our K-12 lesson plans and activities for their "Data Jam" in a new magazine called *Polynya* (published by the Museum of Anchorage and supported by AAAS). *Polynya* is freely distributed and creates activities for middle school students based on research done by women across all races and ethnicities, to help middle-school girls living in the north see women as trailblazers of arctic Indigenous Knowledge and western science.

5. Outreach to federal, state, and local management agencies: ARC-LTER research relates directly to managing huge expanses of public wild lands in Alaska. We give tours of our research sites, and regular briefings to Bureau of Land Management (BLM), Arctic National Wildlife Refuge, Department of Natural Resources, Alaska Fish and Game, and North Slope Borough managers during visits to their offices in Anchorage, Fairbanks, and Utqiagvik. We interact with agencies in the permitting process for our research, and Alaska Fish and Game uses our research to set angling policies and regulations. Contacts with the North Slope Borough have increased as our research takes us to areas of subsistence hunting, and occasionally we invite Borough officials to speak at our Toolik Talking Shop seminars.

6. National and International Research Planning and Organization: Scientists associated with ARC-LTER serve on useful advisory boards or panels. Examples from the past 6 years include participation in SEARCH (the Study of Environmental ARctic CHange), the National Academy of Sciences Polar Research Board, the US DOE Environmental Science Molecular Laboratory User Executive Committee, and the United Nations Environmental Programme, Environmental Effects Assessment Panel. We continue to serve as Advisory Committee members of the UAF TFS.

7. Broadening Participation: In late 2020, Gough formed a 12-member ARC DEI Committee to develop a DEI plan and focus on efforts to broaden participation and promote inclusivity; the plan was approved by the ARC-LTER community in Spring 2021. The plan will be updated annually given input from the broader ARC community. The plan emphasizes recruitment and retention of under-represented students, making the ARC-LTER and Toolik communities more welcoming, and will help us increase interactions with Indigenous students and communities. Two committee members are from TFS (Dunleavy and Bret-Harte). In 2021-2022 we held virtual happy hours for junior scientists at our annual meetings, held a follow-up virtual orientation with new project personnel, and created a "Welcome to Toolik" guide for project newcomers. Gough and senior RA Messenger serve on the LTER Network's DEI Committee that meets monthly to learn from other sites and share challenges and successes.

Results from Supplemental Funding: We received two supplemental funding awards (2019 and 2020). The 2019 award (\$25,000) purchased an Acoustic Doppler Channel Profiler to assess river flow rates even during high-flow when other methods are dangerous. The 2020 award (\$59,958) supported two Research Experience for Teachers (RET) teachers for 1 month at Toolik (but precluded by COVID). Instead, education coordinator Morrison worked with the teachers to develop lesson plans and Data Nuggets based on LTER data and associated projects at Harvard Forest and Northern Arizona University. We hope to use these funds to support these teachers at Toolik once the pandemic restrictions are lifted.

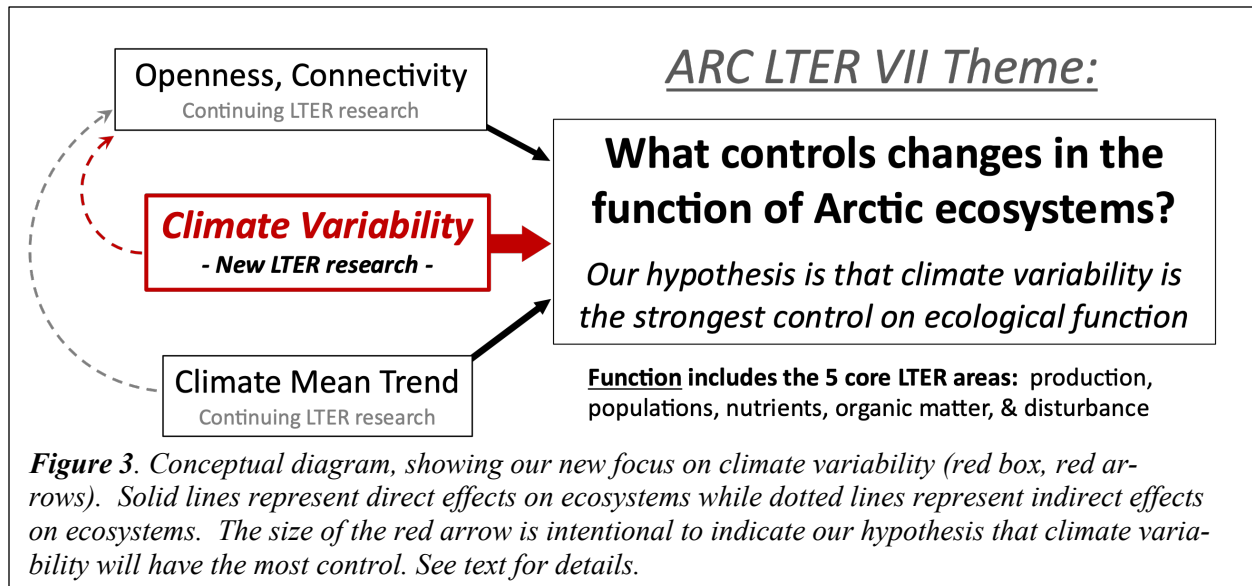
Response to Previous Reviews: NSF held a site review in June 2019 at Toolik Field Station. The review was strongly positive, with favorable comments about our research design, productivity, and exciting new areas of inquiry. The review report did, however, suggest several areas for improvement: **(1)** “The application of the conceptual model is least developed in the terrestrial system and deserves closer exploration by the research group.”, **(2)** “...better definition of future ARC syntheses is needed, with more consideration of alternate models recommended”, **(3)** “Opportunities may exist for more participation and leadership in cross-site LTER syntheses.”, **(4)** Project interaction could be enhanced by holding more regular meetings with investigators, **(5)** “... ARC could do more to broaden participation of underrepresented groups into their education programs”, and **(6)** “...forthcoming IM challenges include future decisions on upgrades to software used to archive data in a readily searchable form.”

Since the review and in the renewal proposal we have made the following improvements: **(1)** We published papers applying our conceptual framework to terrestrial systems to explicitly address project hypotheses (Rastetter & Kwiatkowski 2020, Rastetter et al. 2020, 2022, *In review*). **(2)** A substantial component of the renewal will be new synthesis of our long-term data to test how climate variability affects ecological dynamics, and a proposed new activity (Question 2, activity #3) will synthesize alternative models (e.g., meta-community dynamics) with the openness and connectivity concepts. **(3)** We completed a complex, cross-site synthesis project led by ARC with 8 LTER sites and 11 coauthors using the Multiple Element Limitation (MEL) model to examine responses of 12 ecosystems to elevated CO₂, warming, and 20% decreases or increases in precipitation (Rastetter et al. *In review*). Our openness concept of ecosystem N and P cycles played a key role in evaluating the response of these terrestrial ecosystems that ranged from forests to grasslands to tundra. **(4)** We will switch to quarterly meetings for the (a) ARC-LTER executive committee, (b) ARC-LTER graduate students, and (c) ARC-LTER DEI committee, in addition to our annual all-hands meeting in March (led by lead-PI Griffin) for science and field planning. We will add a second all-hands meeting (virtual) at the end of the growing season to connect collaborators and debrief from the field season. **(5)** We now have an active DEI committee led by Gough to improve DEI and to disseminate our efforts to the broader ARC participants and the LTER Network DEI committee. In the Broader Impacts section we describe new initiatives to improve DEI in our project and at our field site. **(6)** We made progress on IM challenges, in part through transferring the grant from MBL to Columbia. We updated the web page from Drupal 7 to Drupal 9, rebuilt links to EDI and ADC data repositories, and began exploiting EDI search functions. These efforts will continue, including webpage transfer to Columbia and decreased reliance on a local database (see Data Management).

III. PROPOSED RESEARCH

The overall goal of the ARC-LTER program is to *develop a predictive understanding of the low arctic landscape including tundra, streams, lakes, and their interactions, based on the framework of a terrestrial to aquatic continuum*. Our continuing research has shown how ecosystem openness and connectivity impact responses to disturbance, including climate change, and in doing this research we learned that climate variability is likely a stronger driver of ecosystem structure and function than is the mean trend in climate (e.g., warming). Thus, our recent research results, plus a body of ecological literature, provide the rationale for adding the role of climate variability to our LTER conceptual diagram and new research.

Climate is the long-term average of weather, and we refer to weather as daily to annual variation and climate as multi-year averages of weather. For simplicity we write “climate variability” but stress that the time scales will be matched to specific questions and activities. For modeling studies our weather generator (described below) analyzes long-term meteorological records to generate a climate record of more variable or less variable weather with the same long-term mean as the unmanipulated control. Below we **(1)** present results supporting the conceptual framework, **(2)** discuss the theoretical and empirical role of “climate variability” in ecology, and **(3)** propose research questions and activities that address research gaps identified by integrating our findings and the literature.



3.1 Conceptual framework

In our conceptual diagram, climate variability interacts with the climate mean trend and system openness and connectivity to control arctic ecosystems (Fig. 3). Our hypothesis is that the strongest control comes from climate variability. Climate variability also impacts the openness and connectivity of ecosystems, and this indirect control on ecosystem function is also new to our research program.

Our previous research established that terrestrial and aquatic ecosystem functions are driven by climate (e.g., mean warming) and disturbance (Shaver et al. 2013, Gough et al. 2012, Sistla et al. 2013, Mack et al. 2011, Pearce et al. 2015, Crump et al. 2012, Cory et al. 2013, Kendrick and Huryn 2015, Daniels et al. 2015, Budy and Lueke 2014, Budy et al. 2021). For example, Pearce et al. (2015) showed that recovery from thermokarst failure (a climate-warming disturbance) is slow, and residual effects can persist for 100+ years. Climate warming affects the rate of biomass accumulation, and Shaver et al. (2013) found a remarkable panarctic convergence in ecosystem C metabolism (photosynthesis, respiration) that is predicted from just three variables: leaf area, air temperature, and photosynthetically-active solar radiation. A third example is Daniels et al. (2015) showing that increased inputs of nutrients and DOC from land to water associated with climate warming could differentially impact the structure and function of benthic vs. pelagic communities in arctic lakes. This research on climate and disturbance led to our current (2017-2023) theme by suggesting that biogeochemical and community openness and connectivity might modify the effects of climate change.

Recently we made advances in understanding how openness and connectivity, disturbance, mean climate trends, and climate variability control ecosystem structure and function. For example, Rastetter et al. (2021) found that open ecosystems experience higher N losses following disturbance than do closed systems, and Rastetter et al. (2022) showed that grazers affect the terrestrial response to warming. Warming and nutrient supply altered community structure of terrestrial systems (McLaren and Buckeridge 2019), and a fire disturbance altered community structure as well as canopy height (Klupar et al. 2021). By extension, warming will increase disturbances like fire or thermokarst failure and the loss of N will scale positively with ecosystem openness. Openness also increases ecosystem connectivity, and connectivity of even the more closed terrestrial systems is critical on the land-water continuum. This increased connectivity is because nutrients and C accumulate from land in the watershed, and are exported to biogeochemically-open lakes and streams where these exports support the bulk of aquatic productivity. We found that mean climate warming and increased disturbance will facilitate this transfer (Rastetter et al. 2004,

Bowden et al. 2014, Kling et al. 2014, Daniels et al. 2015, Kendrick et al. 2018, Neilson et al. 2018, Abbot et al. 2021). For example, thawing of permafrost promotes the movement of DOC in groundwater to surface waters (e.g., Neilson et al. 2018, O'Connor et al. 2019), which can increase the subsequent release of CO₂ to the atmosphere from microbial respiration (Cory et al. 2013, Nalven et al. 2020, Romanowicz et al. 2021) and from photochemical oxidation (Cory et al. 2014, Bowen et al. 2020a, Ward & Cory 2020). However, across this land-water continuum we still lack knowledge of how climate variability affects ecosystem processes. We have studied parts of this continuum, for example showing how variable floods affect stream ecosystems (e.g., McNamara et al. 2008, Iannucci et al. 2021, Shogren et al. 2021), but integrated at the landscape level there is little or no synthetic understanding of how climate variability affects the functioning of terrestrial plants and animals, coupled to groundwater flow and soil processes, coupled to riparian zones and finally to lakes and streams.

3.2 Rationale for the importance of climate variability

We have 3 justifications for integrating climate variability into our framework: (1) analyses of our long-term data, (2) new modeling simulations, and (3) past research on the role of climate variability.

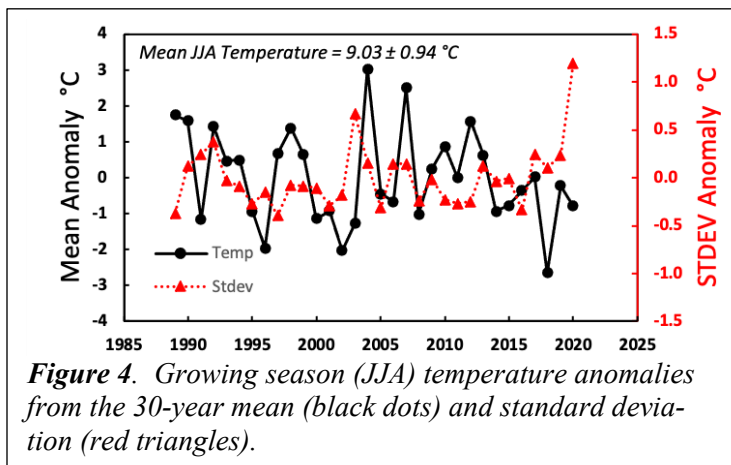


Figure 4. Growing season (JJA) temperature anomalies from the 30-year mean (black dots) and standard deviation (red triangles).

3.2.1 Our first justification for studying climate variability is an analysis of our long-term data. Our 30-year climate record at Toolik has interannual variability in growing season temperature, with anomalies of $\pm 3^{\circ}\text{C}$ (Fig. 4, black dots). In addition, the record of daily temperature variability within the growing season (red triangles) is independent of changes in the mean. For example, years where the average temperature was about 1°C below the mean (e.g., 1995 and others) correspond to a wide range of variation within the season (standard deviations

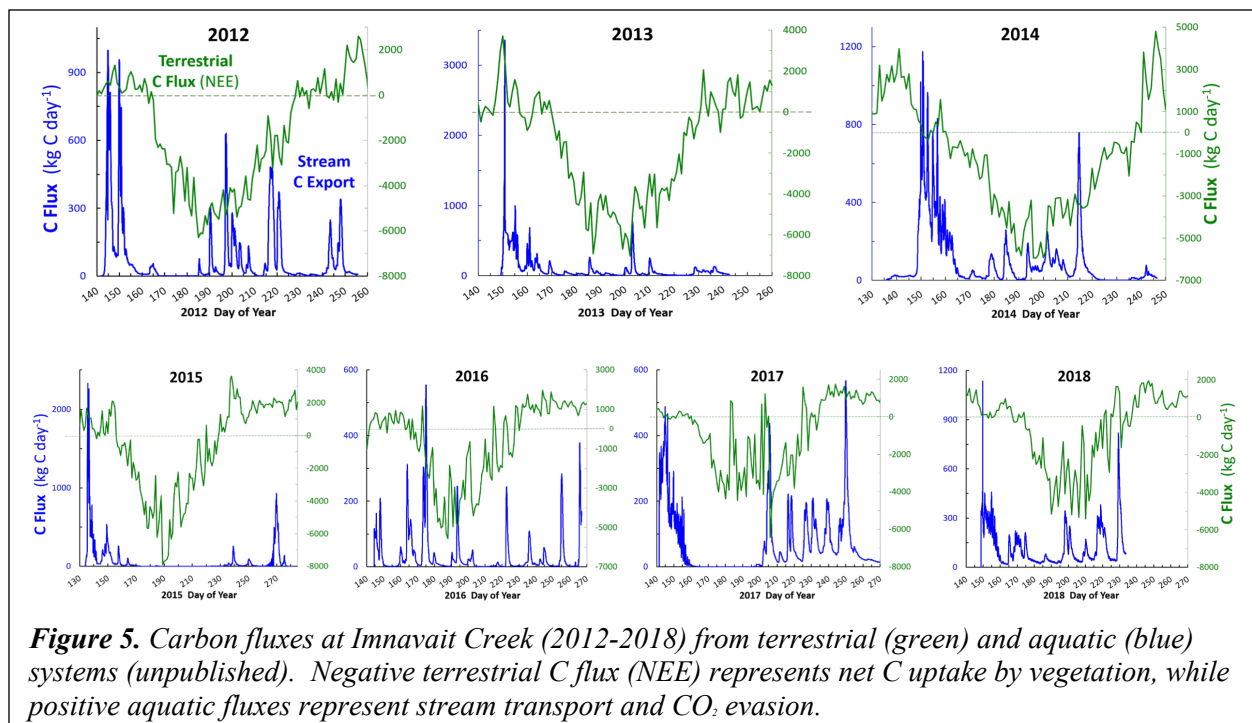


Figure 5. Carbon fluxes at Innavait Creek (2012-2018) from terrestrial (green) and aquatic (blue) systems (unpublished). Negative terrestrial C flux (NEE) represents net C uptake by vegetation, while positive aquatic fluxes represent stream transport and CO₂ evasion.

ranging from lowest to highest on record). This independence allows statistical investigation of the role of climate variability in our long-term climate data. While this particular analysis was confined to the growing season and based on mean monthly temperature, it can be extended in many ways, e.g., to include shoulder seasons, examine decadal patterns, or consider short-term diel fluctuations.

A second analysis shows great variability in terrestrial and aquatic C flux at the Imnavait Creek watershed (Fig. 5, above). The terrestrial system varies between a C source and sink within each year (Euskirchen et al. 2017), while the more open aquatic system consistently loses C through lateral transport and DOC respiration or photomineralization to CO₂ and degassing to the atmosphere (Kling et al. 1991, Cory et al. 2014). However, beyond the expected drawdown of C by photosynthesis on land in the summer and aquatic loss of C during snowmelt and rain events, there is high variability within and across years that is not easily explained by mean climate trends or disturbance. In the proposed research we will determine how climate variability affects C dynamics and C balance of the catchment. For example, if the terrestrial system does not compensate for increased aquatic C losses due to storms with an equal or greater increase in C uptake, the landscape loses C. Thus, we suggest that climate variability (increased storms, heat waves, or cloud cover) will itself act as a driver of ecosystem function.

3.2.2 Our second justification for studying climate variability comes from new modeling simulations using 10 years of ARC-LTER environmental data to drive the MEL model (Rastetter et al. 2013) calibrated for tussock tundra (Pearce et al. 2015). With a weather data generator, we changed precipitation variability $\pm 50\%$ by adjusting the average duration of consecutive wet and dry days. Similarly, we changed temperature variability by $\pm 3^\circ\text{C}$ and irradiance variability by $\pm 4 \text{ MJ m}^{-2} \text{ day}^{-1}$. We used 10 sets of simulated 100-yr weather records with observed variability (control), higher variability, and lower variability in all three weather variables, individually and in combination, to drive 100-yr simulations with the MEL model (90 simulations total).

Over the 100-year simulation, increased variability in weather caused a loss of soil and total C from the system (Figs. 6, 7). Decreased variability increased vegetation C with no significant change in soil C (left

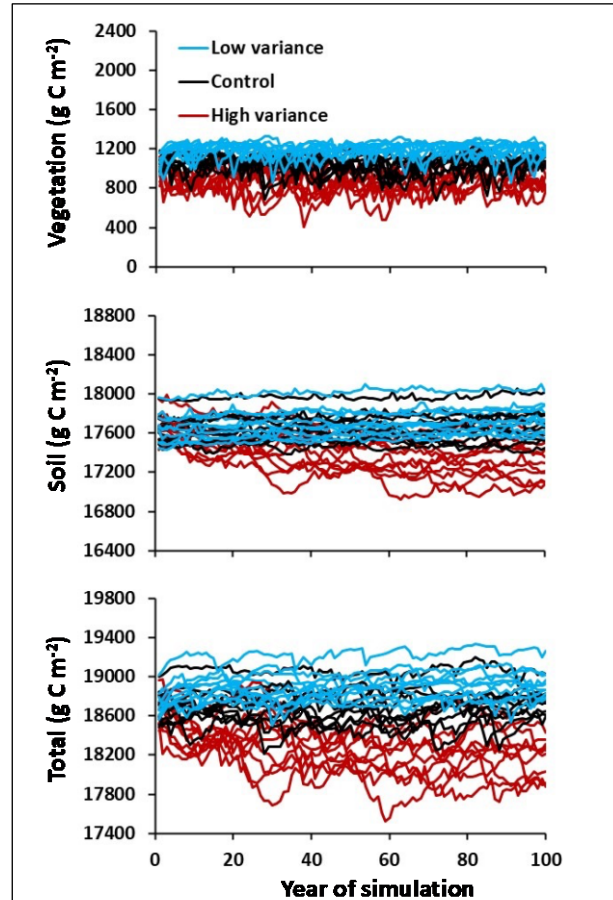


Figure 6. Simulated responses of tussock tundra to control (black), low (blue), and high (red) variability of precipitation, shortwave radiation, and temperature using synthetic weather records. Simulations use the MEL model and a single parameter set. Graphs show responses to 10 replicate weather records for control (same variability as Toolik met station), low (same precipitation over 38% more days, 9% fewer bright and 93% fewer dim days, and 3 °C lower temperature variability), and high (same precipitation in 36% fewer days, 4.5% more bright and 76% more dim days, and 3 °C higher temperature variability) variability simulations. All weather records were adjusted to the same mean precipitation, temperature, and irradiance, just the day-to-day variability changed. Simulations are first initialized by running the model for 1000 years under the control weather (ten times through the control synthetic weather record).

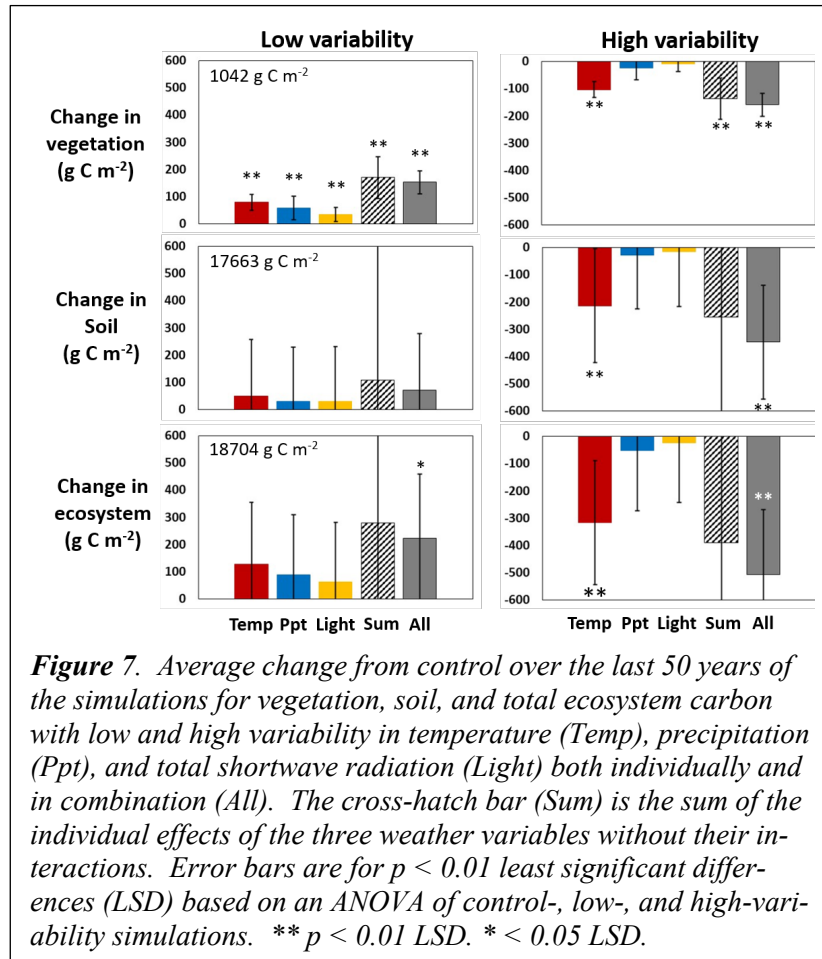


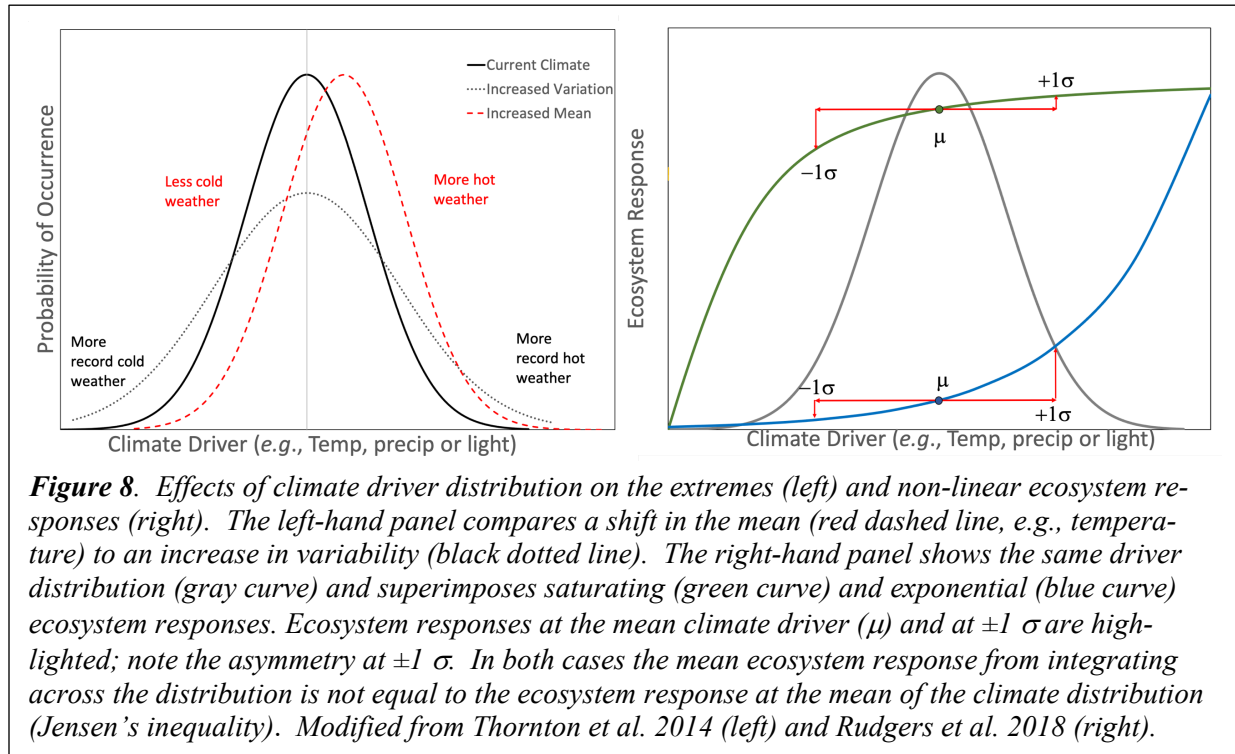
Figure 7. Average change from control over the last 50 years of the simulations for vegetation, soil, and total ecosystem carbon with low and high variability in temperature (Temp), precipitation (Ppt), and total shortwave radiation (Light) both individually and in combination (All). The cross-hatch bar (Sum) is the sum of the individual effects of the three weather variables without their interactions. Error bars are for $p < 0.01$ least significant differences (LSD) based on an ANOVA of control-, low-, and high-variability simulations. ** $p < 0.01$ LSD. * $p < 0.05$ LSD.

increase in variability could offset C gains associated with the mean trend of climate change. However, to fully assess the relative strengths of these offsetting effects, we must understand the controls on ecosystem responses to variability, including the influence of response nonlinearity.

3.2.3 Our third justification for studying climate variability is based on a growing body of relevant research, in part related to nonlinearities. Many ecosystem processes respond non-linearly to environmental drivers. Because of this nonlinearity, changes in variability can alter the mean rates of ecosystem processes (e.g., Rastetter et al. 1992, Rudgers et al. 2018) and processes might be disproportionately affected by high-frequency variability. For example, plant respiration increases exponentially with temperature (Heskel et al. 2016), whereas photosynthesis has a unimodal temperature response (Sage & Kubien 2007). Similarly, photosynthesis saturates in response to light but at a maximum rate determined by $[CO_2]$, leaf N content, and temperature (Blackman 1905). Plant growth is episodic and responds to extreme events like drought, heatwaves, and storms (Lipiec et al. 2013), and the response of soil microbes to rain is transient (Lee et al. 2004, Romanowicz et al. 2021). In response to environmental variability these nonlinear processes can have unexpected effects that differ from the mean response (e.g., Jensen’s inequality, Ruel & Ayres 1999, Evans et al. 2008, Medvigy et al. 2010; Fig. 8). Despite this expected dependence of the response on variability, most studies of climate change effects focus on average climatology (Field et al. 2012, Thornton et al. 2014). Furthermore, typically these average climatologies are derived from model predictions at monthly or longer time scales and thus lack the high frequency signals known to affect ecosystem processes.

panels Fig. 7). In contrast, increased variability decreased both vegetation and soil C (Fig. 7). Furthermore, in the higher variability scenario, the weather variables interact synergistically on soil and total C loss (i.e., the combined effect is larger than the sum of their individual effect). Vegetation responses dominate changes in total ecosystem C to decreased variability, and soil responses dominate changes in total ecosystem C to increased variability.

These simulations indicate that changed weather variability might result in a 1-2% change in ecosystem C over time. In a mean climate change analysis using the same model, but with no change in weather variability, ecosystem C increased by about the same amount in response to the combination of a doubling of CO_2 , a $\sim 3^\circ C$ warming, and either a 20% increase or a 20% decrease in precipitation (Rastetter et al. *In review*). Thus, an in-



From a population and community perspective, environmental variation has long been recognized as a critical control on system structure at numerous spatial and temporal scales across levels of biological organization (e.g., Hutchinson 1961, May & MacArthur 1972, Chesson & Warner 1981). For example, the classic work of May and MacArthur (1972) suggests that environmental variability limits niche overlap among species (see also Cannon et al. 2009, Hoorn et al. 2010). Chesson & Warner (1981) considered environmental variability and generation times, and concluded that more variable environments actually increase the likelihood of species coexistence. Beyond the theory of species coexistence, which is related to the community openness research at ARC-LTER (e.g., Bret-Harte et al. 2004, McClaren & Buckeridge 2019, Klupar et al. 2021, Slavik et al. 2004), examples of environmental variability effects in ecology include Hastings and Caswell (1979) who consider climate variability and the success of annual vs. perennial life histories; Claireaux and Lefrançois (2007) who link climatic variability to fish physiology; Schimel and Clein (1996) who link microbial activity and biomass to the frequency of arctic freeze-thaw cycles; Rubenstein and Lovette (2007) who argue that environmental variability causes cooperative breeding in birds; and Righetti et al. (2019) who find that temperature variability defines latitudinal patterns of phytoplankton. These are a few important examples of how environmental variability can influence communities by altering ecological processes and biogeochemistry.

Summary. Biogeochemical, community, and landscape responses to climate variability are poorly understood, yet will modify the response of arctic ecosystems to climate change (mean trends) and disturbance. For example, the interaction of climate variability with biogeochemical fluxes will help determine the future arctic C sink, the magnitude and even the direction of which are poorly known (e.g., McGuire et al. 2018). Our conceptual framework assumes that the biogeochemical characteristics of a system set the stage on which community processes act, and the community structure of a system sets the potential for various biogeochemical processes. The degree of biogeochemical openness and connectivity (e.g., nutrient turnover relative to throughput, movement of materials on the landscape) as well as community openness and connectivity (e.g., introductions of species, movement of species) further constrain ecosystem responses, tie the landscape together, and influence the large-scale patterns of both structure and function.

In this proposal, we will develop a synthetic understanding of the arctic landscape based on these principles by expanding our conceptual framework to include climate variability and its interactions with climate mean trends and ecosystem openness and connectivity.

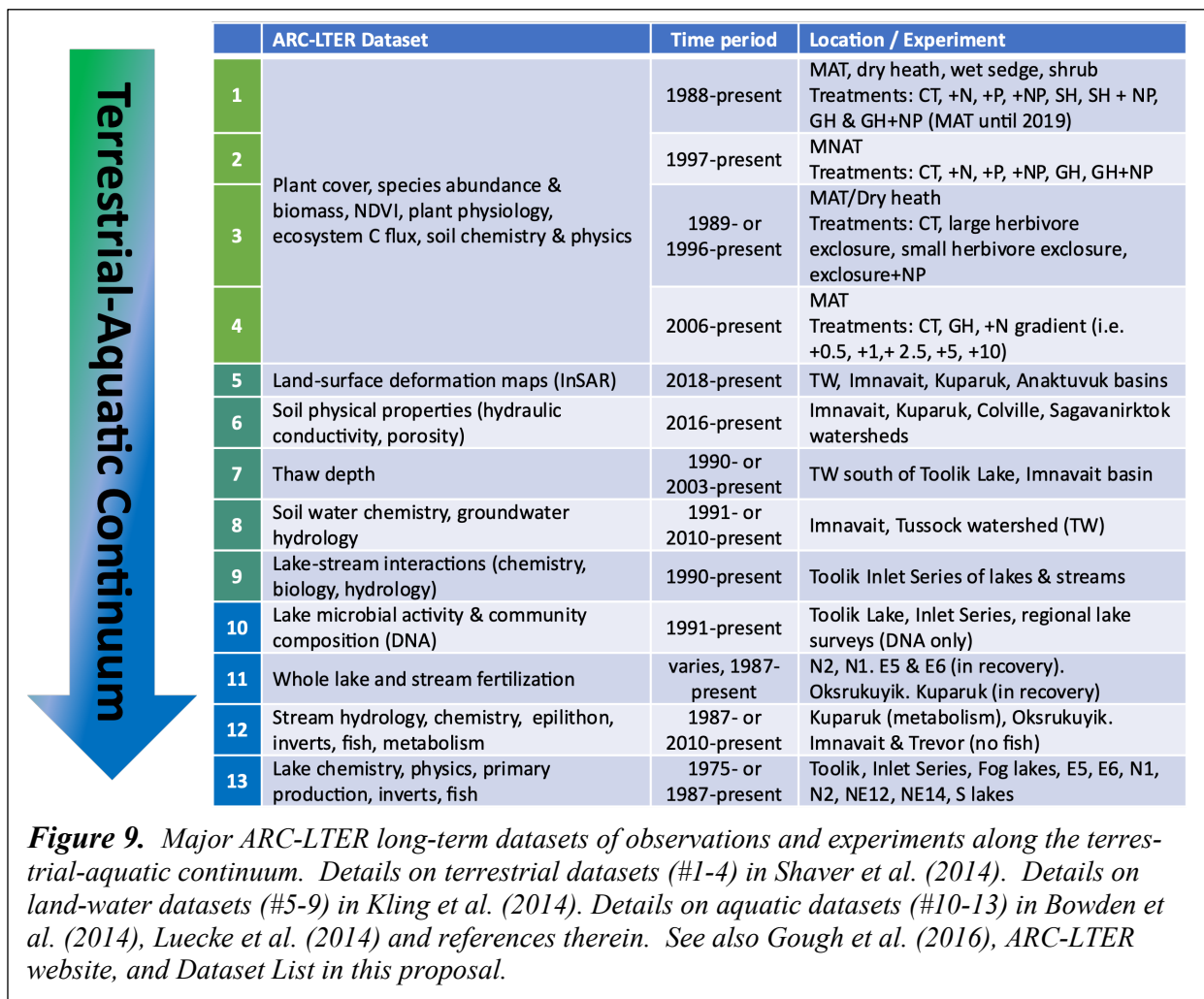
3.3 Research Activities

We have three overarching research questions:

- Q1. How does climate variability affect the openness and connectivity of arctic ecosystems?**
- Q2. How does climate variability affect key consumers and their influence on ecosystems?**
- Q3. How does climate variability affect carbon dynamics along the terrestrial-aquatic continuum?**

These are separate questions but together they integrate our research on the terrestrial-aquatic continuum. Below we provide an overview of ongoing activities in our research (supported by many of the same datasets and experiments for all 3 questions), followed by a summary of how we use models to help synthesize the research, and more detailed descriptions of the rationale and new activities for each question.

Overview of ongoing activities for Q1 – Q3. All of our LTER long-term datasets will contribute to answering the above questions on the role of variability in climate and environmental drivers. The aquatic and terrestrial research sites and supporting datasets are shown in Fig. 9. For **terrestrial ecosystems** we will continue to monitor physical, chemical, and biological responses to a suite of experiments developed over 46 years on landscapes of different ages where contrasting tundra types (e.g., wet sedge, moist acidic



and non-acidic, shrub, and dry heath tundra) are subjected to identical, replicate manipulations of nutrient inputs (N and P fertilizers), air temperature (plastic greenhouses), light (shading), and herbivore exclusion (Shaver et al. 2014). In addition, we will continue monitoring thaw depth and groundwater chemistry (established 1991) at the Toolik and Imnavait Creek sites (Kling et al. 2014). In **aquatic ecosystems** we will continue long-term monitoring of physical, chemical, and biological variables in our sentinel streams (tundra and mountain, 2nd to 4th order) and both shallow and deep lakes (Bowden et al. 2014, Luecke et al. 2014); *physical* includes water temperature, discharge, and lake stratification; *chemical* includes nutrients, major ions, dissolved and particulate organic matter; *biological* includes primary production and biomass, aquatic consumer species and growth (microbes, benthic and pelagic invertebrates, fish), and stream ecosystem respiration. We will follow the recovery from long-term nutrient fertilization of the Kuparuk River and Lakes E5 and E6, and sample less frequently several sites that represent important regional differences in tundra types or landscape ages. Finally, we will continue opportunistic data collection of ecological responses from unexpected disturbances such as fire (Steketee et al. 2022) or thermokarst failures (Budy et al. 2021). All observations support answering our ongoing and new questions on the effects of climate variability, openness, and connectivity on ecosystem processes, including reanalyzing datasets on different timescales (up to 4 decades of data) or where we have experimentally altered the variability in drivers, such as nutrient addition experiments (terrestrial and aquatic) that in effect reduce the variability of nutrient inputs to the system. All of our datasets have been or will be used to help parameterize and validate our modeling of terrestrial processes (e.g., Rastetter et al. 2020) that connect to aquatic systems (e.g., Neilson et al. 2018). In the next sections we provide background information to justify the suite of new modeling, observations, and experimental activities for our research.

Summary of New Modeling Activities. Our 3 main questions each use new modeling activities to help integrate the project along the terrestrial-aquatic continuum. The models are used to study openness and connectivity of ecosystems on the landscape, and how climate variability affects ecosystem function. Modeling can explore questions (e.g., longer timescales, logistically unfeasible manipulations) that are impossible to address in other ways. We will use both simple, heuristic models and more complex, quantitative models (see Rastetter 2017). Simple, heuristic models are easier to interpret, can provide insight into general ecological patterns, and are a powerful way to generate hypotheses and analyze results. Complex models are more difficult to parameterize and implement but provide more quantitative predictions and can help develop and constrain the heuristic models.

We will continue to use the MEL model (Rastetter et al. 2013, Pearce et al. 2015, Jiang et al. 2015) to analyze the effects of interactions between increased weather variability and climate trends on ecosystem function. We already used MEL to study climate trends (Jiang et al. 2016, 2017, Rastetter et al. *In review*) and produced preliminary simulations to examine the effects of weather variability (Figs. 6, 7). We propose to continue this analysis to examine interactions between climate change and climate variability. We hypothesize that increased weather variability will negate ecosystem C gains or exacerbate C losses associated with warming and elevated CO₂ (Q3, *New Activity #1*).

We will modify our groundwater models (Neilson et al. 2018, O'Connor et al. 2019) to determine the effects of climate variability on dissolved C (DOC, DIC, CO₂, CH₄) and oxygen (O₂) transport down toposequences to streams. We are specifically interested in how variability in O₂ transported into soils from rainfall will set redox conditions and drive the abiotic oxidation of DOC to CO₂ (Q3, *New Activity #3*). We can link groundwater model outputs to surface waters (Merck and Neilson 2012, Neilson et al. 2018, King et al. 2020) to study the effects of climate variability, especially temperature, light, and rainfall, on C processing and CO₂ fluxes. We will modify our surface-water models (e.g., Merck and Neilson 2012, King and Neilson 2016, King et al. 2019, 2020) to include photochemical reactions (Cory et al. 2015, Li et al. 2019) and microbial activity (Cory et al. 2013, 2014) to study the controls on C balance of surface waters (Q3, *New Activity #4*).

We will use the simple terrestrial model (Rastetter et al. 2021) to examine interactions among landscape units in terms of connectivity. Our hypothesis is that the buffering effects of increased water and nutrient

fluxes downslope will make downhill landscape elements less susceptible to weather variability. We will modify this simple model to run on a daily time step and be responsive to the weather drivers needed for our analysis. Output from the MEL model will help develop and constrain this simple model using an approach analogous to that used by Williams et al. (2001).

QUESTION 1: How does climate variability affect the openness and connectivity of arctic ecosystems?

Background and rationale. Our current grant has focused on the openness and connectivity of biogeochemistry and of communities. We confirmed that openness and connectivity are linked and strongly affected by the variability of the environment. For example, intense rain events can create large pulses in the movement of elements across the landscape (e.g., McNamara et al. 2008) and can provide transit pathways for fish and other aquatic organisms between otherwise isolated lakes. In contrast, prolonged dry periods can constrain element movement (Merck et al. 2012) and trap organisms in isolated pools and lakes (Golden et al. 2021). Thus, increased variability in climatic drivers should have important effects on openness and connectivity of the tundra landscape.

Recently we helped develop theory and modeled the effects of biogeochemical openness on the recovery of terrestrial ecosystems from disturbance (Rastetter et al. 2020). Following a disturbance (red dotted arrows in Fig. 10), we define three phases of recovery: *Phase 1* in which the ecosystem continues to lose nutrients (thereby increasing connectivity) because the recovering vegetation cannot take up nutrients as fast as they are released by the soil (black dotted lines cross the total-ecosystem N isopleths right to left, Fig. 10). *Phase 2* in which plant and soil-microbial N-cycling processes come into near balance, the ecosystem reaccumulates nutrients (thereby decreasing connectivity), and the ecosystem reaches a quasi-steady state (black dotted lines turn to cross the total-ecosystem N isopleths left to right and converge on the “Balanced-Accumulation Trajectory” [BAT]). *Phase 3* in which the ecosystem accumulates nutrients slowly through these quasi-steady states along the BAT toward the true steady state (i.e., tracing the thick dashed lines from left to right, Fig. 10).

Ecosystem openness exacerbates nutrient losses and increases connectivity to downslope systems in *Phase 1* (*Phase 1* trajectories slant more to the left in the more-open ecosystem than in the less-open ecosystem, Fig. 10), but speeds recovery in *Phases 2* and *3* because of the large external source of nutrients. We propose that the BAT is a defining characteristic of an ecosystem and that its properties are set by the interactions among plant processes, soil-microbial processes, and climate. In this proposal, we will use this framework to examine the long-term effects of climate change compared to the increased variance in climate drivers (temperature and precipitation). We hypothesize that warmer average temperatures will

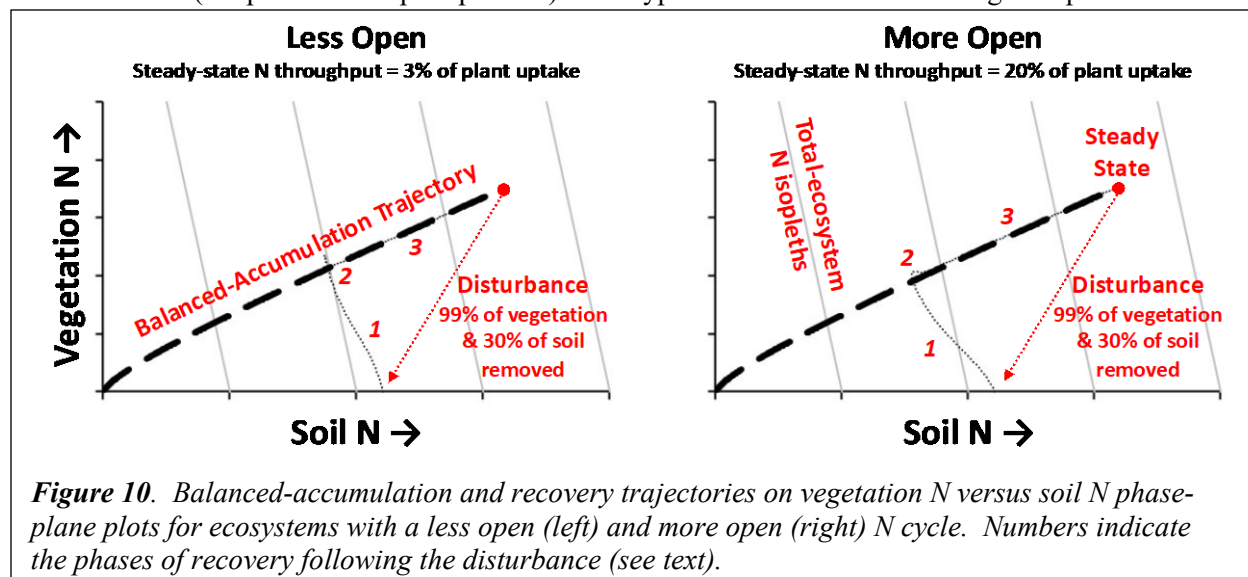


Figure 10. Balanced-accumulation and recovery trajectories on vegetation N versus soil N phase-plane plots for ecosystems with a less open (left) and more open (right) N cycle. Numbers indicate the phases of recovery following the disturbance (see text).

accelerate the release of nutrients through the mineralization bottleneck and stimulate plant growth, resulting in a net transfer of nutrients from soil to vegetation. Thus, the BAT should rotate counterclockwise in Fig. 10. If the stimulation of plant growth is strong enough, the ecosystem might retain or augment its nutrient capital and the steady state will move parallel to the total-ecosystem N isopleth or possibly cross it left to right. Alternatively, if the stimulation of plant growth is limited, the ecosystem might lose nutrient capital, potentially increasing landscape connectivity. Either way, increased climate variability will act like small disturbances, thereby perpetually diverting the ecosystem from recovery along the BAT. The ecosystem will therefore spend more time in *Phase 1* recovery, causing it to lose nutrients. In preliminary simulations, most of the nutrient loss is from soils rather than vegetation (Fig. 7), indicating that increased climate variance will rotate the BAT counterclockwise, and the loss of nutrients will move the steady state right to left across the total-ecosystem N isopleths in Fig. 10.

New Activities - Q1

Our proposed research on how climate variability affects the openness and connectivity of arctic ecosystems will study vegetation and biogeochemical cycles in moist acidic tundra along a nutrient gradient (e.g., Heskell et al. 2012, Prager et al. 2017, 2020), in warming plots (e.g., Shaver & Jonasson 1999, Lang et al. 2012, Heskell et al. 2013, 2014), and in nearby Alder stands (e.g., Heslop et al. 2021). This research extends the theoretical framework from our current LTER and is supported by ongoing model development (Rocha et al. 2018, Rastetter et al. 2020, 2021). Arctic terrestrial ecosystems are typically relatively closed, both biogeochemically and in community structure for vascular plants. Fertilization experiments demonstrate co-limitation by N and P (e.g., Klupar et al. 2021), and the removal of nutrient limitation typically results in a shift in plant functional types towards woody deciduous shrubs (Shaver et al. 1997, Bret-Harte et al. 2001, 2004) with variable effects on tundra biogeochemistry (e.g., Mack et al. 2004, Sistla et al. 2013). What we do not yet understand is how climate variability will affect nutrient inputs and turnover rates, and thus ecosystem openness and connectivity. Similarly, we do not know how climate variability will affect community openness or its functional consequences. In three new activities we will use models, observations, and experiments to answer the following questions:

New Activity #1: How does variable nutrient availability affect biogeochemical connectivity?

New Activity #2: To what degree can N fixation compensate for variation in N inputs?

New Activity #3: How does climate variability affect plant community composition and in turn ecosystem function?

Proposed Research - Q1

New Activity #1: How does variable nutrient availability affect biogeochemical connectivity?

Fertilization experiments have been a key part of the ARC-LTER since its inception, first to determine if the tundra was N limited and later as a climate change analog because warming will lead to increased rates of N mineralization (Shaver & Chapin 1991, 1995). We learned recently that warming-induced thawing of previously frozen nutrients is a similarly important source of new nutrients (Pearce et al. 2015). In 2006 a tussock tundra fertilization gradient experiment was started with 4 randomized blocks, each of which has a control and 5 treatments: 0.5, 1, 2, 5 and 10 g N m⁻² yr⁻¹ (with P at 0.5 of N levels). These treatments modify the mean nutrient levels but not the variability in inputs. We will use this ongoing experiment along with a new variability manipulation (see below) to assess the degree to which fertilization and variability in fertilization rate, including from climate-driven variability in thaw depth and soil nutrient release, alters tundra biogeochemistry (*New Activity #1*) and community structure (*New Activity #3*). Specifically, we can test whether nutrient input variability will alter system connectivity to the downslope ecosystem *despite* the relatively-closed nature of the terrestrial system.

Fertilization increases nutrient inputs; how these inputs affect ecosystem function depends on the degree

to which fertilization also affects nutrient losses and internal cycling (along with any changes in other nutrient inputs, e.g., biological N fixation, see *New Activity #2*). We predict that when the plant-soil system is nutrient limited it will retain added nutrients without an increase in downslope losses and connectivity, but that when the system is nutrient saturated it will lose more nutrients downslope (and proportionally more inorganic than organic nutrients). Along the fertilization gradient, therefore, we predict greater losses of nutrients at higher fertilization levels, although we don't know exactly which levels of nutrient additions will approach saturation. With regard to variability, we predict that variable fertilization will increase biogeochemical connectivity by stimulating N losses. Our reasoning is that the high fertilization years will exceed the capacity for the ecosystem to take up nutrients, leading to leakier nutrient cycles, but we cannot yet predict the transient response between the constant and variable treatments. We will test the effects of variability in nutrient inputs on biogeochemical connectivity by adding a new treatment of variable nutrient addition.

Approach: To the existing nutrient gradient experiment we will add a manipulation of nutrient variability in each block. This new treatment will receive an *average* of $2 \text{ g N m}^{-2} \text{ yr}^{-1}$ ($1 \text{ g P m}^{-2} \text{ yr}^{-1}$) over the next six years, but with a different amount added each year. To isolate the effect of variability (rather than time since the treatment began), we will also start a new $2 \text{ g N m}^{-2} \text{ yr}^{-1}$ treatment in each block. Simultaneously establishing this new $2 \text{ g N m}^{-2} \text{ yr}^{-1}$ treatment will let us account for both natural variation and the slow response time of arctic tundra. With the variable nutrient treatments, we will test whether increased variability in nutrient inputs (a major consequence of increased variation in temperature across years) increases lateral biogeochemical losses (connectivity). Furthermore, using the newly established $2 \text{ g N m}^{-2} \text{ yr}^{-1}$ plots with ambient variability we will determine whether the form of N loss (inorganic, DIN vs. organic, DON) changes as a function of time since treatment onset by comparing to the $2 \text{ g N m}^{-2} \text{ yr}^{-1}$ plots established in 2006. We will quantify potential nutrient losses (pore water concentrations), inputs (biological N fixation, described in the next section), and atmospheric deposition, which is measured by the NADP at Toolik, and internal cycling (uptake rates from vegetative concentrations and productivity, and net mineralization). Measurements of ecosystem structure and function will be continued and extended to the new plots, including: species composition and abundance, NDVI (for LAI and productivity), plant phenology, micrometeorology, periodic biomass harvests, C flux measurements, and leaf and root elemental analyses. A basic N budget will be quantified this summer on the current LTER project and in the final year of the experiment. In addition to comparing along the fertilization gradient and through time on each manipulation, we will also compare these variables between the 2006 plots and the new plots. For example, the 2006, $5 \text{ g N m}^{-2} \text{ yr}^{-1}$ plots will be compared to the variable nutrient plot in the year it receives $5 \text{ g N m}^{-2} \text{ yr}^{-1}$.

New Activity #2: To what degree can N fixation compensate for differences in N inputs?

The degree to which climate variability affects the openness of the N-cycle depends on biological N fixation, which is the dominant natural input of N in many arctic ecosystems (Barsdate & Alexander 1975, Hobara et al. 2006). Unique among natural inputs of mineral elements, biological N fixation can feed back to N cycling. For example, increases in N supply can cause declines in N fixation, as occurs in tundra lichens (Weiss et al. 2005) and in benthic oligotrophic lakes (Gettel et al. 2013) at Toolik. In addition to these N cycle feedbacks, N fixation in arctic ecosystems is regulated by biophysical factors such as temperature, moisture, and light (Hobara et al. 2006), by top-down control (Bazely & Jefferies 1989), and by differences among individual N-fixing taxa (Stuart et al. 2021a).

Climate variability likely affects N fixation via many of these drivers. For example, temperature variability likely increases N fixation directly due to its nonlinear temperature response (Prévost et al. 1987, Liengen 1999, Bytnerowicz et al. 2022) and Jensen's inequality (Bernhardt et al. 2018), whereas precipitation variability could stimulate N fixation (via increased N losses) or inhibit it (via prolonged drying). Over longer timescales, prolonged warm periods would result in increased N mineralization, which would likely inhibit N fixation.

Although most N fixation in arctic ecosystems occurs via bryophytes, lichens, and free-living N fixers, the rapid (Tape et al. 2006) but patchy (Tape et al. 2012) expansion of alder (*Alnus viridis*), a symbiotic N-fixing shrub capable of large fluxes of N, represents a major potential shift in the arctic N cycle.

Approach: Our multi-pronged approach includes, first, short-term manipulations of temperature and moisture to quantify response functions of bryophytes, lichens, free-living N fixers, and alder, using the continuous measurement system developed by Griffin and Menge (Bytnerowicz et al. 2019, 2022). Second, we will measure N fixation in the long-term field experiments (2006 fertilization gradient and new variability treatment, greenhouse, shading, and herbivore exclusion) using $^{15}\text{N}_2$ incubations (as in Weiss et al. 2005, Stuart et al. 2021a,b) to assess background rates and determine responses to the longer-term consequences of climate change. Third, we will measure N fixation in alder patches, also using $^{15}\text{N}_2$. Fourth, we will combine the results with past work studying N fixation near Toolik (e.g., Weiss et al. 2005, Hobara et al. 2006, Gettel et al. 2013, Holland-Moritz et al. 2021, Stuart et al. 2021a,b) to inform a series of models from simple heuristic models (e.g., combining Menge et al. 2009 and Bernhardt et al. 2018) to the more complex MEL (e.g., Rastetter et al. 2001) to land models (e.g., Kou-Giesbrecht et al. 2021) to explore the effects of climate variability on N fixation in ways that are impossible in the field.

New Activity #3: How does climate variability affect plant community composition and in turn ecosystem function?

Fireweed (*Chamerion angustifolium*) has recently appeared in our tundra experiments, but only in the highest N treatments (Fig. 11). To our knowledge this is the first time a new species with a broad geographical range has moved into our experimental plots. Fireweed is a prolific seeder and the cottony seeds can disperse widely. However, to date the occurrence appears to be highly contained within the experimental plots (see photos). As the common name suggests, this species is promoted by fire, which releases nutrients. The appearance of this species in our fertilization plots suggests that high levels of N lead to greater community openness, but the precise mechanism for this response is unknown as are the larger consequences for the ecosystem. We will more fully describe the function of this species and the plots in which they are found across a variety of scales. We hypothesize that seedling germination is directly stimulated by high N concentrations, and that fireweed has physiological advantages over other tundra species at high N supply (but sparse literature exists describing key physiological processes in this species). We predict that this species will have low N-use efficiency making it less competitive in low N settings, but able to grow rapidly in the high N plots where N limitations are eliminated.



Figure 11. Fireweed (*Chamerion angustifolium*) has appeared in our high N plots in both tussock (left) and dry heath (right) tundra. This species is more commonly seen in disturbed areas in boreal forests or along roads but has never been found in our experimental plots. The occurrence of fireweed is confined to only the high fertilizer plots.

Approach: We will use growth chambers, greenhouses, and field experiments, and a variety of gas exchange, chlorophyll fluorescence, and isotopic techniques to quantify the rates of photosynthesis, respiration and transpiration and their responses to light, temperature, and CO₂ (as in Heskell et al. 2014). Leaf nutrient concentrations will be measured and nutrient use efficiencies will be calculated. Additionally, the occurrence, abundance, spread, and phenology of fireweed will be monitored. At the plot level the contribution of fireweed to the NDVI/LAI trends will be analyzed. Interannual variation in weather, climate, and fireweed abundance and performance will be analyzed. We will collect seeds from all flowering plants for further germination and process-level experiments. The contribution of this species to the C and nutrient budgets of these plants will be estimated. Further investigation of the nutrient concentrations, relationships between canopy N and C uptake (Williams & Rastetter 1999), and canopy light absorption (Williams et al. 2014) will be used to first quantify the key physiological responses, and then to model C exchange and its response to environmental variability (Shaver et al. 2013, McLaughlin et al. 2014, Williams et al. 2014, Prager et al. 2017).

QUESTION 2: How does climate variability affect key consumers and their influence on ecosystems?

Background and rationale. Consumers in ecosystems span the range from heterotrophic microbes to small and large herbivores to omnivores and predators. Early research linking consumers to ecosystem structure and function includes Elton (1927) reminding us that ‘big fish eat little fish’ and introducing pyramids of biomass and energy into ecology, and Lindeman’s (1942) study of “trophic dynamics” that established microbes as the dominant recyclers of C and nutrients. Later studies showed that grazers can control primary production (Pitelka 1964, McNaughton 1985), top-down predators can control ecosystem structure (Hairston et al. 1960, Paine 1966) and function (McQueen et al. 1988, Carpenter & Kitchell 1993), consumers can control biogeochemical cycling (Pomeroy & Alberts 1988, Atkinson et al. 2017), and species interactions influence C cycling (Schmitz & Leroux 2020). Despite this long history, surprisingly few studies on this topic have addressed the role of climate variability (Koltz et al. 2018a).

Prior ARC-LTER research has shown the importance of consumers in arctic ecosystems. Microbes control organic matter degradation on land and water (e.g., Crump et al. 2003, 2007, Cory et al. 2013, Nalven et al. 2020, Romanowicz et al. 2021), invertebrates influence C and N cycling in soils (Koltz et al. 2018b) and litter breakdown in streams (Benstead & Huryn 2014), herbivores influence plant growth (e.g., Gough et al. 2012, Min et al. 2020, Roy et al. 2020, Rastetter et al. 2022), and predators influence ecosystems on land (Koltz et al. 2018c) and in lakes and streams (Luecke et al. 2014, Budy et al. 2021, Deegan et al. 1997, Golden & Deegan 1998, Bowden et al. 2014). We also have shown that mean climate trends, primarily warming, influence consumers (e.g., Benstead et al. 2005, Budy & Luecke 2014, Budy et al. 2021). For example, warming (1) altered microbial metabolic activity and community composition (Adams et al. 2010), (2) affected soil invertebrates in combination with shading by shrubs (Asmus et al. 2017), (3) reversed the trophic cascade from predatory spiders in soils (Koltz et al. 2018c), and (4) could reduce Arctic char populations (Budy & Luecke 2014).

However, similar to studies in other regions, we know very little of how climate *variability* affects consumers. Adams et al. (2015) examined natural variability in stream temperature, discharge, and nutrients, and found that microbial activity and community structure rapidly responded to storms. Analysis of a 17-year LTER data set showed no influence of stream temperature, discharge, and winter severity on the long-term survival of grayling (Buzby & Deegan 2004). Yet, variation in stream discharge and temperature influenced juvenile and adult arctic grayling growth (Deegan et al. 1999) and drought greatly influenced grayling genomic and population structure (Golden et al. 2021). Finally, variation in climate influences seasonality and phenology in avian consumers, with direct effects on foraging and growth (Ricklefs 1968, Tremblay et al. 2005, Oliver et al. 2018, Pérez et al. 2016, Boelman et al. 2017). Despite some bird species adjusting breeding phenology in response to environmental variability (Boelman et al. 2017), a predictive understanding of population dynamics remains elusive because of the lack of data on interactions among changing conditions in stopover vs. breeding habitats and predicted increases in extreme

events. The overall importance of consumers in ecosystems, and our prior results from the ARC-LTER, provide the rationale for studying consumer responses to climate variability and how those responses will affect community composition and ecosystem processes.

New Activities - Q2

Our proposed research along the terrestrial-aquatic continuum has three new activities. The research is grounded in the fact that (1) the Arctic has permafrost, which directly affects soil organisms such as microbes, and (2) the fauna exhibit physiological, morphological, and behavioral adaptations that allow them to thrive in harsh and variable environments (e.g., Finch & Rose 1995, Martin 2001, Boonstra 2004, Beaumont et al. 2011). For example, in response to variable weather, arctic consumers can shift the timing of their life history stages (Oliver et al. 2020, Sheriff et al. 2013, Post & Forchhammer 2008). However, variability in conditions might exceed what consumers are adapted to (e.g., Post & Stenseth 1999, Høye et al. 2007, Gilg et al. 2012). A better understanding of how climate variability affects consumers will help predict the abundance, species composition, or in some cases even persistence of consumers as climate changes, and in turn their impacts on ecosystem function.

We will focus on the key consumer groups of microbes, fish, rodents, and birds, spanning the terrestrial-aquatic continuum and studied by ARC-LTER or associated projects. Our first new activity is on the *response* of fish and bird communities to climate variability, because of their reliance on and importance in arctic ecosystems. Every year millions of migratory birds from all over the world rely heavily on the Arctic for food and breeding (Johnson & Herter 1990). Grayling and lake char are the dominant fishes in Alaskan arctic streams and lakes (Deegan et al. 1999, Hershey et al. 1999), important in circumpolar freshwaters (Jonsson and Jonsson 2001), and critical food for Indigenous People and larger predators such as lake trout, Arctic char, grizzly bears, and some migratory birds. The second new activity focuses on the *influences on ecosystem function* from fish and microtine rodents (i.e., voles and lemmings) as they respond to climate variability. The importance of fish is described above, and rodents are the most abundant and regionally important herbivores in most tundra systems (Batzli et al. 1980, Oksanen et al. 1997, Callaghan et al. 2004, Olofsson et al. 2012, 2013). The third new activity focuses on the influence of climate and hydrologic variability on microbial species composition and their ability to consume and degrade DOM in lakes and streams (e.g., Kling 1994, Crump et al. 2003). The new activities include observations, experiments, and models that complement and expand on long-term datasets and understanding gained from ongoing ARC-related research.

***New Activity #1:** How does variability in climate affect key consumer communities?*

***New Activity #2:** How does variability in climate affect the influence of higher trophic levels on ecosystem function?*

***New Activity #3:** How does variability in climate affect the genomic potential and metabolic functioning of microbial communities as species move from soils to streams to lakes?*

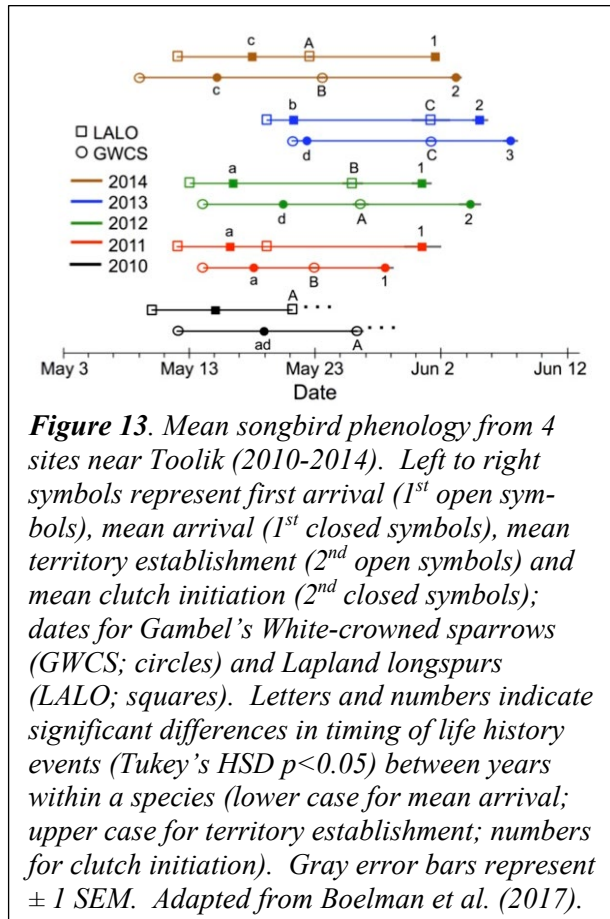
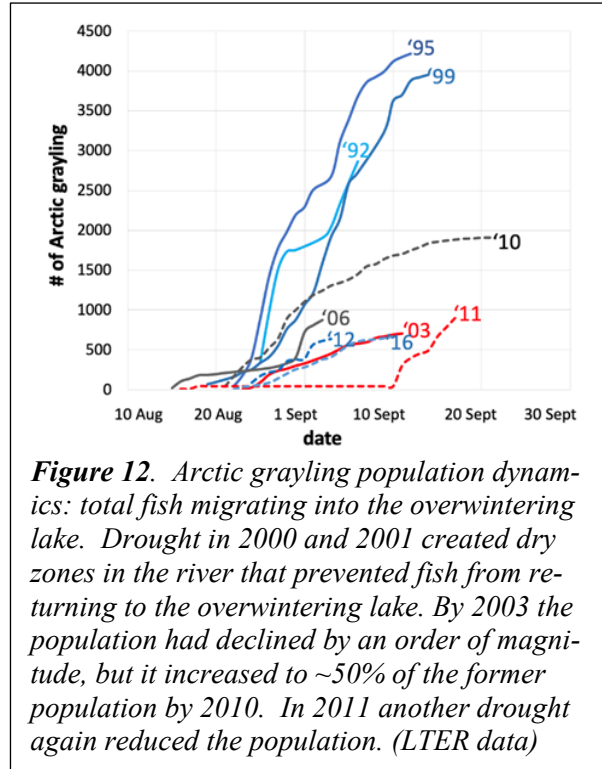
Proposed Research - Q2

New Activity #1. How does variability in climate affect key consumer communities?

Fish. The dominant impacts of climate on fish relate to movement and growth. Lake drying from climate change (Smith et al. 2005) or shifts in hydrology that close lake access can limit fish movement and their ability to colonize lakes (Hershey et al. 1999, 2006) and create genetic differentiation in populations (Golden et al. 2021, Klobucar et al. 2021). In streams, droughts are problematic because grayling require connectivity (interlinked waterways) for local population health and persistence and to migrate into overwintering lakes (Buzby & Deegan 2004). For example, sections of the Kuparuk River dried up in 2000, 2001, and 2011, stranding grayling in isolated pools and preventing migration upstream to Green Cabin Lake where they overwinter (Fig. 12). Such habitat fragmentation also causes genetic isolation in Kuparuk grayling, and might interfere with recolonization and their metapopulation resilience to climate change by restricting movement of better adapted populations (Golden 2016, Golden et al. 2021).

Predictions from experiments and modeling of the effects of climate warming on fish and their prey indicate that higher temperatures in lakes can increase fish growth rates, but only with sufficient invertebrate consumers as food (Budy & Luecke 2014, Klobucar et al. 2018, Pennock et al. 2021). In the Kuparuk, modeling of future climate change impacts on the food web predicts variable responses in prey items, and thus variable responses in fish populations (Wan et al. 2008). Thus, there is a need to understand and predict responses of fish to climate and environmental variability.

Approach. In LTER lakes and streams (Fig. 9) we will continue our long-term fish monitoring of community composition, population size and age structure, growth rates, and movement through stream-lake networks, but with modifications to increase sampling frequency during weather extremes of temperature and hydrology, including in shoulder seasons when possible. Parallel measurements of fish surveys and environmental



conditions (standard LTER protocols) will be conducted in the Kuparuk and Oksrukuyik watersheds; we will specifically compare our data to the complementary NEON data in Oksrukuyik Creek. Tracking of fish location and movement behavior in these surveys will use PIT tags (Buzby & Deegan 2004, Golden et al. 2021). An intensive study of migration into and out of Green Cabin Lake in the Kuparuk headwaters, and characterization of population size and structure of grayling, char, and lake trout, will be done twice during the grant using existing protocols (Buzby and Deegan 1999, 2004, Fig. 12). These data, added to the long-term LTER measurements, will also help inform modeling studies of fish and food web responses to climate variability (see Bowden et al. 2014, Budy & Luecke 2014).

Birds. Waterfowl arrive on their breeding grounds when much of the tundra is still covered in snow and ice (Prop & de Vries 1993, Madsen et al. 1998), and their reproductive success depends in part on the timing of their arrival versus access to snow-free breeding grounds (Prop et al. 2003, Bêty et al. 2004). Research near Toolik showed that variation in spring conditions can alter the phenology, stress physiology, and reproductive success of migratory songbirds (Oliver et al. 2018, Boelman et al. 2017,

Chmura et al. 2018, Krause et al. 2016a,b, Perez et al. 2016) (Fig. 13). However, while some birds adjust their arrival and clutch initiation to variation in the timing of spring conditions others do not (Tombre et al. 2008), suggesting that variability might be exceeding what at least some species have adapted to in the past. Because the summer breeding period is key to species success, the impacts of variable climate on that success are critical to understand, especially considering that avian responses might result in new patterns of migratory overlap among bird species (Patterson & Guerin 2013), altered host and pathogen life cycles (Altizer et al. 2013), and consequently in a rapid increase in the abundance and distribution of avian diseases in the Arctic (van Hemert et al. 2014).

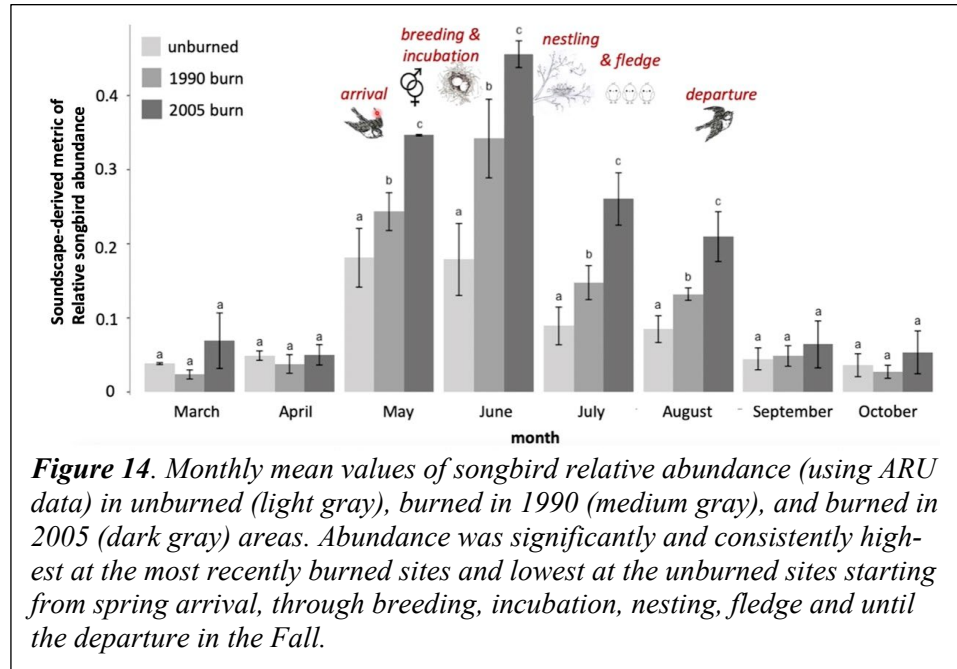


Figure 14. Monthly mean values of songbird relative abundance (using ARU data) in unburned (light gray), burned in 1990 (medium gray), and burned in 2005 (dark gray) areas. Abundance was significantly and consistently highest at the most recently burned sites and lowest at the unburned sites starting from spring arrival, through breeding, incubation, nesting, fledge and until the departure in the Fall.

Approach. Three consumer monitoring efforts started during our previous LTER grant will be combined with our LTER environmental data and analyses. This will increase the number of systematically studied consumer species, sample sizes, and the spatial and temporal extent of data used to study how variable environmental conditions impact resident and migratory arctic consumers. **First**, we will incorporate bird count data in the Toolik region from NEON (2019 and ongoing) into our analyses. **Second**, we will incorporate a network of audio recording units (ARUs) that have been autonomously collecting soundscape data near Toolik (March-October, 2010-2015, 2019-ongoing) including the NEON Oksrukuyik site (coordinated by Boelman, lead PI on this NNA project and LTER co-PI). The value of these ARU data especially for songbirds, waterfowl, ptarmigan, and flying invertebrates, including sound-derived concurrent weather conditions (e.g., rain, wind), is seen in the seasonal responses of songbird abundance including behaviors on burned tundra (Fig. 14). **Third**, we will incorporate 3 decades (1991-present) of avian movement tracking and concurrent meteorological conditions from the recently compiled Arctic Animal Movement Archive (AAMA; Davidson et al. 2020). By combining this multi-species, multi-decadal dataset of avian locations and movements with our temporal data on weather and environmental conditions (including productivity of prey for some bird species), we can determine how climate variability affects birds.

New Activity #2. How does variability in climate affect the influence of higher trophic levels on ecosystem function?

Fish. Variability in climate and hydrology can restrict fish movement within stream and lake networks, and effects on fish abundance and location have three main impacts on ecosystem food webs and function. First, similar to anadromous salmon migration, grayling can transport nutrients to and from headwater lakes such as Green Cabin Lake in the Kuparuk headwaters

Fish. Variability in climate and hydrology can restrict fish movement within stream and lake networks, and effects on fish abundance and location have three main impacts on ecosystem food webs and function. First, similar to anadromous salmon migration, grayling can transport nutrients to and from headwater lakes such as Green Cabin Lake in the Kuparuk headwaters, and could alter biogeochemical cycling or increase nutrients for primary producers (Deegan & Golden *In prep*). Second, grayling provide trophic subsidies for large piscivorous fish (e.g., lake trout and char) that remain in lakes year-round (Klobucar et al. 2020, Fig. 15), but river fish trapped in warm pools even if they later escape reduces body condition and thus their subsidy value (Golden 2016). Third, fish controls on consumers lower in the food web (their prey) can be strong in arctic freshwaters (e.g., O'Brien & Evans 1992, Deegan et al. 1997, Lienesch et al. 2005, Klobucar & Budy 2020, Budy et al. 2021). Given this importance of fish in the trophic dynamics of freshwater ecosystems, we clearly need more knowledge on how climate variability might reduce or increase fish abundance, condition, and growth.

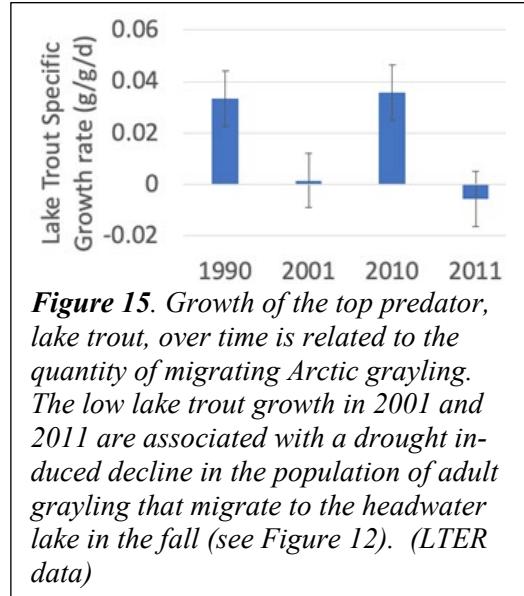


Figure 15. Growth of the top predator, lake trout, over time is related to the quantity of migrating Arctic grayling. The low lake trout growth in 2001 and 2011 are associated with a drought induced decline in the population of adult grayling that migrate to the headwater lake in the fall (see Figure 12). (LTER data)

Approach. The research approach and data collection is the same as in *New Activity #1*, but the analysis will focus on how consumers affect ecosystem function (trophic subsidies, population abundances, biogeochemical cycling, primary and secondary production). We will continue data collection on fish in key lakes and streams (Fig. 9) and analyze our measures of climate and other environmental variability using our standard LTER protocols (e.g., discharge and water levels, producer and consumer biomass, fish movement) to determine the relations between environmental variability, fish, and ecosystem connectivity and function.

Microtine rodents. Voles and lemmings are the most abundant and regionally important herbivores in most tundra systems (Batzli et al. 1980, Oksanen et al. 1997, Callaghan et al. 2004, Olofsson et al. 2013). In contrast to caribou and other herbivorous mammals who are infrequent visitors or at low population densities (Batzli et al. 1980, Lenhart 2002) and thus have low grazing impacts (Callaghan et al. 2004), the rodents are resident year-round, ubiquitous, locally abundant, and can sequester nutrients and thus control vegetation growth (Pitelka 1964) or directly consume vegetation in substantial amounts despite their small size (Olofsson et al. 2013, Batzli et al. 1980). In fact, Olofsson et al. (2012) found that rodents in northern Sweden caused a decrease in plant biomass detectable by satellites (NDVI) during the growing season following peak rodent years. Recent work near Toolik showed that herbivore population cycles intensify the impact of grazer-mediated processes on ecosystem biogeochemistry (Roy et al. 2020), and the presence or absence of herbivores can shift arctic tundra from a C source to a C sink (Min et al. 2021, Rastetter et al. 2022)

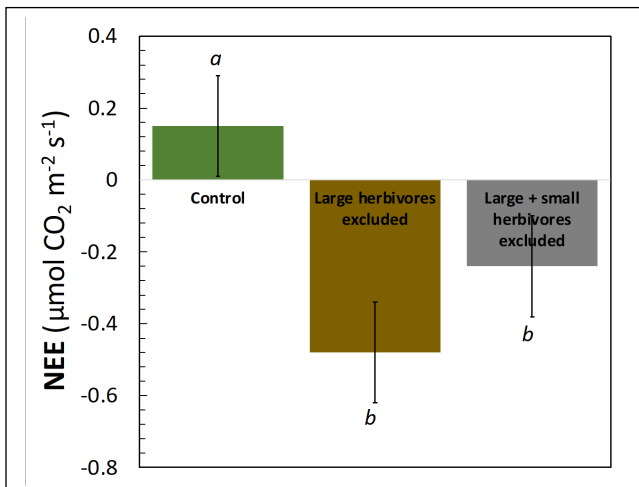


Figure 16. Net Ecosystem Exchange (NEE) after 21 years of exclusion of large (brown bar) and large and small (gray bar) herbivores in dry heath tundra. Herbivory causes the ecosystem to shift from a C sink (negative NEE) to a C source (positive NEE). Adapted from Min et al. (2021).

(Fig. 16). However, we still lack an understanding of how climate variability will influence the controls that these consumers have on community composition and ecosystem processes.

Approach. We will expand the LTER herbivore exclosure experiment (started in 1996) in dry heath tundra (Gough et al. 2007, Linden et al. 2021, Min 2021) to include more recently established plots in moist acidic tussock tundra. We will monitor the effects of rodents on ecosystem function in replicated plots that exclude lemmings and voles in both tundra types, in coordination with an ARC-LTER affiliated project started in 2017 (and shares co-PIs with the LTER). Vegetation species abundance, canopy complexity and phenology, leaf and soil nutrient concentrations, plot-level carbon exchange, and net primary productivity will be compared between the rodent exclosures and control plots (methods in Min et al. 2001, Steketee et al. 2022, Roy et al. 2020). In addition, we will use the NEON small mammal dataset (since 2019) to provide estimates of the spatial and temporal variability of ambient rodent density. We will analyze these datasets to determine how climate variability controls ecosystem responses both in the presence and absence of rodents.

New Activity #3: How does variability in climate affect the genomic potential and metabolic functioning of microbial communities as species move from soils to streams to lakes?

In the ‘Inlet Series’ of streams and lakes (the I-Series lakes) draining into Toolik Lake, we found that landscape-level connections among terrestrial, stream, and lake ecosystems affect patterns of chemistry and biology among sites (Kling et al. 2000, Crump et al. 2007). We also found that downslope transport and inoculation of soil bacteria strongly influence the microbiome composition (Crump et al. 2012) and activity (Adams et al. 2014, 2015) in streams and lakes, indicating a surprising openness of the microbiome and high community connectivity on the landscape. This ‘openness and connectivity’ relies on the conceptual ideas of meta-community ecology (e.g., Holyoak et al. 2005, Adams et al. 2014), and our findings have stimulated further research in other environments on this ecological topic of microbiome assembly and function (e.g., Ruiz-González et al. 2015, Staley et al. 2016, Teachey et al. 2019, Urycki et al. 2020). Here we will build on the concepts of openness, connectivity, and meta-communities to test how climate variability modifies microbial community assembly and in turn genomic potential and expressed activity (metabolism of DOM) in space and time.

In Toolik Lake, species connectivity across the landscape strongly influences microbiome composition and thus their ability to degrade DOM (e.g., Judd et al. 2006, 2007, Adams et al. 2014). Many bacteria and Archaea species (OTUs) in the lake were initially detected in upland soils and small headwater streams (Crump et al. 2012). For example, 58% of the bacterial taxa and 43% of the archaeal taxa were observed in upland habitats, and the 39 most common species in Toolik were found upslope in soils or headwater streams. Because these common taxa in the lake were classified as “rare” in upslope environments (<0.1% of sequences), rare taxa transferred into the lake must undergo species sorting (e.g., competition and predation) to form the resultant lake community. These results suggest that terrestrial environments serve as critical reservoirs of microbial diversity in lakes, and that the patterns of diversity in surface waters are structured by initial inoculation from upslope habitats. However, we also found that environmental variability, such as rainfall, strongly determines the stream microbiome at any given time (Fig. 17). What is unknown is how these shifting microbiome communities affect microbial activity in streams, or in receiving

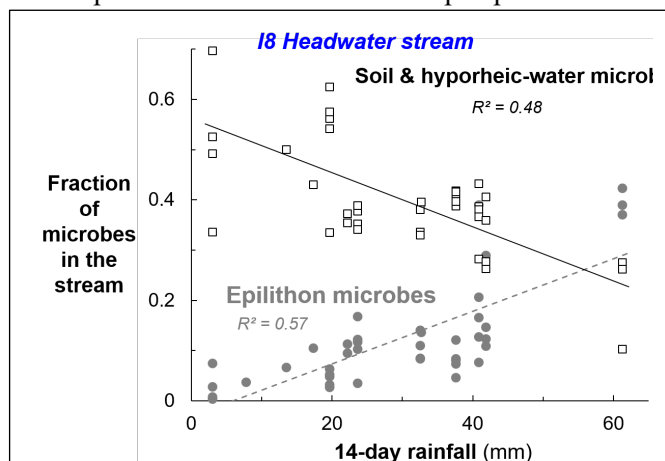


Figure 17. Rainfall dilutes soil and sediment microbes (open), and washes more epilithon microbes (closed) into the stream. (LTER data)

lakes. We will study the activity and function of these microbial taxa on the terrestrial-aquatic continuum using metagenomics and metatranscriptomics to test whether community openness and influence of climate variability translate into functional importance for ecosystem processes (e.g., metabolism of DOC and DON), or if openness is mainly a passive transfer of inactive microbes.

Approach. In the Toolik Inlet Series of lakes and streams we will use genomics approaches (methods in Nalven et al. 2020, Romanowicz et al. 2021) to answer two questions: first, whether microbial species moving from soils to streams to lakes are passive or if this community openness is also functionally important in the metabolism of DOM to produce inorganic C, N, and P; and second, how climate variability and especially rainstorm amounts and frequency affect microbiome composition and activity. Field samples collected from streams during dry and rainy periods will be analyzed with rainfall intensity as the independent variable (as in Fig. 17). We will also experimentally alter environmental conditions to replicate moving between ecosystems (e.g., adding DOM from soil water compared to DOM in stream or lake water), and measure the metatranscriptomic response to assess which species respond and on what time-scales. These experiments also allow us to measure the similarity of microbiomes among ecosystems as an index of community openness and connectivity, how that shifts with climate variability, and what changes in function (microbial activity) result.

QUESTION 3. How does climate variability affect C dynamics along the terrestrial-aquatic continuum?

Background and rationale. Theoretical linkages between environmental variability and ecosystem properties point to the severity of the arctic environment as an extreme and thus useful case for studying ecological function (May & MacArthur 1972). The Arctic is experiencing accelerated rates of climate change and variability (Cohen et al. 2012, Huang et al. 2017, Easterling et al. 2000, Vonk et al. 2019), and the future of northern latitudes as a sink or source of C is in question (McGuire et al. 2018). The release of thawed soil C to the atmosphere in the next 50-150 years is the strongest potential impact on the atmosphere from any natural system, and this *arctic amplification* could dramatically increase global warming (Bowen et al. 2020a). Furthermore, several studies highlight the link between environmental variability and C dynamics. Schaefer et al. (2011) showed variable freeze-thaw cycles can lead to permafrost C loss, and Ruel & Ayres (1999) showed that increased variation in light can reduce daily C assimilation in boreal shrubs. In Toolik Lake, Evans et al. (2008) found that variability in the light field caused by internal waves and patchy clouds affects photosynthetic C gain. Finally, in Innvait Creek increased variability in soil temperatures in one year was followed by substantial ecosystem C loss to the atmosphere for the following 4 years (Euskirchen et al. (2017). Given these examples, we propose to study the importance of climate variability on C dynamics, and using models described below we will compare the effect of variability to the effect of mean climate trends.

Prior ARC-LTER research characterized how mean trends of climate change act as a disturbance, for example by increasing mean temperature (Rastetter et al. 2020) or by addition of nutrients to terrestrial (Shaver & Chapin 1991, 1995)

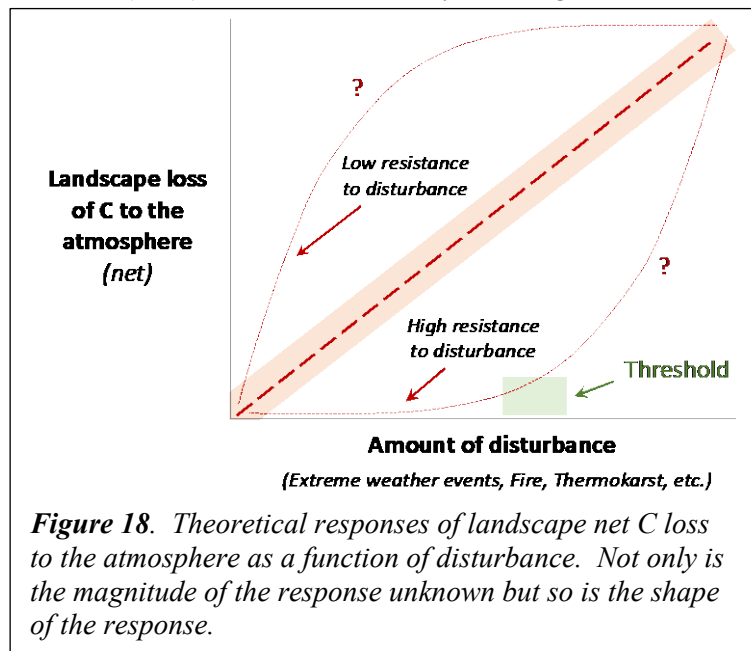


Figure 18. Theoretical responses of landscape net C loss to the atmosphere as a function of disturbance. Not only is the magnitude of the response unknown but so is the shape of the response.

and aquatic (Luecke et al. 2014, Budy et al. 2021) systems as expected from thawing permafrost. We quantified lateral and atmospheric C losses from surface waters (Cory et al. 2014, Eugster et al. 2020, Bowen et al. 2020a), and showed the importance of ecosystem openness and connectivity in hydrology and biogeochemical cycles (Neilson et al. 2018, O'Connor et al. 2019, 2020). In this proposed research we add investigations of how climate *variability* affects biogeochemical cycles; the hypothesis is that climate variability will increase disturbance (e.g., extreme weather, thermokarst), which will increase the landscape-level loss of C laterally and to the atmosphere (Fig. 18). However, we are unsure of how openness and connectivity will control, or respond to, the resistance of ecosystems to disturbance. We are *not* proposing to determine an absolute landscape-level C balance for the region, although we have estimated C balances for aquatic (Eugster et al. 2020) and terrestrial (Euskirchen et al. 2017) habitats, but instead we will determine the mechanistic controls on C balance and how they respond to climate variability.

New Activities – Q3

Our proposed research studies biogeochemical cycles along the terrestrial-aquatic continuum (e.g., Cory & Kling 2018), including the use of models (e.g., Neilson et al. 2018, O'Connor et al. 2019, King et al. 2020, Rastetter et al. 2021). The first new activity determines climate variability effects on plant photosynthesis and respiration (net production of organic matter), and the second and third activities examine organic matter degradation (DOM to CO₂) in soils by microbes and abiotic redox reactions, including the effects of thawing permafrost (Fig. 19). The fourth activity determines how DOM exported from land is degraded to CO₂ in lakes and streams by coupled microbial-photochemical processes (Fig. 19). [We use “DOM” for all dissolved organic matter, DOC when referring specifically to C, and SOM for soil organic matter.] What we need to know is how variability in climate, in hydrology, and in permafrost thaw dampens or accelerates this DOM processing along the continuum. In these new activities we will use models, observations, and experiments to answer the following questions:

New Activity #1: How does variability in climate control C balance in tundra ecosystems?

New Activity #2: How does variability in permafrost thaw control microbial degradation of DOM?

New Activity #3: How does variability in hydrology control the abiotic degradation of DOM by iron-mediated redox reactions?

New Activity #4: How does variability in climate and hydrology control the coupled microbial and photochemical oxidation of DOM in streams and lakes?

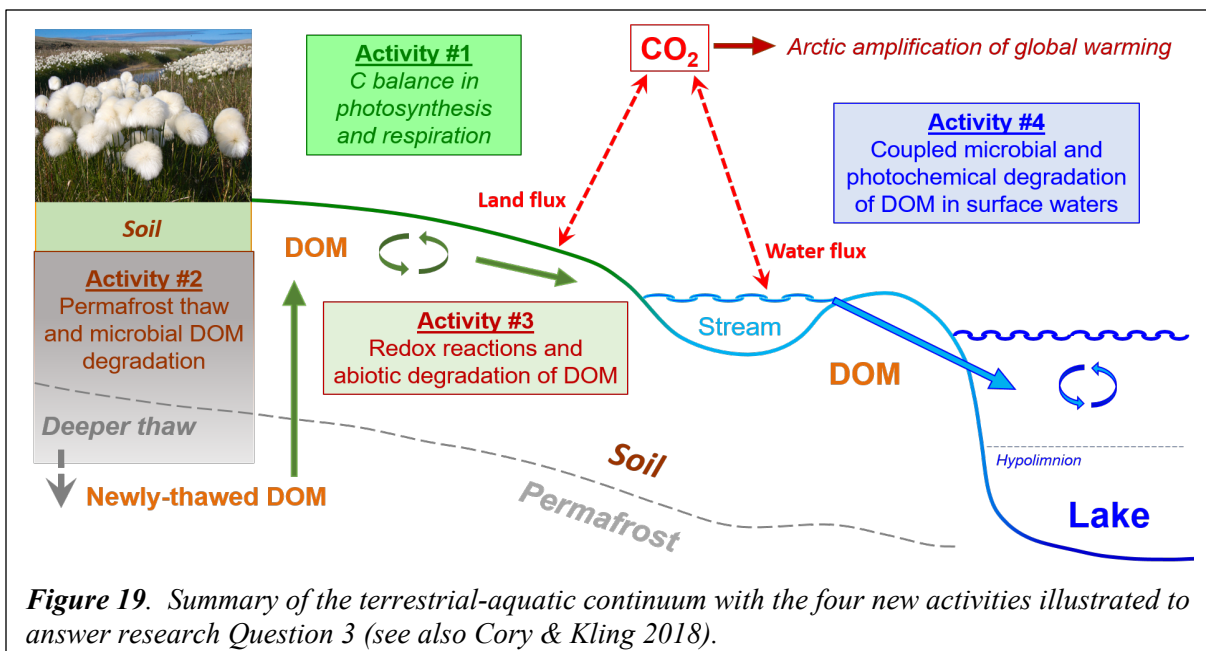


Figure 19. Summary of the terrestrial-aquatic continuum with the four new activities illustrated to answer research Question 3 (see also Cory & Kling 2018).

Proposed Research – Q3

New Activity #1: How does variability in climate control C balance in tundra ecosystems?

Uncertainty in the estimated annual gross primary productivity of the Arctic is unacceptably high and compromises predictions of the future strength of the arctic C sink (Rogers et al. 2021), and thus arctic amplification of climate change. Arctic tundra has a large impact on global biosphere-atmosphere exchange due to the enormous size of the biome, huge C stores in permafrost, and the uncertainty in both the magnitude and direction of the net carbon flux (Beer et al. 2010, Pan et al. 2013, Fisher et al. 2014, Fisher et al. 2018). Furthermore, the rapidly increasing and highly variable temperatures in the Arctic can result in large C releases to the atmosphere, stimulating the climate feedback (Commane et al. 2017). Given that annual C storage in arctic vegetation is the small difference between two large C fluxes (photosynthesis and respiration), process-level studies of arctic vegetation are urgently needed (e.g., McLaughlin et al. 2014). Photosynthesis has a saturating response to light and a broad temperature optimum while respiration has a small but sharp response to light (the Kok effect, Heskell et al. 2013b) and increases exponentially with temperature. This combination of responses will have a strong but currently un-quantified response to climate variability (Ruel & Ayres 1999). Below we describe how we will quantify and integrate these potential responses in photosynthesis and respiration in arctic tundra.

A. Photosynthesis. C uptake by photosynthesis is heavily constrained by light absorption and temperature in arctic plants (McLaughlin et al. 2014, Heskell et al. 2013a, 2014, Magney et al. 2017, Rogers et al. 2019, Min et al. 2022) and these drivers vary substantially over time scales from seconds to decades and spatial scales from leaves to landscapes. In this activity we will quantify the physiological responses to varying light and temperature. We recently discovered that canopy structure plays an important role in light absorption and thus C uptake (Min et al. 2022). Using Structure-From-Motion (SFM, described below) we found significant differences in the average amount of light that heath vegetation received when subjected to herbivore grazing. These structural differences are also reflected in net ecosystem exchange (NEE) and gross primary productivity (GPP); canopy structure quantified using SFM showed the heath tundra was a C source, while traditional methods (no canopy structure) predicted this system was a C sink (Min 2022).

B. Respiration. The exponential increase in respiration with temperature results in a higher C loss with greater temperature variability (assuming a similar or higher mean). Our LTER-related studies showed that plant respiration at 25°C was 3x higher than rates in the tropics (Atkin et al. 2015) but had a similar response to temperature (Heskell et al. 2016). At the leaf scale we found that arctic plants have increased respiratory flexibility due to their variable engagement of the respiratory alternative oxidase (Kornfeld et al. 2012). At a plot scale both dry heath and tussock tundra are precariously balanced between C source and sink because respiratory fluxes and their exponential response to temperature easily outpace photosynthetic C uptake in the Arctic due to warming and cloud cover (Min 2021), and due to continued soil respiration during the autumn shoulder season when GPP is limited (Watts et al. 2021). Thus the interactive effects of variable warming and canopy structure must be determined, and we will test two recent hypotheses from the literature. First, that warming and disturbance have opposing effects on GPP (warming increases GPP while disturbance decreases GPP) but have additive effects on respiration (warming increases respiration directly while disturbance increases respiration indirectly by creating warmer conditions) (Rogers et al. 2021). Second, that increasing shrub height alters the thermal environment and this results in larger C losses. The implication is that expansion of tall shrubs can amplify shallow soil warming, increase seasonal thaw depth, and increase soil C cycling rates, all of which could lead to increased C loss and further permafrost thaw (Kropp et al. 2021).

Approach: Leaf-level gas exchange and chlorophyll fluorescence will be used to quantify short-term and small-scale responses to light, temperature, and long-term responses to nutrients (methods in Griffin et al. 2013, Heskell et al. 2014, Atkin et al. 2015, Heskell et al. 2016, O’Sullivan et al. 2016, Rogers et al. 2017). The ARC-LTER has a long history of innovation in measuring and modeling arctic C exchange (e.g.,

Shaver et al. 2013, Min et al. 2022), and we will extend this work by reanalyzing archived chamber flux data from a variety of different tundra types and by optimizing estimates of canopy structure and light absorption. First, the data reanalysis will determine if the antecedent variability in key drivers affects model parameters of photosynthesis and respiration rates, and if these effects depend on the degree of biogeochemical openness. Second, we will optimize estimates of light absorption using SFM, a photogrammetric method for deriving three-dimensional structure and leaf area index (LAI) from digital imagery (Min et al. 2021). We will extend this work to other tundra types and to experimental plots with altered nutrient availability. Our improved understanding and quantification of light absorption can then be used to test for the effects of variability in climate and environmental drivers of C gain. We will test the response of C uptake to variability at even larger scales with similar reanalysis and scaling exercises using eddy covariance data from the collaborating LTREB data (led by A. Rocha), the NSF-AON project (the LTER shares co-PIs), and the NSF-NEON data (see Project Management).

New Activity #2: How does variability in permafrost thaw control microbial degradation of DOM?

Globally about half of the CO₂ flux from land to atmosphere is due to microbial respiration of organic matter in soils, and the majority of soil C worldwide is in permafrost (Tarnocai et al. 2009, Hugelius et al. 2014) where soils are being thawed and C mobilized as climate warms (Hinzman et al. 2005, Jorgenson et al. 2006). Estimating the degree to which climate change will be amplified by greenhouse gases released from thawing permafrost is arguably the prime question that science has to answer for society today. Right now, our best answer for the future C balance of the Arctic comes from models that have large uncertainties and whose predictions cross zero; i.e., they predict by 2100 the Arctic could be either a source or a sink of C to the atmosphere (McGuire et al. 2018). This uncertainty is in part because the models do not include important processes such as photochemistry (Bowen et al. 2020a; see *New Activity #4* below), and because we know too little about the genomic potential of microbes to degrade thawed permafrost C and produce CO₂ and CH₄ (e.g., Chen et al. 2021).

Thaw depth and duration have increased in permafrost soils (Serreze et al. 2000, Euskirchen et al. 2006, Barichivich et al. 2012, Kling et al. 2014). Once permafrost thaws the SOM degradation is regulated by microbial genomic potential, hydrology, and redox conditions. In permafrost soils, water is confined by the shallow ice table to the upper thawed zone and results in waterlogging and thus periodic or persistent reducing conditions that support anaerobic metabolism (e.g., Lipson et al. 2015, Herndon et al. 2015, Romanowicz et al. 2021). However, warming also has increased rainfall intensity, frequency, and water accumulation (Kumar et al. 2012, Spence & Phillips 2015, Bintanji & Andry 2017), and thus permafrost thaw and hydrological changes in precipitation and drainage will likely lead to greater fluctuations in water levels and redox status. Yet few or no studies have investigated how thaw duration or variability in redox status has affected the soil microbiome.

Recent studies of microbial responses to permafrost thaw in lab incubations show rapid shifts in composition within a few

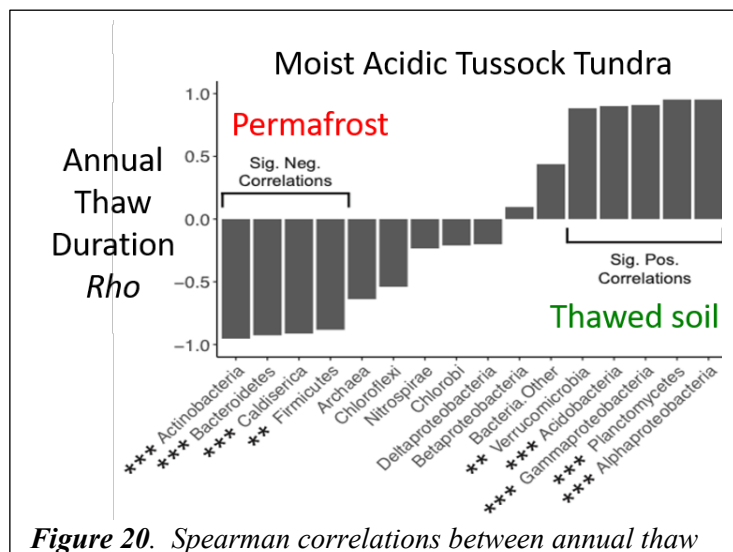


Figure 20. Spearman correlations between annual thaw duration and microbial taxa in the soil profile of MAT at Toolik. Correlations are arranged from rho values of -1 to 1 (left to right) to show relationship with annual thaw duration (left side microbes are from permafrost depths and right side microbes are from thawed surface layers). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. LTER data.

days of thaw (Mackelprang et al. 2011, Coolen and Orsi 2015), but these results disagree with *in-situ* soil warming experiments that show little or no change in permafrost microbiome composition (e.g., Rinnan et al. 2007, Biasi et al. 2008, Lamb et al. 2011, Deslippe et al. 2012). Our recent LTER research combined multi-decade thaw depth records with fine-scale measurements of soil microbiome composition from the annually-thawed surface ‘active layer’, through the transition zone of intermittent thaw, and into the permafrost. We found that variability in annual thaw duration by depth was positively correlated with dominant taxa in the active layer and negatively correlated with dominant taxa in the permafrost (Fig. 20). Microbiome composition in the transition zone was statistically similar to that in the permafrost, and the implication is that recent decades of intermittent thaw have not yet induced a shift from permafrost to active-layer microbes.

Approach. We will experimentally thaw soils at realistic temperatures and time periods (in the lab) as informed by our long-term LTER data (soils thawed up to 3 months representing the summer). We will include treatments that vary the amount of water saturation and thus redox conditions as soils thaw (see Romanowicz et al. 2021), and measure the genomic potential (metagenomics) of soil microbiomes thawed for different lengths of time in anoxic and oxic conditions, measure the microbial metatranscriptome response over time, and determine the lability (ease of degradation) of SOM in the transition zone and permafrost compared to OM decomposition in surface soils (methods in Ward et al. 2017, Nalven et al. 2020, Romanowicz et al. 2021).

New Activity #3. How does variability in hydrology control the abiotic degradation of DOM by iron-mediated redox reactions?

Studies of the coupling between iron (Fe) and C cycling at terrestrial-aquatic interfaces have focused on SOM stabilization by Fe minerals (Chen et al. 2020). However, Fe redox cycling can also lead to the oxidation of SOM to CO₂ (Lipson et al. 2010, Trusiak et al. 2018, Chen et al. 2020). We showed that Fe redox cycling in soils can oxidize as much DOM to CO₂ as does microbial respiration of DOM in arctic surface waters (Page et al. 2013). Upon oxidation of reduced ferrous iron (Fe(II)) by O₂, reactive oxygen species (ROS) including hydroxyl radical (•OH) are produced in proportion to Fe(II) concentrations; •OH then oxidizes DOM to CO₂ (Fig. 21). Our results, combined with field observations of Fe-rich waterlogged soils across the Arctic, suggest that O₂ supply to soils likely limits •OH production (Walpen et al. 2018, Trusiak et al. 2019). The •OH (and subsequent CO₂) produced from Fe redox cycling during precipitation events that bring atmospheric O₂ into soils can be about 3-5 times greater than that from static, waterlogged conditions (Trusiak et al. 2019). Thus, we suggest that the abiotic oxidation of DOM to CO₂ depends on hydrological variability (precipitation and groundwater movement) and associated soil redox status (Trusiak et al. 2019). We hypothesize that soils with high variability in precipitation and thus variable redox conditions will oxidize more DOM to CO₂ than will continuously waterlogged soils.

Approach. We will continue our long-term LTER measurements of soil water chemistry in the Toolik and Imnavait basins (Fig. 9) to explain differences in transient redox status and Fe redox cycling by landscape age, toposequence position (dry hilltop to wet valley

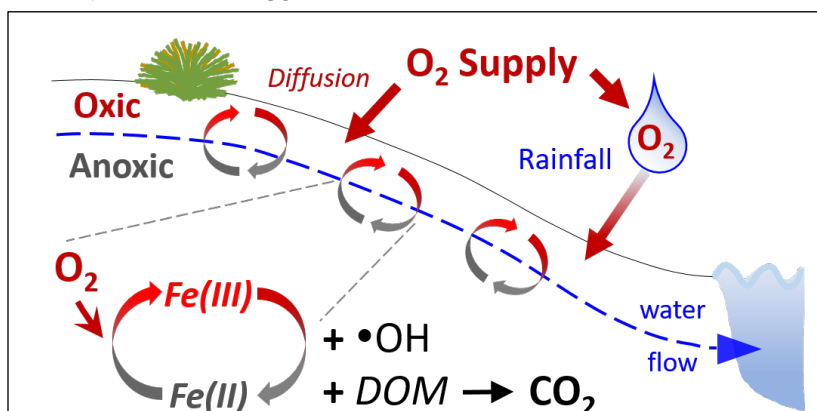


Figure 21. Variability in the frequency and intensity of precipitation events may control the CO₂ produced from redox cycling of iron, given that rain events add more O₂ (or expose more soil to O₂) than diffusion of O₂ from air. Addition of O₂ initiates redox reactions of Fe that oxidize DOM to CO₂.

bottom), and vegetation type (Page et al. 2013, Trusiak et al. 2018, 2019, Romanowicz et al. 2021). The prior and ongoing data collection inform and parameterize models we have used to (1) determine ground-water flow and surface-subsurface exchanges of DOC along an arctic terrestrial-aquatic continuum (Neilson et al. 2018, O'Connor et al. 2019), and will build to (2) determine reactive transport of DOC, nutrients, Fe, O₂ in a variety of soil and landscape settings (methods in Shuai et al. 2017, Zheng et al. 2019, Liao et al. 2021, Ferencz et al. 2021). A weather generator (see above) will analyze Toolik area climate and develop scenarios of increased and reduced variability in precipitation (supplying O₂), and we will perform data-model experiments where model responses to hydrology perturbations (drought, storm intensity or frequency) are analyzed to determine the effects on C-Fe redox cycling and the abiotic production of CO₂ from DOM.

New Activity #4: How does variability in climate and hydrology control the coupled microbial and photochemical oxidation of DOM in streams and lakes?

Microbial mineralization of DOM to CO₂ is generally considered the dominant pathway from organic to inorganic C in surface waters, but we showed that photomineralization of DOM to CO₂ is at least as important for arctic C budgets (Cory et al. 2014, Bowen et al. 2020a) and can stimulate C processing in other environments (e.g., Bowen et al. 2020b). In addition, we know that variability in environmental drivers (e.g., light, hydrology) is more important for photochemical than for microbial CO₂ production (Crump et al. 2003, Cory et al. 2014). For example, areal (water column) rates of CO₂ produced from photomineralization increase with more photon flux at the water surface (i.e., sunny vs. cloudy days), with more sunlight-absorbing chromophoric DOM (CDOM), and with more water surface exposed to sunlight (i.e., lake area or river width) (Cory et al. 2015); these controls all vary with precipitation, sometimes in opposite directions. For example, a preliminary comparison of a relatively wet (cloudy) vs. dry (sunny) summer (2014 vs. 2015, respectively) showed that the Kuparuk River produced 30% more CO₂ from photomineralization in the wet than in the dry summer, because greater CDOM in the wet year spread over a larger surface area of river more than offset the lower photon fluxes due to clouds.

What we do not know is how greater variability in precipitation frequency or intensity will affect CO₂ production from photomineralization and microbial respiration. We hypothesize that the effect of greater variability in precipitation frequency or intensity on CO₂ production depends on (1) inputs of CDOM from soils, and (2) location in the river or lake network. Soil inputs of CDOM can differ from headwater to higher-order streams (e.g., Neilson et al. 2018), and DOM inputs from storms (along with temperature) affect microbial processing rates (Adams et al. 2015). In addition, photomineralization depends on exposure to sunlight and thus on water residence times, which differ between headwater streams, larger rivers, and lakes (Cory et al. 2015). Therefore, we predict that photomineralization will be controlled by the *combined effects* of CDOM, photon availability, and surface area in surface waters, and that microbial respiration will respond mainly to variations in DOM and temperature.

Finally, in basins with interconnected streams and lakes (the Toolik inlet series, Fig. 9), the same controls and processes of photochemistry occur as in streams but the importance of light and microbial activity is higher because as water column depth increases the total amount of CDOM increases and thus limitation by light is stronger; the deepest lakes have dark bottom waters, but microbial activity still occurs. Connected streams and lakes can strongly influence one another (Kling et al. 2000, Crump et al. 2007), but no study to our knowledge has analyzed how variability in weather events alters the basic controls on photo-bio degradation of DOM integrated across the lake district and landscape (Cory & Kling 2018).

Approach. Prior and ongoing data will be analyzed to assess patterns of change in water chemistry, photochemistry, and C measurements with weather variability, and to inform development of a model that moves water, heat, and C through surface water networks and incorporates microbial activity and photochemical reactions (methods in Merck and Neilson 2012, Li et al. 2019, Cory et al. 2014, 2015, Neilson et al. 2018). The transport and fate of water, heat, and C in streams or lakes follow the same physical principles, but require different modeling approaches. The river model will use our previous work to account

for downstream movement (water and C mass), lateral inflows, and heat transfer at river bottom and surface interfaces (King et al. 2016, 2020, King and Neilson 2019). In stratified waters (e.g., ponds and lakes) the majority of water movement and heat transfer occurs in the epilimnion, but mixing can homogenize vertical layers to varied depths. This will be modeled as a one-dimensional system with 3 layers where the volume of the bottom two layers (metalimnion and hypolimnion) will be held constant, and the top layer can vary (following methods of Merck and Neilson 2012). The river and lake models will include photochemical and microbial reactions (methods in Cory et al. 2014, 2015, Li et al. 2019). The river and lake models will be linked with our groundwater model (Q3, *New Activity #3*) (methods in Neilson et al. 2018, O'Connor et al. 2019) to provide DOM inputs from land to surface waters. As with *Activity #3* above, we will use a weather generator and data-model experiments to determine how variance in hydrology affects coupled photo-bio degradation of C and CO₂ production.

IV. BROADER IMPACTS

Intellectual Contributions: The Arctic is one of the fastest warming regions on Earth and its response to climate change will foreshadow future changes in other biomes and might accelerate climate warming from C released in thawing permafrost. Determining the strength of this “arctic amplification,” and communicating the results to society, is a responsibility that the ARC-LTER is positioned to assume. The objectives of the ARC-LTER project for 2023-2029 are to understand how climate variability ranks as a driver of changes in ecosystem function (e.g., C balance) relative to the mean trends from climate change (e.g., warming). The concepts and results from our project will have broad application to other biomes and landscapes, such as in comparisons with the Sevilleta LTER that investigates the effects of changes in climate mean and variance in dryland ecosystems. In addition, increased variability of daily temperature reduces economic growth independent of (and on top of) the mean trend in temperature, with low-income regions most vulnerable to the effects of temperature variability on economic growth (Kotz et al. 2021). Our Schoolyard activities will help communities “relate and connect” with climate variability in the Arctic by engaging them in learning about how where they live might respond to climate variability and be vulnerable to economic and other impacts.

Broadening Participation: Since the last renewal we have increased awareness of the lack of diversity, equity, and inclusion (DEI) in ecology (e.g., NSF 2019) and the challenges to making progress on DEI (Morales et al. 2020, Bowser & Cid 2021). Fieldwork can be more of a barrier than a gateway for underrepresented students (URMs) or other participants (e.g., K-12 teachers) compared to White participants for many reasons (Morales et al. 2020, Bowser & Cid 2021). Our mid-term site review was also a call to action for the ARC-LTER to more aggressively broaden participation. We are doing so in multiple ways guided by a DEI Action Plan adopted in Spring 2021 and updated in Spring 2022. The ARC-DEI Committee, chaired by Gough, meets monthly to share best practices from the LTER Network DEI Committee and engage with UAF DEI staff to make Toolik Field Station (TFS) more welcoming and inclusive to promote a sense of belonging (Halliwell et al. 2020). ARC-DEI provides suggestions to project leadership regarding inclusion at all levels of participants, as described below and in the Project Management Plan. During the next six years the ARC-DEI Committee will continue activities including: providing resources for project members on best practices for recruiting and retaining URM participants at all levels, helping develop a TFS code of conduct, creating pre-field season orientation opportunities (e.g., short videos of life at TFS), and providing social activities to keep participants engaged in LTER activities after completion of the field season (e.g., virtual happy hours, DEI office hours). Our approaches align with recommendations from the mid-term review and recent literature on best practices.

Education, Mentoring, and Outreach: Due to our remote setting (no local schools), the ARC Schoolyard program, led by Ms. Amanda Morrison, is focused on teacher professional development through the Research Experiences for Teachers (RET) program. Morrison has 11 years of experience coordinating 26 RET teachers engaged in arctic ecology, serves on the LTER Education and Outreach Committee, and is co-leader of their RET subcommittee. She will oversee the RET program (2 teachers per

year) and coordinate new and ongoing educational partnerships with existing programs (e.g., PolarTREC, Earth Camp, TUCSE [Towson University STEM Excellence Center]). She also will ensure that our 2 REU students per year are engaged in educational activities with the teachers. Morrison participates in a new NSF-funded BIORET project focused on global change biology where teachers are recruited in pairs from schools serving URMs to work with a researcher team at one of three LTERs (including ARC-LTER), and they collaborate as a group. This funding will increase the number of teachers to create a cohort approach, recommended to give teachers an identity as equals in a group, which in turn can advance student problem-solving and learning (Morales et al. 2020).

Morrison has built relationships with Alaska K-12 administrators and teachers to ensure that our activities reach students in Alaska. For example, in summer 2021 she worked with the curriculum coordinator at North Star Borough School District in Fairbanks, AK to recruit local K-12 teachers. In addition, she speaks with the Alaska Rural Innovation and Student Engagement group, a monthly meeting of rural school districts, to recruit rural AK teachers to the RET program. These activities will continue.

In the new grant Morrison will coordinate a synthesis effort to compile existing and future arctic education curricula. We will link to our ARC-LTER website the arctic ecology curricula developed by PolarTREC teachers that is already freely available, vetted, and often peer-reviewed in educational journals (e.g., Taterka & Cory 2016), and these materials will be promoted via science education societies and conferences and the ARC-LTER annual meeting. Morrison and Co-PI Cory will continue to work with PolarTREC to help support teachers new to TFS working with LTER PIs.

Another new effort to increase recruitment and retention of URMs will collaborate with Earth Camp at the University of Michigan run by Dr. Jenna Munson. Earth Camp's goal is to get URM students outdoors and exposed to ecology and environmental science concepts and careers. Earth Camp serves a cohort of ~60 high school students per summer in an 8 day residential camp experience; each cohort participates for all four years of high school. During the first summer each cohort learns about ecology and environmental science through outdoor activities around Ann Arbor, MI, with year four culminating in field work in Wyoming. Earth Camp has graduated 66 students (99% URM, >50% Black) from Detroit, Southfield, Ypsilanti, and other Michigan cities. Ninety-five percent of Earth Camp alumni have gone to college majoring in STEM. Our support of students and teachers in Earth Camp will result in a module for students on arctic ecology, modified from existing curriculum in coordination with the participating teachers and Ms. Morrison. This exposure to arctic ecology will help the students understand issues facing the arctic region and also empower them to apply for REUs at remote field stations; ARC-LTER will actively recruit REUs from Earth Camp graduates.

Finally, because multiple approaches help broaden STEM participation, we will work with TUCSE (at Gough's home institution). They provide outreach programs to Maryland's K-12 schools, such as virtual field trips and professional development workshops for teachers in STEM; teachers in Baltimore area schools will be recruited for RET activities at ARC-LTER.

Undergraduate and graduate students, postdocs, and technicians. We will support two REU students per year at Toolik, recruited through ARC-DEI, Earth Camp, and our collaborators at minority-serving institutions (MSI). Gough is at Towson University, where 50% of students are URMs, and collaborator McLaren is at UT El Paso, an MSI. The ARC-DEI will assist PIs with recruiting and retention strategies for URM participants at the graduate, postdoctoral, and technician levels. We will support a graduate student site representative to attend the LTER network meetings and to create an ARC community of graduate students with information and science exchanges year round.

Data accessibility. Concomitant with our DEI goals we will increase accessibility to our data for students, educators, and researchers who cannot travel to the Arctic. RETs collaborating with ARC-LTER have published one Data Nugget, with three more in progress. We will contribute several signature datasets on arctic ecology and weather variability to the Alaska Data for Undergraduate Educational Mod-

ules (AK DatuM). We will also hold a "how to use LTER data" session at our annual meeting to introduce and train new graduate students and postdocs on how to access and use LTER data; what we learn in this activity can be exported to the LTER Network or other scientific societies (ESA, AGU).

Outreach to the General Public. ARC-LTER personnel will give presentations to the general public, schools, and community organizations in Alaska and near home. Building more connections with Alaska teachers will facilitate feedback from these communities. We will promote our activities via social media and with Alaskan communities via radio station contacts (via TFS).

Outreach to Federal, State, and Local Management Agencies. We will continue to work closely with BLM, Alaska Fish and Game, and North Slope Borough for annual permitting and provide data and briefings to these agencies on request.

National and International Research Planning and Organization. We will continue ongoing interactions with national and international colleagues and organizations. Kling is a co-PI on the NSF SEARCH project to co-produce knowledge about rapid arctic change with Indigenous and business groups for decision makers. Other ARC personnel have engaged in activities with ISAC (International Study of Arctic Change) and ACIA (Arctic Climate Impacts Assessment). ARC personnel also engage with NEON, the TFS steering committee, and international arctic research networks (e.g., International Tundra Experiment, ShrubHub, Herbivory Network) by contributing data for meta-analyses and collecting data with common protocols.

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