Arctic LTER Site Review
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NATIONAL SCIENCE FOUNDATION ARCTIC PROGRAM

NATIONAL SCIENCE FOUNDATION LTER NETWORK LONG TERM ECOLOGICAL RESEARCH

THE ARCTIC LTER PROJECT AT TOOLIK LAKE, ALASKA
NSF SITE REVIEW 2019

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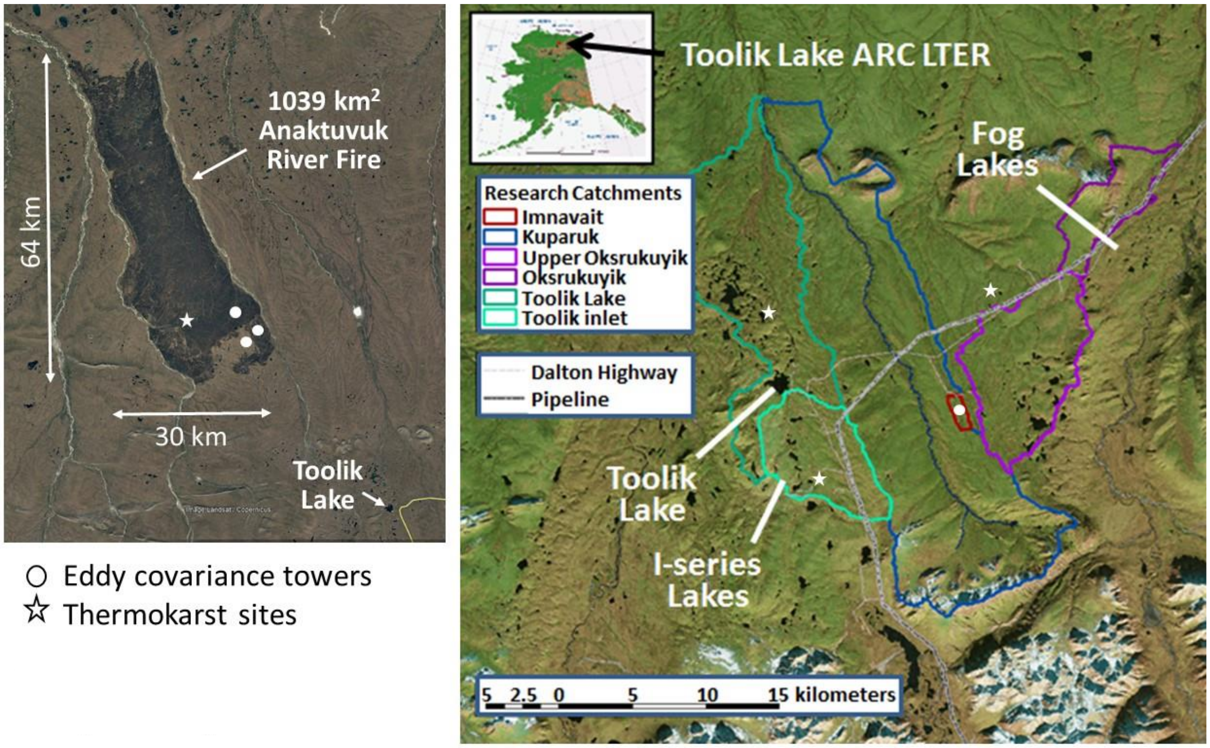

Figure 1: Major Arctic LTER study sites and place names.

1. INTRODUCTION

The Arctic LTER Site

Research in the Toolik Lake area began in 1975, shortly after the opening of the Haul Road (Dalton Highway) built to support construction of the Trans-Alaska Pipeline. From its beginnings, research near Toolik Lake has included studies on terrestrial (e.g., Shaver and Chapin 1980), stream (e.g., Peterson et al. 1983), and lake (e.g., O’Brien et al. 1979) ecosystems. With this broad perspective of arctic ecology, the Toolik Lake site became part of the LTER network in 1987.

Toolik Lake is located on Alaska’s North Slope in the north-facing foothills of the Brooks Range (68°38’N, 149°43’W; elevation 720 m). Long-term study sites of the Arctic LTER include the entire Toolik Lake watershed, the adjacent upper Kuparuk River watershed down to its confluence with the Toolik Lake watershed, Imnavait Creek - an intensively studied sub-watershed of the Kuparuk, and the Oksrukuyik River watershed to the northeast of the Kuparuk (Fig. 1). Additional studies are conducted in the 1000 km^2 Anaktuvuk River Burn site 40 km NNW of Toolik Lake and various thermokarst disturbances within helicopter range of Toolik Field Station (thermokarst failures are caused by local thawing of ice-rich permafrost). These intensive sites are supplemented by occasional surveys that extend more broadly across the North Slope.

The Toolik area is underlain by spatially continuous permafrost to a depth of ~200 m, is covered with vegetation characteristic of low-latitude arctic tundra, has several tundra streams and rivers, and is dotted by both deep and shallow lakes, some of which are connected by streams and rivers and others that are isolated on the landscape. This area is typical of the northern foothills of the Brooks Range, with no trees, complete snow cover for 7 to 9 months, winter ice cover on lakes and streams, and no stream flow during the winter. Tussock tundra vegetation of sedges mixed with dwarf deciduous shrubs and low evergreens is the dominant vegetation type, but there are extensive areas of dry heath tundra on ridge tops and other well-drained sites, shrub-dominated water-tracks on hillslopes, wet-sedge meadows in flat, poorly drained areas at the base of hillslopes, and river-bottom willow thickets in riparian areas (Walker et al. 2014; http://www.uaf.edu/toolik/gis/).

The climate at the site is typical of low-arctic regions, with a mean annual air temperature of about -8.6°C and low precipitation of ~320 mm/yr, about half of which falls as snow (Cherry et al. 2014). During the summer the daily average air temperature is 7-12°C with the sun continuously above the horizon from mid-May to late July. An active soil layer above the permafrost thaws each summer to a depth from ~30 cm to 1-2 m depending on topographic position (Shaver et al. 2014).

The glacial tills that cover the hills near Toolik have three different ages, ~300,000 y, ~60,000 y, and 11,500-25,000 y (Hamilton 2003, Walker et al. 2014). These landscapes control several environmental aspects of chemistry and vegetation. For example, surface water chemistry varies with landscape age, with the oldest lakes and streams being very dilute with low amounts of inorganic ions and alkalinity (Kling et al. 2000, 2014). Soils are more acidic in the older surfaces and less acidic in the youngest surface because of differences in leaching of the carbonate-rich glacial till and longer times to build up organic acids (Walker et al. 2014). One consequence of the surface age is differences in vegetation (Walker et al. 2014); for example, there is little or no birch or sphagnum moss in the non-acidic tundra on the youngest surfaces (Gough et al. 2000).

History of Research

The North Slope of Alaska has a substantial history of ecological research (described in greater detail in our ARC site synthesis book, Hobbie and Kling 2014). Expeditions began in the First International Polar Year (1882) including establishment of a year-round observatory at Utqiaġvik (formerly called Barrow). Various natural history collections were made for the next 65 years. After World War II, a Naval Arctic Research Laboratory (NARL) was established at Utqiaġvik (1947-1980) with well-supported laboratories and dormitories, an air force of five planes, remote camps on an ice floe and on a mountain lake, and some small ships. From 1970-1973 the Tundra Biome project of the International Biological Program (IBP, terrestrial and aquatic) was housed at NARL. The overall themes of the Arctic IBP were (1) to develop a predictive understanding of the Arctic ecosystem, (2) to obtain a database for modeling and comparison, and (3) to use environmental knowledge to address problems of degradation, maintenance, and restoration of ecosystems. All the major ecosystem components such as primary producers, decomposers, herbivores, predators, climate and microclimate, and soils, were studied at an aquatic site and a terrestrial site. Process studies were emphasized, as were system budgets for C, N, and P.

The Dalton Highway opened in fall 1974, instantly creating access to a much wider array of tundra and freshwater ecosystems than were available at Utqiaġvik. Researchers were quick to take advantage of this opportunity, and Toolik Lake was chosen as a site for lakes research in June 1975. Research on nearby streams and tundra began in 1976, mostly funded by NSF-OPP and NSF-DEB. As the number and activities of these projects grew, Toolik Field Station (TFS) emerged as a logistics base managed by the University of Alaska. Throughout the 1980s several smaller projects, mostly with NSF funding, began to use TFS. One large multi-investigator project, the DOE-supported R4D project (1983-1991), worked at nearby Imnavait Creek to study landscape response to disturbance.

The Arctic LTER (ARC-LTER)

The Arctic LTER project began in 1987 with the overall goal of understanding all ecosystems that comprise the landscape around Toolik Lake from both a biogeochemical and community perspective. Our objective is to predict responses of the Arctic to climate change and disturbance by understanding the structure and function of these ecosystems and the interactions among them. The core focus throughout has been understanding the controls on response to long-term changes in the environment, but the specific focus evolves continuously, and changes with each funding cycle, as understanding about different mechanisms of ecosystem regulation grows and new opportunities are recognized. This evolution is reflected in the grant titles for our first five funding cycles:

- 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 on ecosystems 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 changes in the arctic system at catchment and landscape scales as the product of: (i) Direct effects of climate change on states, processes, and linkages of terrestrial and aquatic ecosystems, and (ii) Indirect effects of climate change on ecosystems through a changing disturbance regime

An example of a major shift in understanding and how we capitalize on new opportunities is our response to the 2007 Anaktuvuk River fire. This fire seems to be unprecedented as evidenced by the lack of charcoal in the sediments from nearby lakes going back at least 5000 years (Hu et al. 2010); fire as a new component of the North Slope environment is very likely related to climate warming. The fire made us realize that the gradual responses to climate warming upon which we had been focusing might be dwarfed by the responses to punctuated events like warming-induced wildfire or increased thermokarst activity. This new perspective is reflected in the title of ARC-LTER V. The apparently rapid recovery from the fire raised several questions that motivated our current project. Among these are: Following the 6.7 Gg N loss in the fire, where do the nutrients come from to support the rapid recovery of vegetation? Is the plant community recovery from survival of individuals, from a resistant seed bank, or from recruitment from outside the fire scar? Does the disturbance on land propagate to streams and lakes and by what mechanism? How fast do various components of the landscape recover and why? Now at the midpoint of our sixth funding cycle, our current specific focus is:

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

Biogeochemical openness relates to the dependence of a landscape element on external sources of nutrients and organic matter versus internally cycled nutrients and organic matter produced locally by photosynthesis. Community openness relates to the regulation of community structure and function through interactions with organisms in the surrounding landscape versus interactions among organisms within the same landscape element. Biogeochemical and community connectivity of the landscape relate to how readily biogeochemical and community changes at one location propagate across the landscape versus remain isolated to one location. Applications of these concepts to various components of the ARC-LTER are presented in the following sections of this report.

Much of the research of the ARC-LTER is done in collaboration with separately-funded projects that share LTER sites, experiments, data bases, facilities, and personnel. One of the key management challenges of the ARC-LTER is to create a project structure that optimizes opportunities for collaboration and synthesis among such a large and multidisciplinary group. To provide this structure we continue to organize our research into four main components, focused on (a) terrestrial ecosystems, (b) streams, (c) lakes, and (d) landscape interactions. All four components address the same *Core Organizing Question*: *How do openness and connectivity govern the response of arctic ecosystems to disturbances like: (1) climate change and deeper thaw (press) and (2) changes in the magnitude and frequency of wildfire and thermokarst activity (pulse)?*

Overview of the following sections of this document

The following sections of this document describe the Arctic LTER project results and activities in the current funding period, since 1 March 2017 (two field seasons). The initial sections provide examples of the research currently under way at Toolik Lake and at the home institutions of the collaborating P.I.s of the current ARC-LTER project. These will be discussed in greater detail and with additional examples during the ARC-LTER Site Review June 24-26. Following these examples, we provide additional information on education and outreach, project management, and information management. We end with a list of "Current Challenges", highlighting a few issues where progress is slow by our standards, or activities have changed slightly from what was originally proposed because of lessons learned after preliminary investigations. For reference, the project's research activities are summarized in several tables in an appendix at the end of this report: *Table 1*: Major field sites; *Table 2*: Core monitoring and process studies; *Table 3*: The long-term, whole-ecosystem manipulations; and *Table 4*: Current cooperating projects that make use of our long-term experiments, that use our database as both a repository and source of data, and that otherwise advance the goals of the ARC LTER.

2. TERRESTRIAL RESEARCH

The major research goal of the ***Terrestrial subgroup*** *is to develop a predictive understanding of (1) the distribution of tundra ecosystems in the landscape; (2) the controls over their structure, functioning, and biogeochemical cycles; and (3) their interactions with each other and with the local and regional environment. We focus our efforts on investigating the plant and soil communities of the common tundra types with a more recent focus on consumers both above- and below-ground. In the current proposal we focus on how the closed nature of the terrestrial system, both for biogeochemistry and the plant community, affects the response of ecosystem function to disturbance and climate change. Here we highlight findings so far from the four terrestrial questions (activities) in our LTER proposal. Additional details associated with these and other recent findings (and relevant citations) can be found in the Terrestrial section of our current LTER annual report.*

Proposal Questions:

1. *Does warming alter the biogeochemical and community openness of arctic terrestrial ecosystems?*

Finding: **Although warming accelerates the rate of nutrient release from soils, accelerated plant growth, particularly in shrubs, helps retain nutrients in the ecosystem thereby maintaining the biogeochemical closure of these ecosystems. Warming changes the relative abundance of species already in the community, favoring shrubs in particular, but does not result in the recruitment of new species, thereby maintaining the community closure of the ecosystem.**

As tundra soils warm, decomposition and nutrient cycling rates increase, promoting greater net primary productivity (NPP) of the vegetation and in many cases a shift in the plant community away from a tussock-forming sedge (*Eriophorum vaginatum*) towards dominance by deciduous shrubs. These vegetation changes have occurred in our long-term manipulations and have been documented across the arctic landscape in the past decade in response to regional warming (Shaver et al. 2014). After 13 years of experimental warming, biomass of dwarf birch (*Betula nana*) had doubled relative to control plots (Sistla et al. 2013). This shift mimics what has been identified in regions across the Arctic as "shrubbification" (Myers-Smith et al. 2011). Collaborators Michelle Mack and her postdoctoral associate Rebecca Hewitt (unpublished) have recently documented that the roots of several species, including *Betula* and *Eriophorum*, successfully follow the deeper thaw boundary that occurs in the long-term warming plots, allowing these species to access previously frozen nutrients. Recent research using stable isotopes has documented that soils under *Betula* are more "biogeochemically closed" than those under *Eriophorum* because the shrub soils have higher microbial substrate use efficiency and higher nitrogen (N) (Fig. 2; Lynch et al. 2018). These results in combination with Sistla et al. (2013)'s findings that 20

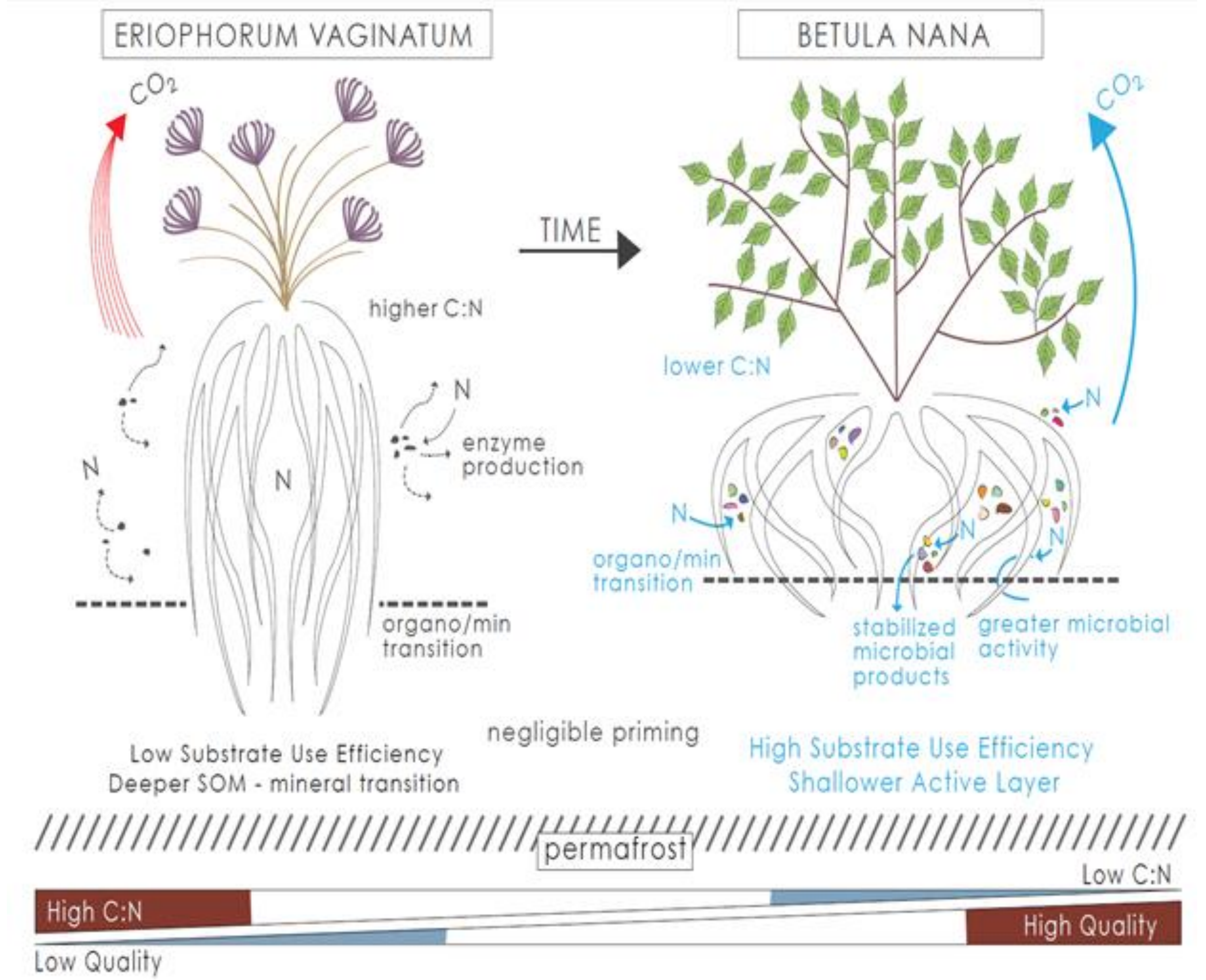

Figure 2: Results of 13C labeling experiment in moist acidic tussock tundra showing that soil microbial communities have greater substrate use efficiency under birch shrubs compared with sedge tussocks resulting in greater retention of new C inputs in shrub soils (Lynch et al. 2018).

years of experimental summer warming resulted in no net change in soil carbon or nitrogen stocks relative to control plots, suggest that terrestrial biogeochemistry might remain relatively closed in response to warming.

The warming experiment described above began in 1989; we have run out of space to sample within these plots. Therefore, as part of our current funding, in 2018 we established new, larger greenhouses in moist acidic as well as in moist non-acidic tundra. We are establishing baseline levels of plant and soil variables with plans to monitor several variables annually. To date in our longer-running experiments we have seen no evidence of plant community opening (i.e., no new species), but data suggest that the arthropod community in experimentally warmed plots is supporting several species that are rare or absent in control plots (AL Asmus unpublished). We will periodically monitor the arthropod community in the newer plots to determine the robustness of this finding and whether community openness differs between plants vs. animals. We anticipate ending the longer-running warming experiments in 2020 after which we will periodically assess plant and soil recovery from this treatment to determine if closure is maintained.

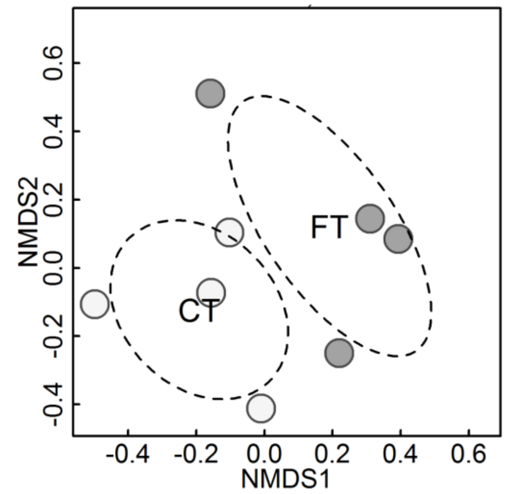

Figure 3: NMDS ordination of the arthropod community in moist acidic tundra in control plots compared to plots fertilized with N and P for 24 years shows distinct shift in community composition (Asmus et al. 2018).

***2**. Are terrestrial consumer communities open under changes in arctic climate?*

<u>Finding</u>: ***Terrestrial arthropod communities have shifted in response to long-term nutrient additions and fire, and small mammals appear to increase abundance in previously burned tundra. Thus, the animal community remains closed with respect to recruiting new species, but there are changes in both the absolute and relative abundance of species already in the community.***

Since 2010, ARC LTER collaborators have been characterizing terrestrial arthropod communities at multiple locations including in long-term nutrient addition plots and at the site of the 2007 Anaktuvuk River (AR) fire. Ph.D. students Ashley Asmus and Amanda Koltz led a study to determine how the ground- and canopy-dwelling arthropods responded to 24 years of nutrient addition. Somewhat to our surprise, we found no significant increases in arthropod community biomass or abundance overall in nutrient addition plots, but we did find a shift in the community structure (Fig. 3; Asmus et al. 2018). The shift towards *Betula* dominance does not support more arthropods, despite the greater NPP and vegetation biomass, but did promote abundance of arthropods that prefer woody plant hosts and reduced abundance of those associated with sedges.

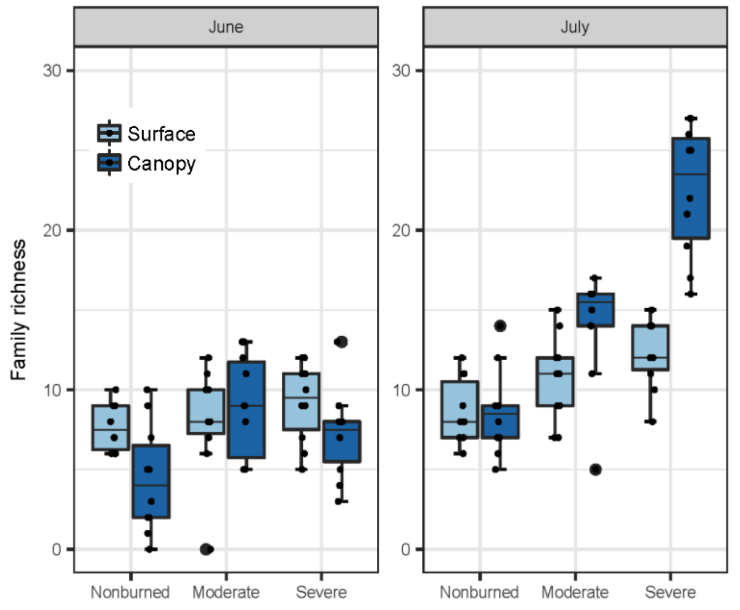

Figure 4: Canopy and ground-dwelling arthropod family richness sampled in control, moderately, and severely burned tundra six years following the fire. Family richness was significantly greater in the severely burned tundra in July suggesting the fire increased arthropod diversity (Koltz et al. *in prep*).

At the site of the AR fire, after six years the arthropod community had greater biomass and abundance and exhibited community shifts relative to moderately burned and unburned areas (Fig. 4; Koltz et al. *in prep*). These results suggest that herbivory has increased as well as detritivory, likely because of the greater soil organic matter availability and greater leaf biomass in the burned areas (Jiang et al. 2017). Intriguingly, data from small mammal trapping show a similar pattern of greater consumer abundance in the severely burned areas relative to unburned control plots over three years post-fire, although species richness was unaffected (R Rowe unpublished). These results parallel measurements of biomass and NPP (Bret-Harte et al. 2013) five years after the fire and continuing measures of GPP (Jiang et al. 2017) as part of a separately funded LTREB project and suggest that the greater nutrient input to the

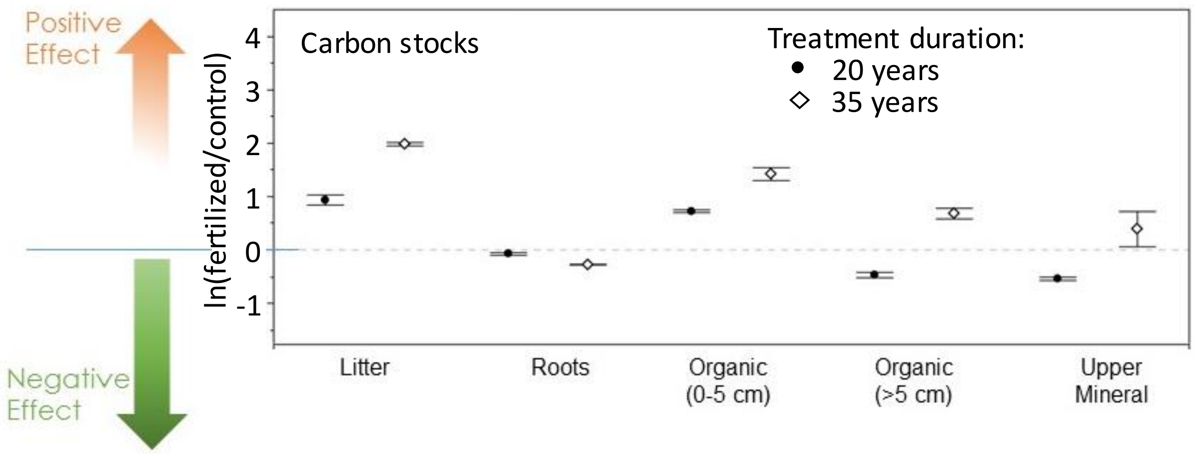

Figure 5: Effect size of carbon stock changes after 20 years (Mack et al. 2004) and 35 years (Machmuller et al. *in prep*) of nutrient addition in moist acidic tundra showing that after 20 years, soils were a net source of C but after 35 years of fertilization, this trend reversed.

plants because of the fire has allowed the support of greater numbers of herbivores, detritivores, and predators.

3. *How do terrestrial ecosystems that have nearly closed plant communities and biogeochemical cycles respond to long-term N and P fertilization, and how do they recover once fertilization stops?* *Finding*: ***In a series of long-term fertilization experiments, the relative abundance of plants shifted in favor of shrubs and a forb, and the plant community opened through the recruitment of three new species. Aboveground NPP and aboveground plant biomass increased in response to added nutrients, but this increase was compensated by a decrease in root biomass. Responses suggest an initial biogeochemical opening resulting in the loss of soil C and N stocks that later shifted to a closure after three decades and a re-accumulation of soil organic matter.***

Previous work at the ARC LTER in moist acidic tundra (MAT) has shown dramatic changes in vegetation and associated ecosystem processes when nutrient limitation is alleviated experimentally (e.g., Chapin et al. 1995, Shaver et al. 2001, Mack et al. 2004). Our longest-running experiment began in 1981 and was sampled periodically through 2015. The plant community change mimicked what has occurred in the warming experiments described above, with dominance shifting towards *Betula* and a forb, *Rubus chamaemorus*. Along with that change, a dramatic reduction in species density occurred such that by 2015, species density averaged 14 species/m^2 in control plots and only 6 species/m^2 in fertilized plots. However, the number of endemic species in the fertilized plots is lower than 6, as three plant species invaded these plots (one grass and two forbs) in the past decade. One of these forb species, fireweed (*Chamerion angustifolium*), now occurs in fertilized plots in all the plant communities in which we maintain these experiments but is not found in paired control plots. These results together suggest that greater nutrient addition supports several plant species that under ambient nutrient conditions are unable to recruit and survive as adults.

One of the benefits of long-running experiments is that we are able to document how changes occur over decadal time scales. In 2015 when we sampled the experimental plots begun in 1981, we were somewhat surprised to find that the trend of decreasing C and N stocks in fertilized plots found in a 2000 harvest (Mack et al. 2004) had reversed, such that the fertilized soils in 2015 had greater C and N stocks than controls (Fig. 5; Machmuller et al. *in prep.*). Along with this finding is one that we had noted in earlier harvests: the increase in aboveground biomass is compensated by a decrease in belowground biomass, particularly fine roots. Thus, total plant community biomass (including mosses and lichens) is unaffected by nutrient addition, even after 35 years and despite a dramatic shift in plant community composition (Shaver et al. 2014 and unpublished). These results together suggest that the soil microbial community changed over time such that the greater litter inputs in the fertilized plots are now building soil C and N stocks back up, and the soil system might be biogeochemically closing relative to the first 20 years of treatment.

We are now following the recovery of this experiment by monitoring the plant community annually and planning soil sampling every few years. This is the first terrestrial fertilization experiment of the ARC LTER to end and allows us to compare recovery trajectories with similar stream and lake experiments ended previously.

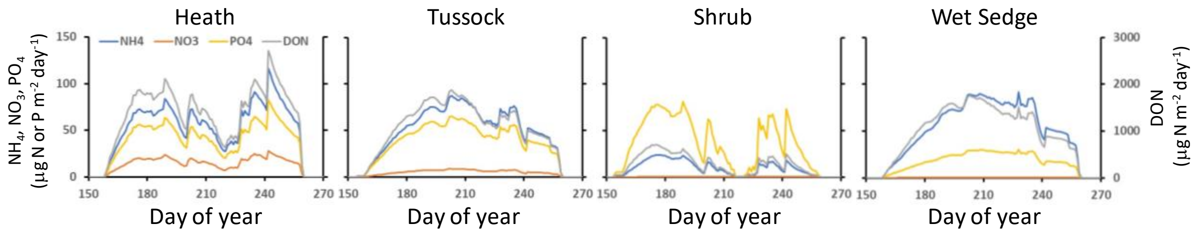

Figure 6: Differences among daily runoff rates for NH_4, NO_3, PO_4 and DON as predicted by the MEL model for the major vegetation types in the ARC LTER. Nutrient export rates are largely governed by the rate of runoff. DON losses are about 20 times the inorganic N losses. Heath has relatively high nutrient throughput (more open system) and shrubs relatively low nutrient throughput (more closed system). The deep peat soils of wet sedge with no mineral soil layer results in stronger P limitation.

4. *How do changes in plant biomass and species composition affect connectivity and losses of nutrients and C to aquatic systems?*
Finding: ***Initial modeling results suggest differences in nutrient loss from landscapes dominated by the four major vegetation types we study.***

In the proposal we discussed the terrestrial group quantifying the plant community and biomass in the areas being intensively studied by the streams, lakes, and landscape interactions groups. Before undertaking this effort, we have generated modeled nutrient loss from the four plant communities we intensively study: dry heath, moist acidic tussock, shrub, and wet sedge (Fig. 6; Rastetter *unpublished*). These results suggest that nutrient loss differs substantially across these communities but that much of this is caused by differences in soil physical structure and hydrological processes (also see Neilson et al. 2018). Given the position of the aquatic research sites in the landscape, we are in the process of determining if additional field measurements are warranted or if the correlations we describe here are sufficient to understanding how the plant community is connected to these aquatic ecosystems.

3. LANDSCAPE INTERACTIONS RESEARCH

Research by the ***Landscape Interactions subgroup*** *focuses on how inputs of materials and species from upland or upstream systems affect downstream ecosystem structure and function. In the current proposal we focus on how system openness and connectivity interact to shape the response of ecosystem function to disturbance, mainly the "pulse" disturbance of rapid thermokarst slumping and the "press" disturbance of climate change. Here we highlight findings so far from the four "land-water" questions (activities) in our LTER proposal.*

Proposal Questions:

1. *How do openness and connectivity influence pulse vs. press disturbances?*
Finding: ***Longer-term press disturbances** (e.g., climate change) **increase land-water connectivity, and the impacts depend on the inherent "system limitations", while short-term pulse disturbances** (e.g., thermokarst failures) **rapidly amplify land-water connectivity but recovery time is relatively short.***

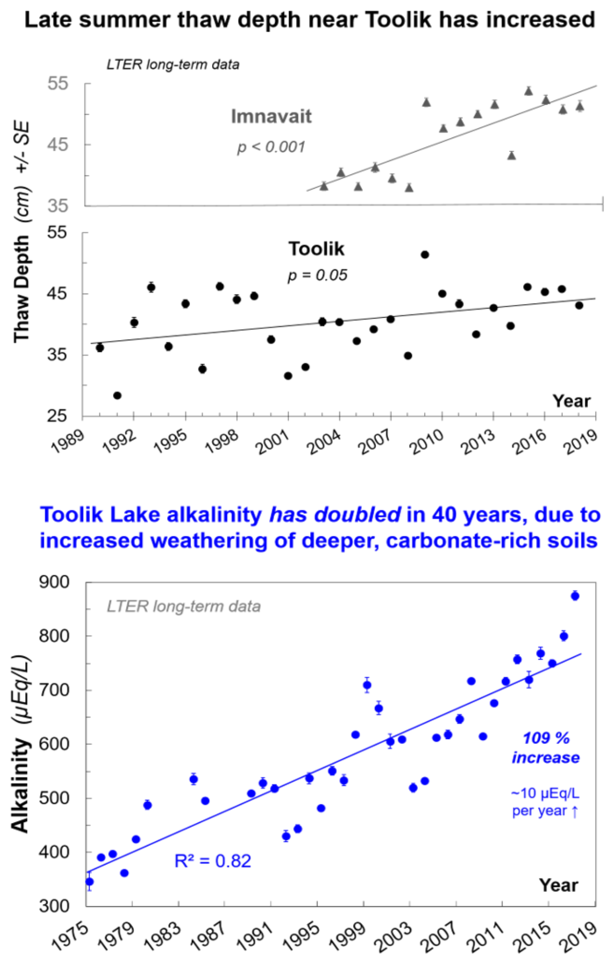

Figure 7: Increases in thaw depth in catchments near Toolik (top) and in alkalinity in Toolik Lake (bottom).

Long-term LTER data now reveal a significant increase in summer thaw depth at Toolik and Imnavait Creek, and an associated dramatic doubling of the carbonate alkalinity in Toolik Lake (Fig. 7). We have evidence that these changes are due to climate warming (Hobbie et al. 2017, Romanovsky et al. 2010), and deeper thaw allows for greater weathering of carbonate-rich rocks in the catchment (Keller et al. 2010, Kling et al. 2014). Clearly this land-water system has high biogeochemical connectivity, and the openness of the aquatic systems make them vulnerable to change. However, the impact of this press disturbance varies depending on the inherent properties of the system. For example, in the very dilute Lake E5, the low alkalinity is just at the limit where molluscs can form shells. Over the last 20 years, however, alkalinity has increased by ~30%, which has removed this limitation and made mollusc populations more likely. Thus, strengthening of the land-water connection with carbonate is poised to impact not only lake chemistry but also the lake food web.

In contrast to this slow deepening of thaw and increased weathering, in permafrost terrain climate warming can also lead to rapid, pulse disturbances when ice-rich soils thaw and destabilize, causing a landslide generically called a 'thermokarst failure'. Thermokarst failures can rapidly transfer terrestrial materials to surface waters (e.g., Bowden et al. 2008, Cory et al. 2013), although LTER monitoring of the thermokarst-impacted Lake NE14 shows that while C and N export from the lake increased 4-fold by the thermokarst, the lake recovered within 3-5 years.

2. *What controls the openness and connectivity of dissolved organic matter flows from land to water?*
Finding: ***Exchanges between overland flow and groundwater control DOM export from land, and the processes affecting land-water connectivity change at different scales.***

Last year we completed an analysis of how openness and connectivity of DOM export from land are controlled (Neilson et al. 2018) and found that different processes are important at different watershed scales. At the scale of a small headwater stream (Imnavait Creek), the groundwater and stream water DOC concentrations are very similar, even across six orders of magnitude of discharge (Fig. 8 *top*). This relative "chemostasis" regardless of discharge is surprising, because during large rainstorms one expects

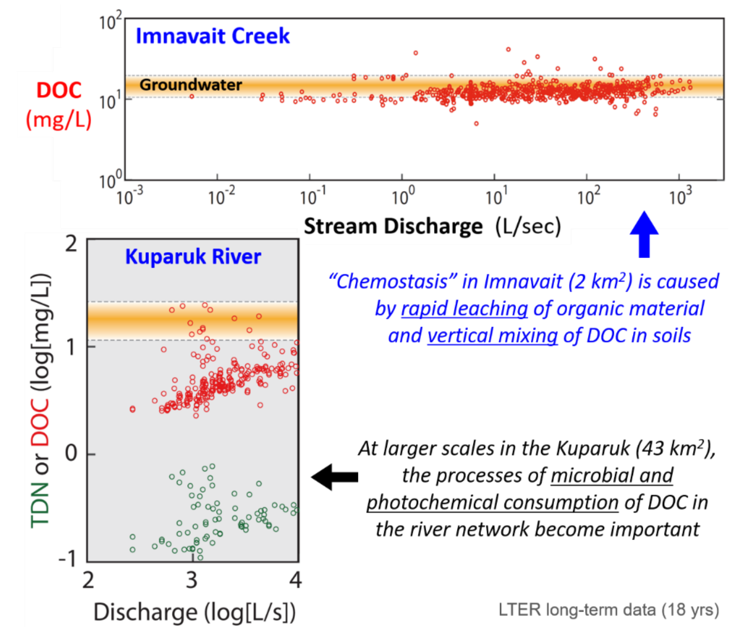

Figure 8: DOC concentrations as a function of discharge in Imnavait Creek (top) and in the Kuparuk River (bottom left).

overland flow carrying the low-DOC character of rainwater to reach the stream. Instead, consistently high DOC concentrations in the stream are likely caused by two processes: first is the rapid leaching of the upper organic mat with rainwater (e.g., Judd and Kling 2002), and second is the consistent and rapid exchange of water from above the land surface with water deeper in the soils that has higher DOC. Hydrologic models show that microtopography on the land surface, caused by vegetation mounds and hollows, creates pressure differentials that drive water into the soil (like bedform-driven hyporheic flow in stream sediments) and thus causes the rapid exchange of overland flow with shallow groundwater. In other words, the water "porpoises" from just above to just below the land surface and back again as it moves downslope. Combined with rapid soil leaching of DOC, this provides a mechanistic explanation of long-term data showing high concentrations of DOC in soils and streams during high flow conditions for both spring snowmelt and summer storms (Neilson et al. 2018). It is also clear that the controls on DOC are quite different than those on inorganic alkalinity and cations. For example, while we see a long-term "press" influence on alkalinity (Fig. 7 *bottom*), there may be strong interannual responses with DOC that are driven by hydrology.

We next tested the importance of these controls on DOC concentrations at a larger scale (4th-order Kuparuk River, adjacent to Imnavait Creek). At this larger scale the pattern of DOC concentrations in soils and surface waters was quite different (Fig. 8, *lower left*). Here, the river water DOC values were consistently lower than the groundwater (soil water) values across a broad range of discharge. We believe that the same mechanisms of rapid leaching of organic mat soils and rapid surface-subsurface porpoising of water moving downslope are occurring in the Kuparuk, but the scale of the river network allows for other processes to overwhelm the relationship observed at Imnavait. This overprint occurs during the longer travel times of water in the Kuparuk and is caused by (1) microbial respiration of DOC to CO_2, and (2) photochemical oxidation of DOC to CO_2. Our

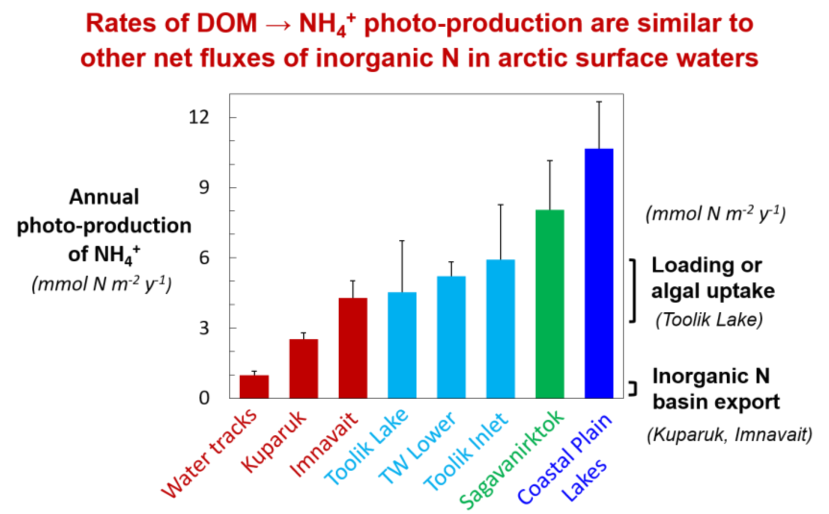

Figure 9: Rates of photochemical conversion of DON to NH_4 in streams, rivers, and lakes near Toolik and further north on the Alaskan coastal plain.

calculations indicate that these two processes reduce the starting groundwater DOC concentrations to values observed further downstream in the mainstem of the Kuparuk (see also Cory et al. 2014, 2015, Neilson et al. 2018). Understanding how "open" these terrestrial systems are to the export of C (and N) from land to water, and what controls the degree of openness, is a first step in predicting how element export might change as thaw depth increases in a warmer climate.

***3.** Do photochemical processes increase land-to-water connectivity?*

<u>Finding</u>: ***The photochemical production of NH_4^+ from DOM strengthens land-water connectivity and could be a substantial source of inorganic N in surface waters.***

Exposing DOM to UV light can produce NH_4^+ (photo-ammonification; Bushaw et al. 1996), which can contribute substantially to the inorganic N required by microbes and algae in surface waters (Smith & Benner 2005, Vähätalo & Zepp 2005). In contrast to the relatively open C cycles in arctic ecosystems, plants and microbes on land are extremely N limited (Shaver et al. 2014), resulting in a closed N cycle, very low connectedness and inorganic N loss, and even N limitation in surface waters, especially in lakes. Yet the dissolved organic nitrogen (DON) concentrations in soils and surface waters are relatively high (Hobbie & Kling 2014), creating the opportunity for photo-ammonification to 'open' the N cycle and help alleviate N-limitation in aquatic ecosystems. Our data so far show that photo-ammonification can produce as much inorganic N as (1) is exported each year from the Kuparuk or Imnavait basins, or (2) is input to Toolik Lake or taken up by algae in Toolik Lake each year (Fig. 9). Our next step will be to better understand the turnover time of photo-labile DON in these systems, and to learn how the general controls on DOM export (question #2 above) affect the rates of photo-ammonification and thus the land-water N connectivity.

***4.** Does disturbance affect the connectivity and transport of microbes from land to streams, and how does changing connectivity influence the genomic and functional potential of the microbial community?*

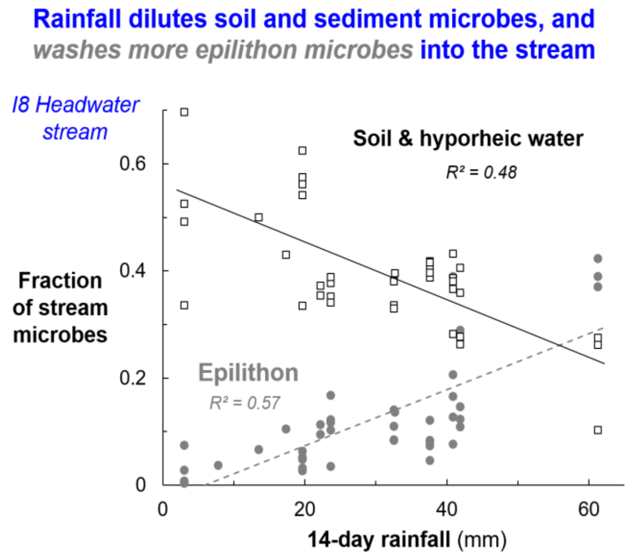

Figure 10: Fraction of microbes in stream water originating in terrestrial soil or stream hyporheic water, or in stream epilithon, as a function of rainfall during the previous 2-week period (i.e., storm events).

<u>Finding</u>: ***The connectivity of microbes from land to surface waters varies with short-term disturbances** (e.g., storm events)**.***

In studying the 'Inlet Series' of streams and lakes feeding Toolik Lake, we showed that landscape-level connections among terrestrial, stream, and lake ecosystems affect patterns of biology among sites (Crump et al. 2007), and we found that downslope transport and inoculation of soil bacteria strongly influence stream and lake microbial community composition (Crump et al. 2012, Adams et al. 2014, 2015). In other words, there is surprising openness of the microbial community and high "community connectivity" moving downslope across the landscape, and the genomics of microbes indicate that many common bacteria and Archaea species (OTUs) found in Toolik Lake were initially observed in upland soils and small headwater streams (Crump et al. 2012). These results suggest that terrestrial environments serve as critical reservoirs of microbial diversity, and that the patterns of diversity in surface waters are structured by initial connectivity and inoculation from upslope habitats.

In this new grant, our analyses show that disturbance in the form of rain events has predictable impacts on what community of microbes dominates the stream water column (Fig. 10). For example, when rainfall and stream levels are low, the highest fraction of microbes in the stream water are those transported from soils or stream sediments. As rainfall increases, the microbes from these sources appear to be diluted, and instead microbial species associated with the epilithon in the stream increase in importance (Fig. 10). This increase in epilithon-associated microbial species might be due to greater turbulence from stronger rainstorms and disturbance. In the second half of the new grant we will analyze genomic and transcriptomic data to determine how this disturbance-altered connectivity affects the genomic and functional potential of the stream microbial community.

4. STREAMS RESEARCH

The major research goal of the ***Streams subgroup*** *is to understand how the structure and function of stream ecosystems are being altered by presses and pulses associated with climate change in the Arctic. While surface air temperature has apparently not changed much in the Toolik region, there are other indicators of climate change that affect streams directly. Among these indicators are warming permafrost that increases the likelihood of thermokarst formation and alteration of flowpaths to streams, as well as an increase in the frequency and duration of droughts that might affect the viability of arctic grayling populations, the primary fish species in these rivers. We are studying these dynamics through a combination of long-term monitoring, manipulative experiments, and collaboration with other projects that are addressing fundamental stream processes in the Arctic.*

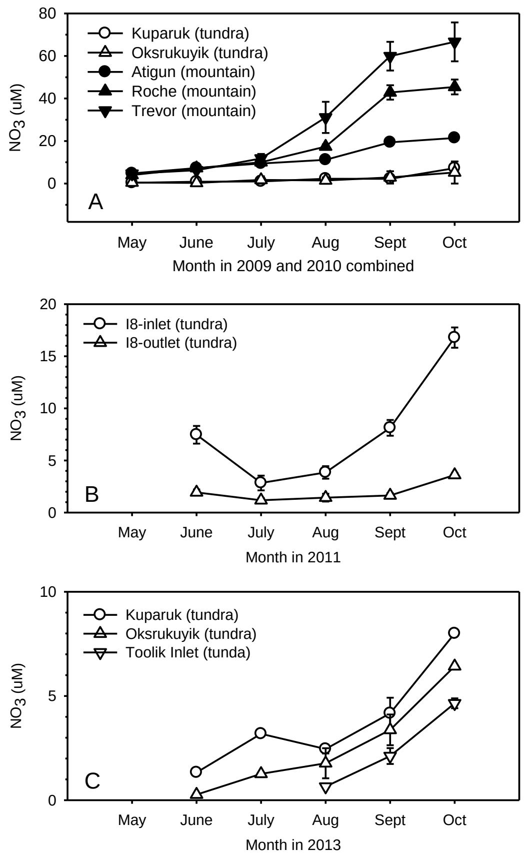

Figure 11: Pattern of nitrate concentrations in the late season for five different watersheds over four different years. Bowden, unpublished data from Arctic LTER database.

Proposal questions

1*. Does the mass flux of nutrients (notably nitrogen) increase during the early autumn season?* *Finding***: *Despite large increases in concentration, notably of nitrate, a rapid decline in discharge decreases the mass flux of nutrients from arctic streams and rivers.***

Beginning in 2013, we altered our stream monitoring to extend longer into the fall season and expanded spatially to include mountain watersheds in the nearby Brooks Range. We were prompted to make these changes by two factors. First, we realized that our historic monitoring program – which was purposefully focused on the period from mid-June to late-August during which the dominant fish (arctic grayling) are present in the river – did not include the fall season. This season is important because streams and rivers continue to flow well into late September and early October and might flow even longer as the

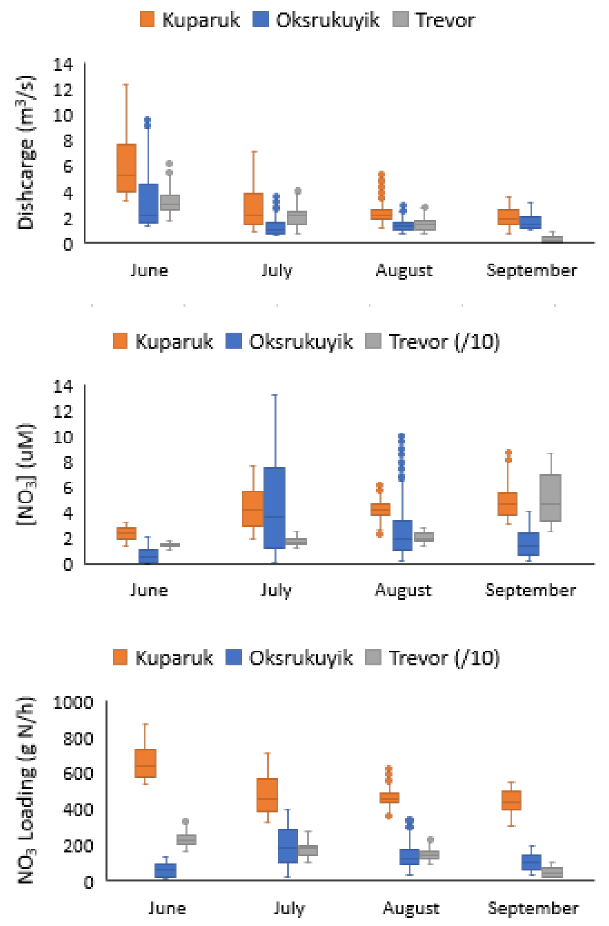

Figure 12: Seasonal patterns of discharge (top), nitrate concentration (middle), and nitrate load in the Kuparuk River, Oksrukuyik Creek, and Trevor Creek in 2016. The data have been binned by month. Note the concentration and load of nitrate in Trevor Creek, the mountain watershed, have been divided by 10. Bowden, unpublished data from Arctic LTER database.

Arctic continues to warm. Second, we had some indications that nutrient concentrations might increase in the fall, after terrestrial demand for nutrients had ceased, but soil microbes could still actively mineralize soil organic matter (Fig. 11). Evidence from another contemporary project corroborated our findings (Khosh et al. 2017). However, at that time we did not have adequate discharge data late into the season that could be used to address whether the total mass flux of solutes increased in the fall. We hypothesized at least four mechanisms that might support such an increase and added late-season discharge and nutrient chemistry to provide a quantitative context. We concluded from this effort that nitrate concentrations in most years and for most watersheds almost always increase late in the season. Notably, nitrate concentrations increase significantly in streams draining mountain watersheds, consistent with the findings of Harms et al. (2016). The evidence is weaker that other important solutes, like ammonium or soluble reactive phosphate, also increase. We have previously demonstrated that these streams are phosphorus limited (Peterson et al. 1985, 1993, Hershey et al. 1997, Slavik et al. 2004) and in general ammonium is preferred over nitrate for uptake by epilithic algae. Consequently, we expect that nitrate might behave more conservatively in these systems than SRP or ammonium. Our new efforts show that in all watersheds we have studied, the decrease in discharge that occurs as watersheds and streams begin to freeze up in the fall is greater than the observed increase in concentration so that the total mass flux is controlled by discharge and generally decreases over time (Fig. 12). These new data also show that in any season and every watershed we have studied, nitrate concentrations decrease (dilute) as discharge increases. This pattern suggests that delivery of nitrate to these arctic streams is source limited (sensu Zarnetske et al. 2018). However, our data also suggest that the source is not rapidly exhaustible and that the concentration-discharge relationship sometimes elevates in the fall. While it seems clear that nitrification is the ultimate source of this nitrate, it is less clear where in the landscape nitrate is produced (Wollheim et al. 2001, Snyder and Bowden 2014, Harms et al. 2016). An important part of our research is to better understand whether future climate change will significantly increase nitrate production and transport to downstream and coastal systems.

***2.** Do arctic grayling provide an important nutrient or energy subsidy to piscivorous fish in larger arctic lakes?*
Finding: ***This initiative is ongoing.***

We are working with the Lakes group to monitor a set of connected lake-stream systems in the Oksrukuyik watershed including the Fog lakes to better understand the importance of grayling from streams to the survival of Lake trout and char. We have worked in these watersheds for many years and developed a considerable body of knowledge about the hydrology, biogeochemistry, and productivity of the streams. We have maintained radio tag reader antennae on the Kuparuk River (3 sites) and Oksrukuyik Creek (4 sites) to track movement of tagged arctic grayling throughout the summer and have deployed and retrieved temperature loggers in the Kuparuk, Oksrukuyik, and I-minus watersheds to help predict timing of arctic grayling migration and to detect flow intermittency.

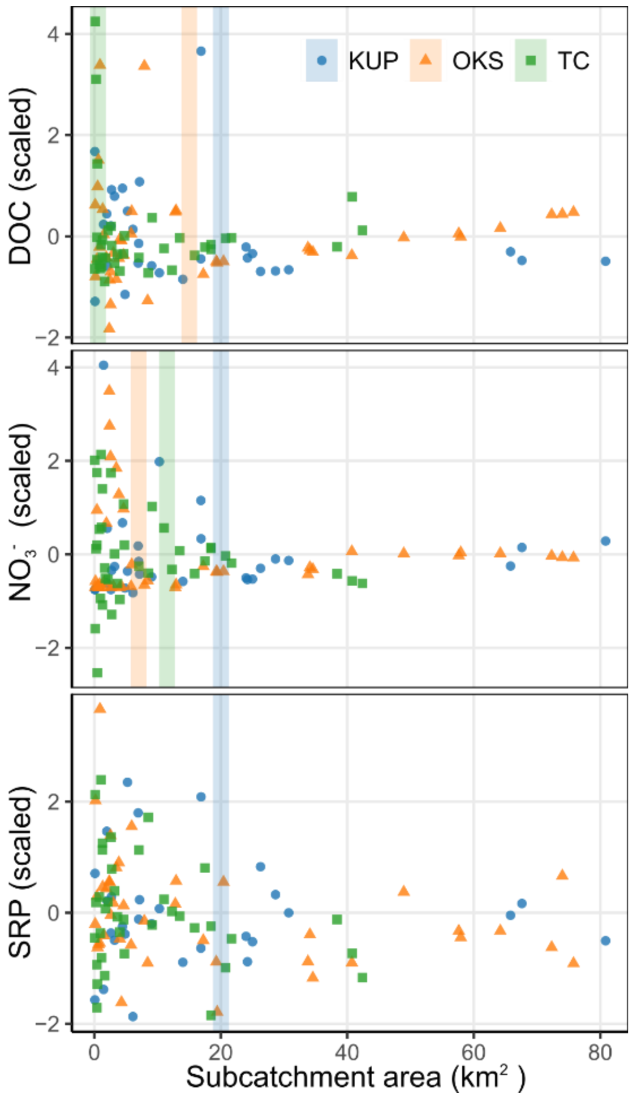

Figure 13: A. Flow-weighted concentrations of DOC, nitrate, and SRP showing variance collapse thresholds across Kuparuk (KUP, blue symbols), Oksrukuyik (OKS, orange symbols), Trevor (TC, green symbols) catchments. The vertical colored bands represent statistical changes in spatial variance among subcatchments based on change point analysis implemented for each catchment separately.

***3.** How do geospatial characteristics interact with river network connectivity to influence biogeochemical and community dynamics in arctic rivers?*
Finding: ***Relatively fine-scale landscape patches drive solute generation in this region of the Arctic, at scales much smaller than the capability of current earth system models.***
(Findings for "community connectivity" will be addressed in the next section.)

This research initiative has been facilitated through a collaboration with Drs. Ben Abbott (Brigham Young University), Jay Zarnetske (Michigan State University), and Arial Shogren (Michigan State University) and has generated two new proposals that are currently under consideration (at NSF and DOE). Dissolved organic carbon (DOC), nutrients, and other solute concentrations are increasing in rivers across the Arctic. These increases are widely attributed to permafrost degradation, either as the press of diffuse active layer thickening or the pulse of relatively discrete thermokarst formation. However, it is unknown whether they stem from enhanced solute sources or diminished solute sinks, which hinders our ability to predict how climate change will alter energy and nutrient availability in terrestrial and aquatic ecosystems. To address these unknowns, we are combining high-frequency water flow and chemistry sensors at catchment outlets with periodic, spatially-extensive sampling through upstream subcatchments to examine how river network connectivity to the land and instream processing (openness) influence the spatial and temporal distribution of key solutes like nitrate and DOC. We are using a new ecohydrological framework (Abbott et al. 2018) to reveal the spatial structure of solute sources and sinks, based on these data. Over the last three years we have synoptically sampled dissolved organic carbon and nutrient chemistry in ~125 subcatchments in three distinct LTER catchments: Trevor Creek (mountain), Oksrukuyik Creek (tundra, lake dominated), and the Kuparuk River (tundra, stream dominated). Subcatchments ranged from 0.1 to 80 km^2. To date, our results show that variance in solute concentrations among subcatchments collapses at spatial scales between 1 to 20 km^2 (Fig. 13), indicating a continuum of diffuse- and point-source dynamics. Across seasons (early to late thaw season), the role of catchment characteristics (e.g., topography, vegetation, surficial geology) interact with biogeochemical processes (e.g., decomposition, nitrification) to create the observed spatial and temporal patterns. For DOC the dominant source-sink function of subcatchments is similar across seasons in all three watersheds and relatively stable for the Kuparuk and Trevor Creek catchments (higher r_s), but relatively inconsistent for the Oksrukuyik catchment (lower r_s). For nitrate, the spatial source-sink function of subcatchments in all three watersheds is somewhat inconsistent, indicating that biogeochemical processing changes differently over the season for different subcatchments within these catchments. There are also major changes in the concentrations of nitrate in the Kuparuk and Trevor Creek watersheds, as noted above. In all watersheds, there is strong in-stream retention of phosphorus (data not shown). Overall, the synoptic sampling approach that we are trialing is showing promise as a means to quantify change detection and identify ecohydrological mechanisms in these Arctic catchments and should have general utility in other regions.

To complement the periodic, spatially intensive synoptic sampling describe above, we have installed high-frequency (every 15 minutes) monitoring of water level, DOC, nitrate, turbidity, and conductivity at three catchment outlets (Kuparuk, Oksrukuyik, Trevor Creek). We are using this information to examine how hysteretic responses to storm pulses change as thaw depth increases over the season. Preliminary high-frequency data from the Kuparuk demonstrate that DOM flux from upland tundra fundamentally shifts from source-limited (dilutes with flow) to transport-limited (increases with flow) as the thaw season progresses (Fig. 14). Collectively, these new initiatives provide a means for us to visualize how connectedness to the land and instream processing (degree of openness) interact to determine the distribution of key solutes in these river networks. Our future efforts will begin to link specific land characteristics (e.g.,

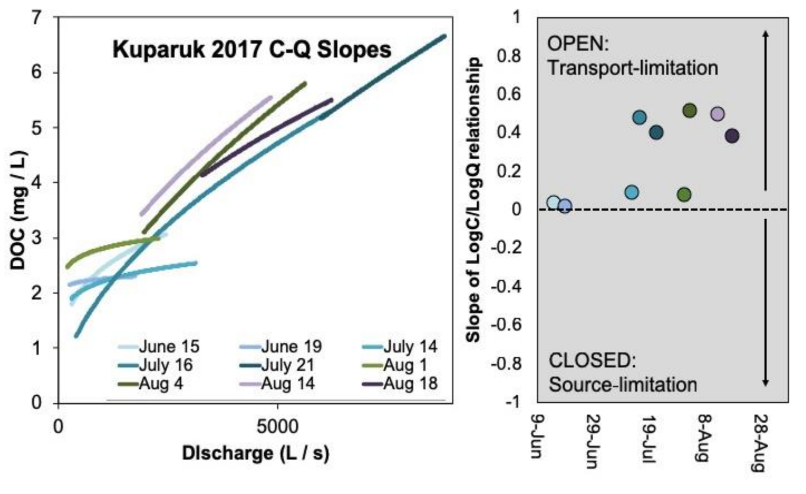

Figure 14: Left panel: Concentration-Discharge (C-Q) relationships for dissolved organic carbon (DOC) across the 2017 summer season in the Kuparuk River derived from a high-frequency (15 minute) optical sensor. Right Panel: Slope of the C-Q relationships, indicating a shift from chemostatic (low slope) to transport-limited (high slope) behavior across the thaw season. The differently colored filled circles in the right panel correspond to the differently colored lines (dates) in the left panel.

topography, vegetation, soils) and processes (e.g., nitrification) to these patterns in space and time.

***4**. Does the genetic composition of fish communities change over time in response to changes in connectivity among aquatic ecosystems?*
Findings: ***Spatially isolated populations of arctic grayling have developed genetically distinct characteristics that could be altered further by future climate change.***

The main goal of this research is an outgrowth of historic research and continuing monitoring supported by the Arctic LTER. The initiative has been facilitated through a collaboration with a previous NSF-funded project led by Drs. Linda Deegan (Woods Hole Research Institute), Mark Urban (University of Connecticut), Heidi Golden (University of Connecticut), and Cameron MacKenzie (formerly Marine Biological Laboratory). The Arctic LTER provided important support to maintain field equipment (PIT tag antennas and readers) and assist with field sampling, and now continues to maintain these antenna installations to maintain the long-term record of fish movement in the Kuparuk and Oksrukuyik watersheds.

We hypothesize in the current proposal that climate-induced changes in the connectivity among aquatic systems will likely change the flow of genetic information, isolating some populations and mixing others. How altered hydrological connectivity changes biodiversity is an important question that will take a long time and considerable effort to address. As a potential approach to address this question, we proposed to test the feasibility of using environmental DNA (eDNA) analyses (Thomsen et al. 2012, Rees et al. 2014, Klobucar et al. 2017, Rodgers et al. 2017) to assess current and future community composition of lakes and streams. With eDNA, we might be able to determine species presence/absence for comparison to our benchmarked lakes with less effort and with better detection of rare species for which we have primers (Biggs et al. 2015, Evans et al. 2016, Kelly 2016). To accomplish this objective, we developed a collaboration with Drs. Meredith Bartron and Aaron Malloy at the Fish Technology Center of the U.S. Fish and Wildlife Service's Northeast Fisheries Center, in Lamar, Pennsylvania. The results from our first full season of eDNA sampling show promise for using this emerging technique to detect seasonal changes in fish abundance. Seasonal migration of arctic grayling has been well-studied in the Kuparuk River; therefore, it provides a unique opportunity to test the efficacy of eDNA sampling against known migration patterns. We repeatedly sampled the Kuparuk River as well as the outlet of its major headwater lake (Green Cabin Lake) – where arctic grayling overwinter – from late May through mid-September in 2017, capturing most of the expected migration period. Detections of arctic grayling eDNA were highest in Green Cabin Lake in May, when fish were staged for outmigration, then dropped off until the fish started to return in early September (data not shown). Similarly, eDNA detections at the downstream site peaked in May and again in late August, presumably during migration from and to Green Cabin Lake. These data should be interpreted with caution, as many additional factors influence eDNA detection in lotic systems (e.g., discharge, temperature, UV radiation, fish behavior and metabolism). However, these initial results are promising.

5. LAKES RESEARCH:

*Research by the **Lakes subgroup focuses on** (1) climate controls on lake states, processes, and linkages to land; (2) how these connections are altered by disturbance; and (3) how climate and disturbance interact to control biogeochemistry and associated productivity and food web dynamics. We combine long-term monitoring at Toolik and many other sentinel and experimental lakes, laboratory experiments, and systems modeling to understand how system openness and landscape connectivity interact to shape the response of arctic lakes to climate change and disturbance.*

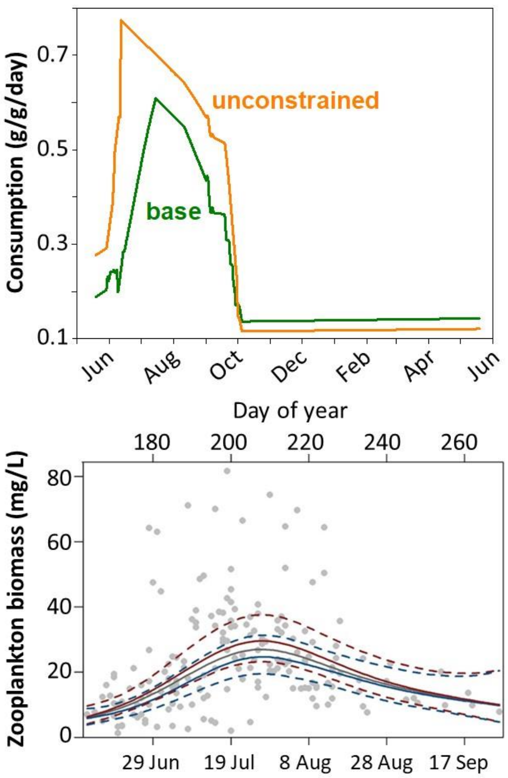

Figure 15: Top. Predicted consumptive demand of adult char under current climate (green) and 5^{o}C warming (orange) over a year. Bottom. Generalized mixed effects additive model ($R^2 = 0.25$, edf = 3.64) of zooplankton biomass in Toolik Lake for a warm (red) and cold year (blue) as a function of day of year ($p < 0.001$) and lake temperature at 3 m ($p = 0.19$) with random effect of sample year. Dashed lines are ± 2se. Gray points are all observed zooplankton biomass from 1987 – 2015 (n = 175).

Proposal Questions:

1. *How will climate change affect metabolic demand and thus the flow of energy through the trophic web to fishes?*

Finding: ***Long-term data and metabolic models indicate fish consumptive demand increases 28-34% under expected warming but observed zooplankton biomass is 19% higher in warm years, indicating a warmer climate might support the increased consumptive demand of fish.***

Using empirical vital rates, population structure, abundance and trend, we predicted the effects of climate change on arctic char (*Salvelinus alpinus*; Budy and Luecke 2014). Climate change resulted in temperatures closer to optimal for char growth (15 °C) and a longer growing season. In the absence of food limitation, an increase in consumption rates (28–34 %) under warming (Fig. 15) leads to faster growth rates (23–34 %). Faster growth predicted under warming resulted in a greater amplitude of cycles in population structure as well as an increase in reproductive output and decrease in generation time. Collectively, these results indicate arctic char are sensitive to changes in the number of ice-free days. More frequent long growing seasons should elevate growth rates of small char, acting like a "resource pulse" and allowing a subset of small char to "break through" the size barrier to become piscivorous, thus setting the cycle in population structure.

Will there be adequate fish food to meet these elevated consumptive demands in a warmer climate? We used a multi-faceted approach to address prey availability to predators in these lakes under changing climate (Klobucar et al. 2018, Zarnetske et al. *in prep*). In arctic lakes, changes in seasonality associated with warming (e.g., temperature, growing season duration) might alter invertebrate prey biomass through influences on physiology and phenology. In a laboratory mesocosm experiment, we measured the response of zooplankton (*Daphnia middendorffiana*) and other invertebrates across three time periods (seasons: early, mid, and late season), and across three temperature and photoperiod treatments (control, increased temperature, increased temperature*photoperiod). In mid-season, we observed significantly increased *Daphnia* abundances, while in the late season, *Daphnia* appeared to be limited by photoperiod. We analyzed long-term variation in zooplankton biomass across years (1983-2015) to see how biomass varied with temperature. These data suggest zooplankton biomass increases nearly 20% in warmer years; however, these estimates could be conservative because of increased consumptive demand by fishes (Fig. 15). The interaction of food and temperature is being further explored as part of our collaborative lake warming project (Barrett and Budy, *in prep*).

2. How will lakes recover from pulse disturbance and does the degree of openness impact recovery trajectories?

<u>Finding (2A):</u> ***We observed significant, albeit lagged (3 apparent thresholds), increases in primary production and fish abundance after low level nutrient input along with concordant decreases in dissolved oxygen. However, post disturbance, lake recovery in a closed lake appears rapid at lower trophic levels and for many physiochemical factors; recovery of higher trophic levels takes more time.***

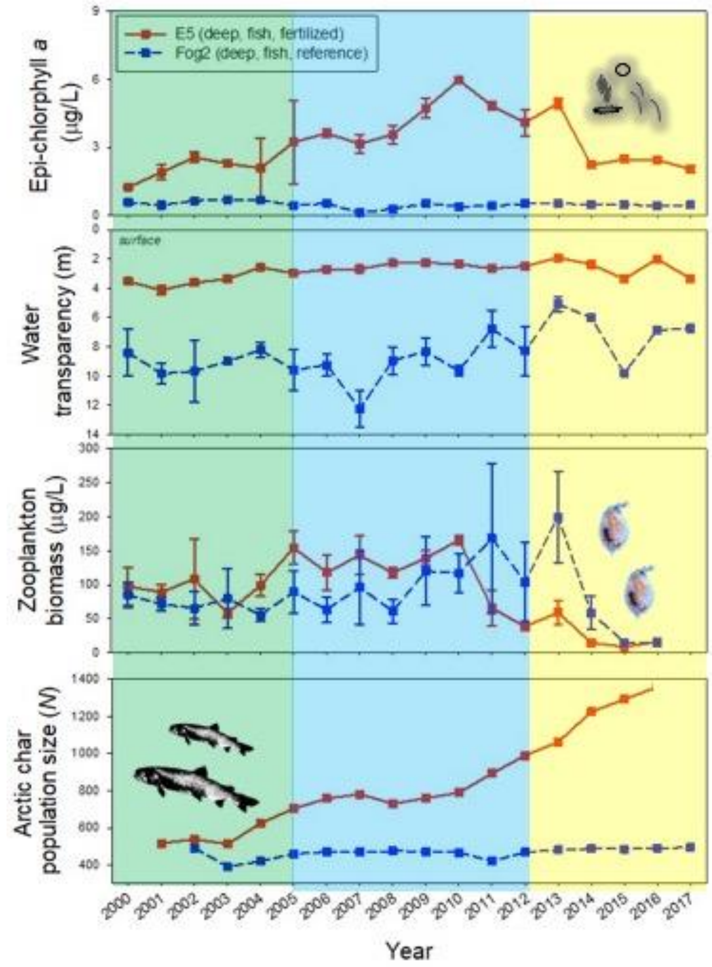

Figure 16: Epilimnetic chlorophyll a, water transparency (Secchi depth), zooplankton biomass, and arctic char abundance over the duration of the study (2001-2013) in deep lakes with fish. The shaded panels illustrate ~ 3 different phases of the response including recovery in yellow.

Following previous, short term high-level lake fertilization experiments, we mimicked natural disturbance and fertilized two paired deep lakes with fish and two paired shallow lakes without fish (not shown here) at low nutrient levels for 12 years and monitored the food web and physiochemical changes in fish (Budy et al. *in review*). Fertilization significantly increased pelagic primary production (chl *a*) 4-fold in the deep lakes, phytoplankton biovolume increased, water transparency declined, and we observed a significant and cumulative decrease in hypolimnetic oxygen in mid-summer (e.g., Fig. 16). Pelagic secondary production responded significantly to the increase in primary production, but not until chl *a* values had doubled by the 5th year of the study, and arctic char increased significantly with the increase in food availability (zooplankton); however, fish response was also lagged. Abundance of char increased 60% by the 5th year of the study, then remained stable, increasing again in the 10th year of the study to a final abundance 120% greater relative to either the reference lake or the beginning of the experiment. The zooplankton population then crashed, presumably because of intense predation pressure. In the recovery stage of this experiment after fertilization was terminated, chl *a* and oxygen concentrations returned to near pre-fertilization conditions in ~4-5 years; however, zooplankton biomass remained at extremely low levels, and the fish population, composed largely of high densities of small adults in poor condition, has also begun to collapse.

Finding (2B): ***Open lakes can act as landscape attenuators of disturbance and change the nature of the material exported downstream.***

Monitoring of an older thermokarst slump (Lake NE14; Kling et al. in prep) indicated the lake acted as a landscape attenuator of the C and N released from the thermokarst disturbance, although C and N export from the catchment still increased. The character of the exported C was likely changed because of interactions with mineral sediments released into the lake, export of C and N downstream was above background levels, and in-lake benthic metabolism was stimulated.

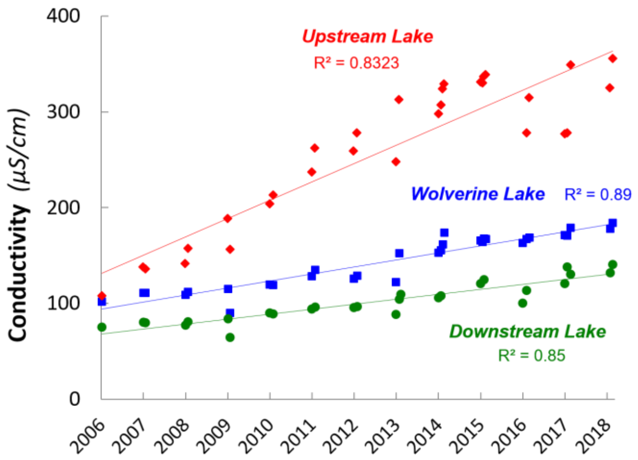

Figure 17: Conductivity increase in three lakes connected in series by streams. The upstream lake is a headwater lake. Wolverine Lake receives the outflow from the headwater lake, has an intermittently active thermokarst slump, and delivers water to the downstream lake.

We took advantage of a recent thermokarst slump in the Wolverine Lake area to examine connectedness of lakes to land and to each other. In the headwater lake, which has a high watershed-to-lake-area ratio, we observed a strong linear increase in conductivity over time (Fig. 17 *upstream lake*). This increase is presumably due to permafrost thawing and the subsequent release of ions from previously frozen soil. In the next lake downstream, Wolverine Lake, there was also an increase in conductivity because it receives outflow from the headwater lake. However, in Wolverine Lake the conductivity increase was muted because of dilution associated with its large size. Although the thermokarst slump had a clear effect on the turbidity of Wolverine Lake, the effect on conductivity is not clear. We have observed that this thermokarst slump is variably active over time, and even when active it does not appear to alter substantially the steady increase in conductivity delivered from the upstream lake. Conductivity increases in the most downstream lake were also consistent over time, but even more muted (Fig. 17). This pattern suggests that the dominant response to warming is due to a regional increase in soil-water conductivity from deepening thaw, which is especially affecting the headwater lakes, and that the connectivity between thaw on land and its impact on lakes is strong, as is the lake-to-lake connectivity moving downstream (see also section above on Landscape Interactions).

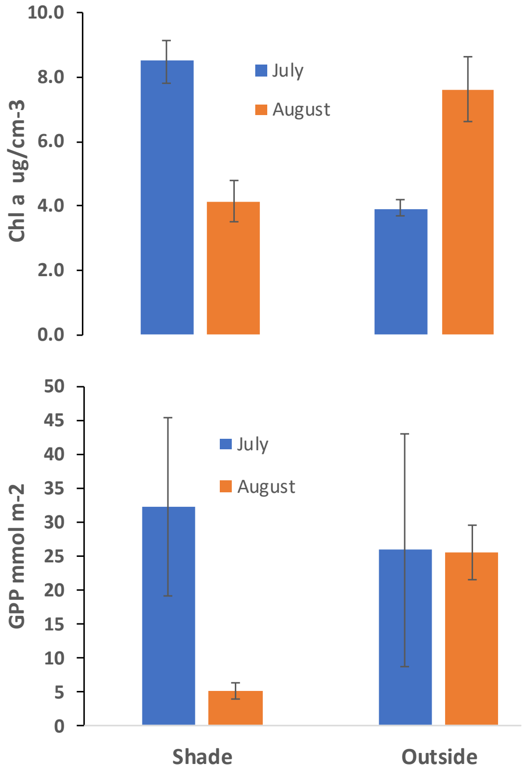

Figure 18: After 3 weeks of shading (July), chlorophyll concentrations were higher in the shade plots but there was little change between shaded and unshaded sediments in GPP$_{max}$.

3. *How will the relative openness of lakes determine the biogeochemical and community response to climate change and disturbance?*

Finding: **Benthic algae respond to low light by increasing chlorophyll concentrations and can rebound to previous levels of production when light is restored for short periods of time, but if shading lasts through the season, benthic chlorophyll and gross primary production decrease dramatically.**

Light reaching the benthos in lakes can be reduced by increased phytoplankton biomass, an increased particulate load from disturbances such as thermokarst slumps, and by increased DOC from land. Previous experiments showed that low-level fertilization increased pelagic production while reducing benthic production (Daniels 2015). While the mechanism was assumed to be light reduction by the phytoplankton, there were other whole-lake changes. To uncouple the role of light from other factors, in a preliminary experiment we reduced light to the benthos by 60% in Fog 2, a relatively clear lake. For the first 3 weeks, we saw an increase in benthic chlorophyll in the shaded areas, and sediment from under shade had similar rates of GPP_{max} as that from nearby unshaded areas (Fig. 18). However, after 6 weeks there was a significant loss of Chl a under shaded areas and a large decrease in GPP. Previous studies showed that the direct grazing of benthic algae in this lake is low, and thus this loss of Chl a might indicate how long algae can persist at low light (Gettle et al. 2007). These observations suggest short-term shading from a disturbance on a closed lake might not have a long-term impact on benthic production, but long-term decreases in light availability, as might be seen in more open lakes (with increased DOC inputs), will reduce the importance of benthic production to overall lake production. This summer we will repeat this experiment in lakes that differ in transparency and DOC concentrations, and also carry out a limnocorral experiment varying DOC and nutrients as outlined in the proposal.

4. *How do closed (isolated) v. open (connected) lakes differ in biogeochemistry, trophic structure, and species composition and in their response to climate change and disturbance?*

Finding (4A): ***Interspecific competition is an important regulatory process that structures fish communities in open and "leaky" (partly open via intermittent inlets and outlets) lakes, while closed lakes are regulated by intra-specific competition.***

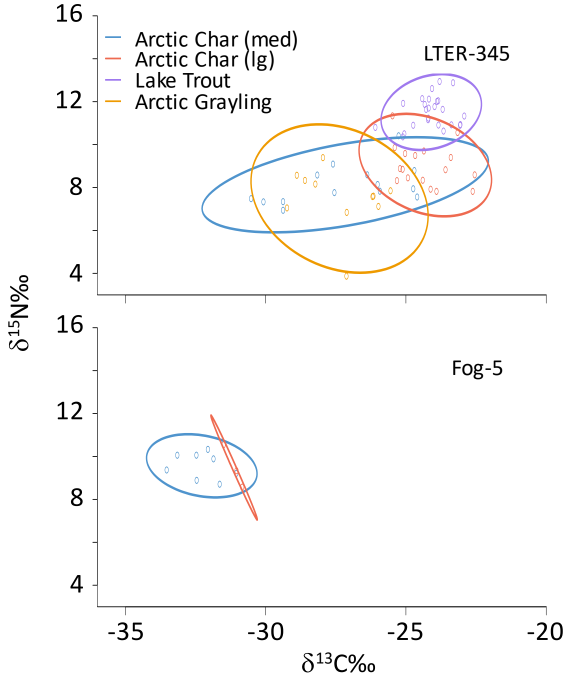

Figure 19: Stable Isotope Bayesian Ellipses (SIBER) ellipses representing arctic char trophic niche space (by size class or species) for individual stable isotope measurements for "leaky" LTER-345 lake versus "closed" Fog-5 lake.

For our comparison of the trophic structure of the fish communities of leaky and closed lakes, we sampled 583 individual arctic char across all seven study lakes (n = 360 in closed lakes; n = 223 in leaky lakes; Klobucar and Budy, *in review*)). Char were significantly larger in the leaky lakes relative to the closed lakes. Across all lakes, trophic position (TP) only increases significantly with length in leaky lakes, where we also captured other apex predator species. Observations of piscivory were rare in closed lakes, and more common in leaky lakes; however, surprisingly, we observed no evidence of grayling providing the hypothesized subsidy to large arctic char or lake trout in these lakes. Arctic char are more densely populated in the absence of other apex predators (closed lakes), where populations are tightly regulated by density dependence (see also Budy and Luecke 2014). Arctic char feed at higher trophic positions (e.g., more piscivorous; Fig. 19) and achieve greater maximum sizes in the presence of other mid-level fish species and apex predators (leaky lakes; Fig. 19). Regardless of size class, across and within the closed lakes, arctic char occupied similar trophic niches with considerable overlap (Fig. 19). In contrast, in leaky lakes, apex predators exhibited significantly different trophic positions (e.g., mean TP for large arctic char = 4.00; mean TP for lake trout = 4.51), and lake trout maintained the highest trophic position, with minimal overlap with large arctic char (19.5% and 6.9%, respectively).

Finding (4B): ***Pre-manipulation data show: (1) the chosen lake pairs are similar to each other both in species composition and in biogeochemistry, (2) greater fish diversity and a more complex food web in open lakes relative to closed lakes, (3) terrestrial sources play a more important role in the food web and flow of energy in open lakes while benthic production is of proportionally greater importance in closed lakes.***

The fish communities of the open lakes I-1 and I-2 (to be experimentally ‘closed’ in Years 4-6) have diverse species assemblages with lake trout and arctic grayling as top predators, whereas arctic char is the only dominant predator in closed lakes (data not shown; lakes to be experimentally ‘opened’ in Years 4-6). In addition, the fish communities of I-1 and I-2 are nearly identical, as are Fog 2 and Fog 3, in terms of species and size distributions, indicating collectively they will provide a suitable set of reference and experimental lakes for the whole lake manipulations. When comparing the food web and diets of lake trout and grayling from these lakes, we see stark differences in the proportion of prey items consumed. In general, arctic char diets in closed lakes are more diverse than arctic grayling and lake trout diets in open lakes, likely because of a lack of interspecific competition and high intraspecific competition. In contrast, coexisting lake trout and arctic grayling in open lakes are using different resources. Lake trout primarily feed on molluscs (>80%), whereas arctic grayling have more diverse diets primarily comprised of trichopteran and dipteran larvae. Prey electivity indices, which consider resource availability, indicate some evidence for interspecific competition for trichopterans; however, results from our niche overlap analysis indicate very little overlap between lake trout and arctic grayling. Further, terrestrial diet sources appear to be important only in open lakes.

6. SYNTHESIS

The ARC LTER supports a wide range of synthesis activities including within-site syntheses, multisite and panarctic syntheses, and network-level syntheses. These activities help us integrate with collaborating projects and help those collaborating projects interpret their results in the context of the core ARC LTER long-term datasets. Our multisite and panarctic synthesis allows us to determine whether results from Toolik Lake can be extrapolated to other sites and ecosystems, testing the generality of our research at Toolik Lake. These activities are our principal means of participating in the LTER Network, promoting the science of long-term ecological research.

Within-Site Syntheses

*Finding 1**: Although air temperature does not yet show a significant warming trend at Toolik Lake, several other indicators of warming indicate that warming is indeed happening.***

The significant 0.5 ^{o}C/decade warming trend detected at Utqiaġvik has not yet been detected at Toolik Lake. However, the Toolik record is much shorter than that at Utqiaġvik and, because of the large year-to-year variability in annual mean temperature, the record at Utqiaġvik did not emerge as significant until about its 45th year of record, about the duration of the record at Toolik. As discussed in earlier sections, Hobbie et al. (2017) examined other long-term time series, several of which indicated that warming is indeed occurring in the Toolik region. They conclude that these indicators of warming respond to temperature slowly enough to average out the year-to-year variation but fast enough to be useful indicators of warming on a decadal time scale. Rastetter et al. (submitted) examined this idea further using the Multiple Element Limitation (MEL) model to examine the response of tundra to warming at a rate of 0.5 °C/decade but with random year-to-year variability equivalent to that in the Utqiaġvik record (Fig. 20). They found that trends in the biogeochemistry of tundra are not likely to emerge as significant for 50 to 100 years.

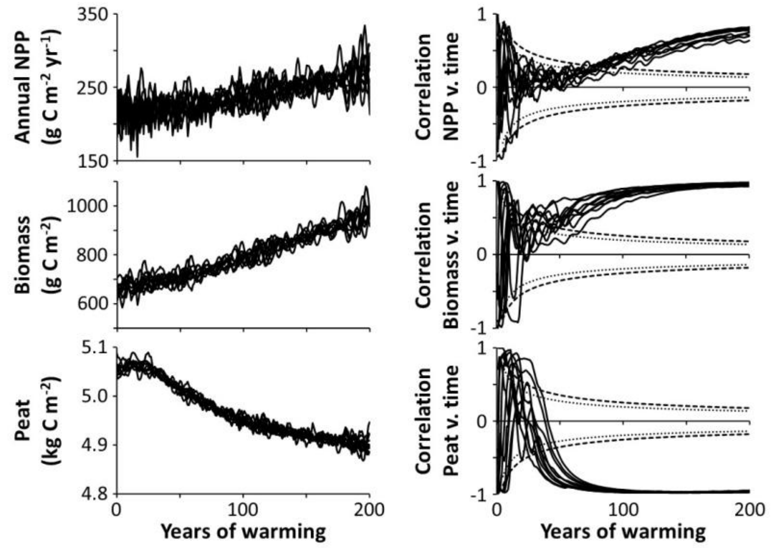

Figure 20: Ten replicate Multiple Element Limitation (MEL) model simulations of responses to a 0.5°C / decade warming for tussock tundra with annual mean temperatures varying randomly about the trend with the same variance as observed in the Barrow record.

*Finding 2**:* ***Warming is predicted to increase the amount of food needed by fish by 28-34%; this increased demand might be partly offset by increases in zooplankton biomass with warming.***

Because fish are ectotherms, their metabolism increases with warming. Using long-term LTER data, Budy and Lueke (2014) calculated that to meet this metabolic need, fish will need to eat 28-34% more than they currently do. In a follow-up study, again using long-term LTER data, Klobucar et al. (2018) found that in warm years zooplankton biomass increased nearly 20%, suggesting that the increased food demand by fish might be partly met by increase zooplankton production. Those predictions are now being tested with laboratory and whole lake experiments.

*Finding 3**:* ***Fertilization alters production, food webs, habitat structure, and ecosystem biogeochemistry, but these responses differ markedly among terrestrial, stream, and lake ecosystems.***

Gough et al. (2016) examined responses of our terrestrial, stream, and lake ecosystems to long-term fertilization. Net primary production increased in all three ecosystems with the expected increases in autotrophic and consumer biomass, detritus and litter, and light reduction to the ground or benthos. Perennial habitat structure increased in terrestrial and stream ecosystems, but not in lakes. Soil temperature decreased in terrestrial ecosystems, but there was no thermal effect in streams and lakes. Dissolved oxygen deceased in lakes, but there was no analogous change in terrestrial or stream ecosystems. Moore et al. (*in prep.*) analyzed food webs in these same ecosystems and found that the rate of C flow and respiration decreased 10-50% in terrestrial soil food webs following fertilization but increased 60-75% in lakes and about 3400% in streams. Nitrogen mineralization declined 40-50% in terrestrial ecosystems, and net N immobilization increased 22% in lakes and 5100% in streams.

These differences in response to fertilizer among the three ecosystems are of course related to their physical and community characteristics but also to differences in the openness of their biogeochemical cycles. To examine these differences, we built a simple heuristic model linking C and N fluxes in an ecosystem (Rastetter et al. in prep). We simulated dynamics of three ecosystems that were

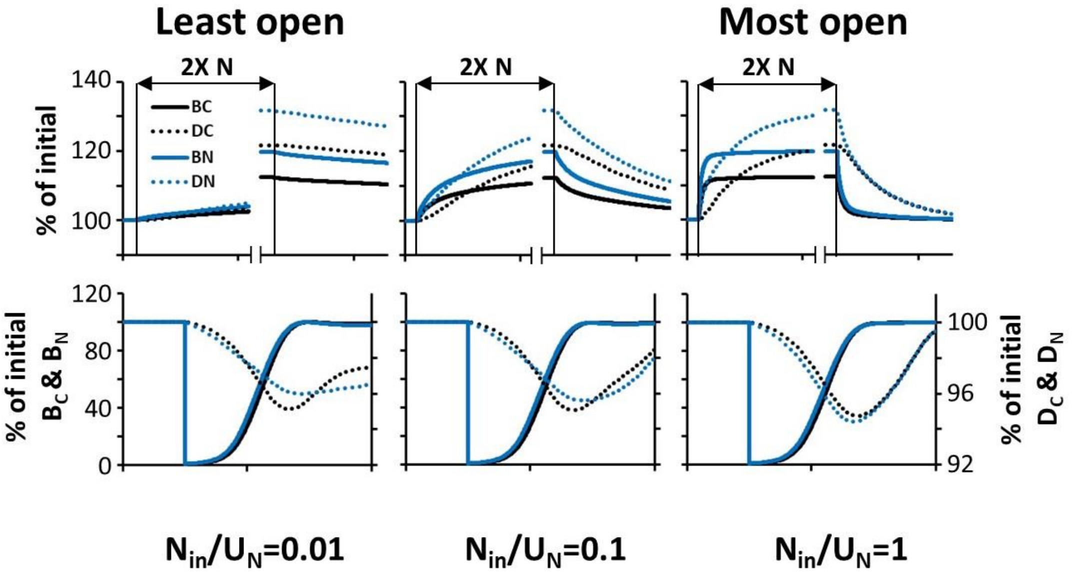

Figure 21: Simulated responses to a doubling of N inputs and recovery after fertilization stopped (upper panels) and to a 99% loss of autotrophic biomass (lower panels). The 3 ecosystems differ in the ratio of N inputs (N_{in}) to N uptake by autotrophs (U_N). Panels are arranged left-to-right from least open (low N_{in}/U_N) to most open. B_C & B_N – autotrophic biomass C & N; D_C & D_N – detrital C & N.

identical except that their biogeochemical openness differed by changing the throughput of N by a factor of 100. Thus, all the internal C and N fluxes and stocks are identical in the three ecosystems but the inorganic N supply to and inorganic N losses from the ecosystem were set at 1, 10, and 100% of autotrophic N uptake; the ecosystem is terrestrial-like and least open with throughput at 1% of autotrophic uptake and is stream-like and most open with throughput at 100% of autotrophic uptake. Relative to the residence time of C (which is identical in the 3 ecosystems), the terrestrial-like, least-open ecosystem responds very slowly to a doubling of N inputs and recovers very slowly when N inputs are returned to their initial values (Fig. 21 *upper panels*). These are the responses we either observed in our long-term terrestrial fertilization or expect in the recovery now that we have stopped fertilization in some plots. The stream-like, most-open ecosystem responds and recovers very quickly, as observed in the Kuparuk fertilization experiment.

We also used this model to examine responses to a disturbance that removes 99% of the autotrophic biomass. The autotrophic component recovers very rapidly in all three ecosystems by scavenging N from detritus (Fig. 21 *lower panels*), as observed in the recovery from the Anaktuvuk River fire. Recovery of the detrital component is fast in the stream-like, most-open ecosystem. However, detrital recovery is slow in the terrestrial-like, least-open ecosystem; if N input rates are not accelerated following fire, it should take over 500 years to recover the N lost in the Anaktuvuk fire even if all normally occurring N losses are stopped.

Pan-Arctic Syntheses

Finding: ***Models predict a net increase in total ecosystem C with warming because of the acceleration of nutrient cycles and the net transfer of nutrients from soils (relatively low C: nutrient) to vegetation (relatively high C: nutrient). However, this net storage might not continue once thaw depth exceeds rooting depth and is easily reversed by disturbances like wildfire and thermokarst erosion.***

In a series of key findings, we have noted a remarkable convergence in canopy function across all the major vegetation types in the Arctic. Williams and Rastetter (1999) found a common relationship between canopy leaf area and total canopy N on the North Slope that optimized photosynthetic gain in all

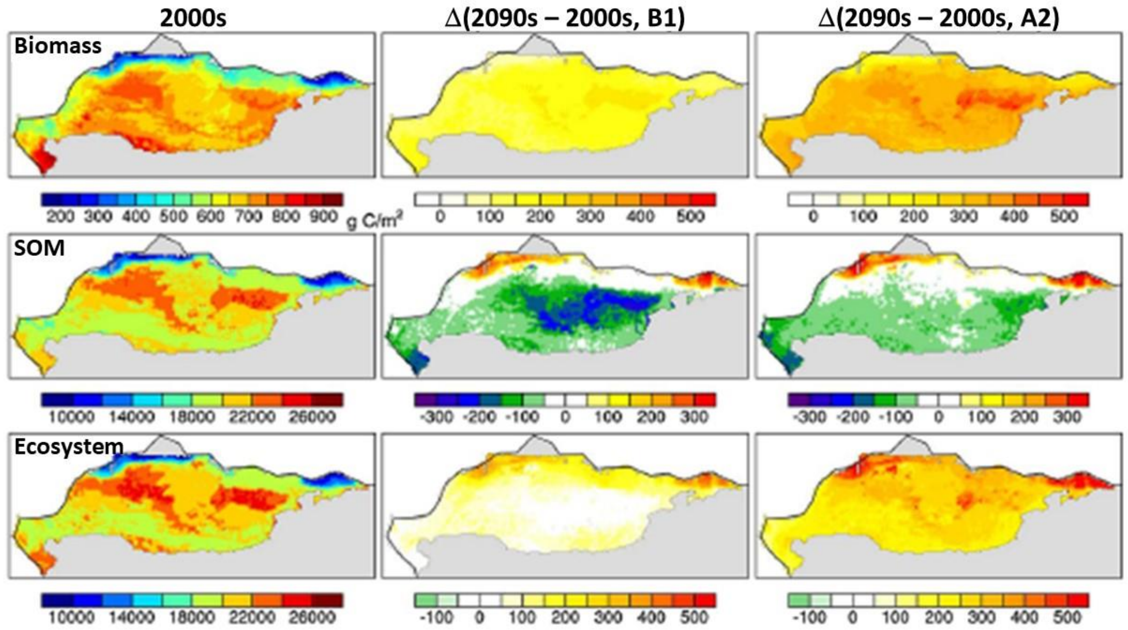

Figure 22: MEL model simulated C stocks for the North Slope and changes in those stocks over the next 100 years under IPCC climate scenarios B1 and A2. (from Jiang et al. 2016).

these vegetation types; this same relationship was found by Street et al. (2012) for other locations in the Arctic (Abisko, Sweden; Svalbard, Norway; Zackenberg, Greenland; and Utqiaġvik, Alaska). Because of this convergence, Shaver et al. (2007, 2013) found that net ecosystem carbon exchange (NEE) can be predicted anywhere in the Arctic using the same parameterization of a simple equation using only three input variables: leaf area, air temperature, and irradiance. This convergence persists even though common-garden studies indicate that conditions are now about 350 degree-days too warm for optimal growth of *Eriophorum vaginatum*, the dominant tussock sedge in the Toolik area (McGraw et al. 2015), and latitudinal differences in *E. vaginatum* ecotypes exists (Curasi et al. 2019).

This background gives us confidence in making projections. Rocha et al. (in prep) assimilated eddy covariance data into a Coupled Carbon and Nitrogen (CCaN) model and used it to extrapolate NDVI trends across the North Slope. They were able to capture the mean rate of NDVI greening detected in MODIS satellite data, but their predictions were less skewed toward faster greening than the MODIS data. This analysis will allow us to relate MODIS greening trends to the C-N biogeochemistry of the North Slope.

We have used long-term LTER data to constrain the Multiple Element Limitation (MEL) model and have tested the model against eddy covariance data in control and moderately and severely burned tundra (Jiang et al. 2015). Pearce et al. (2015) used the model to analyze recovery of tundra from thermokarst erosion, and Jiang et al. (2015, 2017) used it to analyze tundra recovery from wildfire; all these analyses indicate rapid recovery of vegetation, but very slow recovery of soil organic matter resulting in a long-term, net loss of C from the ecosystem. Jiang et al. (2016) used the model to extrapolate changes in ecosystem C in the next 100 years for the North Slope under IPCC climate scenarios B1 (low emissions) and A2 (high emissions). Under both these scenarios tundra is predicted by the model to sequester C (Fig. 22), but not at a rate that would compensate for losses resulting from thermokarst and wildfire disturbance. Thus, the C budget of the Arctic might be determined as much by changes in disturbance regime as by direct responses to climate change.

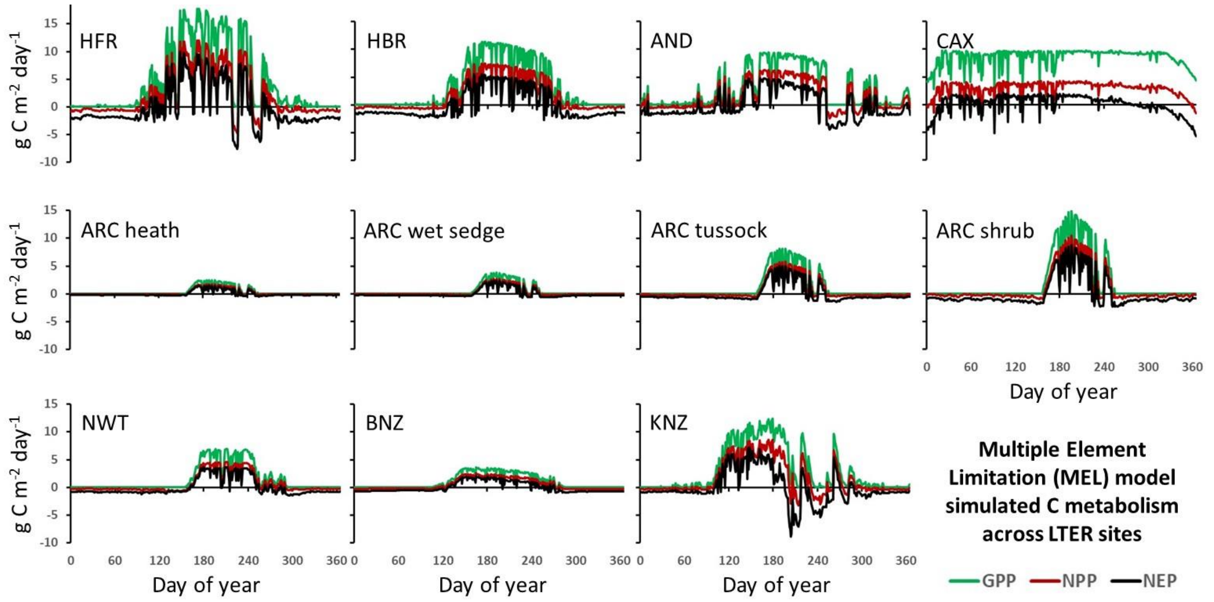

Figure 23: MEL model simulations of daily GPP, NPP, and NEP for the four dominant vegetation types near Toolik Lake (center row) and for several other terrestrial ecosystems in the LTER network and an Amazonian forest. HFR - Harvard Forest, HBR - Hubbard Brook, AND - HJ Andrews, CAX – Caxiuana, Brazil, NWT – Niwot Ridge, BNZ – Bonanza Creek, and KNZ – Konza Prairie.

Network level and global syntheses

The ARC LTER participates in a wide range of network and global synthesis efforts. The LTER Network has long supported and participated in a series of Network-level analyses of ecosystem patterns and properties, published in high-impact journals. Our latest contributions to this series are (1) Gough contributed to an analysis of responses to experimental manipulations of nutrients and climate change variables across several LTER sites (Smith et al. 2015), (2) Griffin contributed to a latitudinal analysis of leaf respiration (Atkin et al. 2015) and a global data base of plant traits (TRY; https://www.try-db.org/TryWeb/Home.php), (3) Budy contributed our LTER zooplankton long term data to a global database aimed at accelerating and facilitating quantitative analysis of temporal patterns of biodiversity in the Anthropocene (Dornelas et al. 2017; BioTIME 8,777,413 records; http://biotime.st-andrews.ac.uk/), (4) Ashley Asmus, a student of Gough's, contributed to an analysis of latitudinal patterns of insect predation (Roslin et al. 2017) and contributed to a network on tundra arthropods (NeAT; https://www.uarctic.org/organization/thematic-networks/arthropods-of-the-tundra-neat/), (5) Gough provides data on herbivore activity to the International Tundra Experiment database (ITEX), and (6) Rastetter et al. (submitted) contributed to a special LTER issue of Ecosphere examining time lags in responses to changes in the environment. (7) Song et al. (2018) used data from the Arctic LTER and several other LTER and non-LTER sites to inform a stream metabolism model that predicts future warming will increase stream ecosystem respiration relative to stream ecosystem production, yielding a net increase of 0.0194 Pg carbon globally from small headwater streams, every year. In addition, ARC LTER has helped facilitate dataset inclusion in various other locations like the Environmental Data Initiative (EDI; https://environmentaldatainitiative.org/), NFS's Arctic Data Center (ADC; https://arcticdata.io/), the Arctic Observatories Network (AON; http://aon.iab.uaf.edu/), and AmeriFlux (https://ameriflux.lbl.gov/). The ARC LTER also contributed data and model development that spawned a new project (Rastetter NSF 1651722) in which the biogeochemistry of several LTER sites is being analyzed using the MEL model (Fig. 23). In addition to the four major tundra types (tussock, heath, shrub, and wet sedge), the model is being used to look at responses to climate change and recovery from disturbance at Niwot Ridge (NWT), Hubbard Brook (HBR), Harvard Forest (HFR), HJ Andrews (AND), Bonanza Creek (BNZ), and the Konza Prairie (KNZ), plus two non-LTER sites, southeastern pine plantations and Amazonian rain forest at Caxiuana.

7. EDUCATION AND OUTREACH

The ARC LTER project maintains a multifaceted education and outreach program. Each component of our program is selected to optimize available opportunities and their institutional resources. With a few carefully-selected activities, our strategy is to reach a diverse audience ranging from kindergarten through graduate students to the public, and to governmental and scientific planning agencies. Except for our Schoolyard and REU programs, these activities are all independently funded but receive support from the ARC LTER in the form of investigator, student, or RA participation, and through access to our field sites, laboratories, and data base. We also provide small subsidies from LTER research or supplemental funds, especially for travel to and logistics costs at the Toolik Field Station (TFS).

1. *ARC-LTER Schoolyard program:* Because of our remote location, we have no local schools with which to collaborate in Schoolyard activities. Instead, our schoolyard program focuses on providing research experiences for K-12 teachers that they can take back to their classrooms and pass on to their students. These activities are supported by ARC LTER schoolyard funds, the NSF-OPP “PolarTREC” program (http://www.polartrec.com/about), and private sources like the Friends of the MBL. Many of these initiatives were developed in partnership with scientists and science educators from other LTER sites **(AND, ARC, BES, KBS, LUQ, SGS, SBS)** and the LTER Network Office. ARC LTER researchers provide an array of opportunities for teachers to engage in arctic ecology at the site (e.g., soil food webs, avian census, arctic grayling, botany, small mammals, lake and stream ecology).

Over the course of 11 years, 22 K-12 teachers from 6 states have participated in this 2-week field and lab experience at Toolik Field Station (TFS). However, their involvement in the program extends beyond working side-by-side with researchers. Before they travel to TFS, Amanda Morrison, our education and outreach coordinator, and the researchers meet online to get to know each other, discuss working and living conditions in the Arctic, and set up expectations for entering into a Professional Learning Community (PLC), which guides the teachers as they develop curricula to deliver to their students (curricula are shared among teachers and with Ms. Morrison and the ARC LTER researchers with whom the teacher worked at TFS). We estimate that curricula developed by the teachers has been taught to a minimum of 3,300 K-12 students (22 teachers, 5 classes/teacher, 30 students/class). This estimate is likely conservative because our teachers tend to stay engaged with the PLC for multiple years and develop their own curriculum, which they use year after year.

In the past, we had an active outreach program with the Utqiaġvik community and schools coordinated by the Utqiaġvik Arctic Science Consortium (BASC). LTER personnel would visit Utqiaġvik to lecture in the “Saturday Schoolyard” series and in the public schools. We also helped set up field experiments near Utqiaġvik that replicated some of those running at Toolik. However, this program could not be maintained when BASC disbanded. In addition, many of the teachers involved in the experiments left Utqiaġvik during the summer when the experiments needed to be maintained and monitored. We therefore need a new model for engagement. In Spring 2019, Ms. Morrison successfully made new connections with the Principal at Utqiaġvik High School and a high school science teacher in Point Ley, Alaska. She will be collaborating with them beginning in Summer 2019 to network and brainstorm ideas on how to integrate research from the ARC LTER into the Utqiaġvik schools’ science curriculum. In early August, Ms. Morrison will spend time in Utqiaġvik to meet with these new collaborators to begin development of educational activities and revitalize our connections with the Utqiaġvik community.

2. *Other Opportunities for K-12 Teachers and outreach to the public*:

Dr. Rachel Cox of the Riverdale Country School in the Bronx, NY brought 3 high-school students and 2 recent Riverdale alumni to Toolik in 2017 to sample mosses in the ARC LTER experimental plots and brought 8 Riverdale students to Toolik in 2018 to sample *Salix* leaves in the ARC LTER plots. In both years they used Toolik as a base to sample spruce at tree line south of Toolik. The students developed posters of their research. Dr Cox and one of the Riverdale alumni, Zachery Halem, presented their work at the TFS meeting in 2019. Dr. Cox plans to return to Toolik with a new group of students every other year.

ARC LTER researchers often give talks for the public. For example, Rastetter presented lectures to the Lawrence School, Falmouth, MA 7th grade science class of one of the ARC LTER Schoolyard teachers and, along with two of the Schoolyard teachers, made presentations to about 60 K-12 teachers and the public at an event hosted by the Woods Hole Science and Technology Education Partnership (WHSTEP; https://web.whoi.edu/whstep/wp-content/uploads/sites/123/2019/03/WinterMeeting2019-Flyer.pdf). Gough has spoken about the Arctic at Career Day at middle school as well as during visits to science classrooms at both elementary and middle schools. Gough also attended that Polar-ICE workshop to better incorporate arctic science into college level courses and develop stories for the public based on research at the ARC LTER. ARC LTER researchers occasionally give talks to Alaskan Native communities in Anaktuvuk Pass, Kaktovik, and Utqiaġvik.

3. *Education of undergraduate and graduate students in arctic research*: Each year we support at least 2 REU students at the Toolik Field Station with LTER supplemental funds, and 2-10 additional undergraduates interact with LTER personnel in association with collaborating NSF grants. REU students are selected via a national search each year and come from a wide range of states and institutions. We promote the training of graduate students on collaborating grants by allowing them access to our experimental plots and providing logistical support (user-days, helicopter time), and we continue to encourage foreign collaborators to send their students to work with us for a summer at Toolik Lake. To promote communication among these students and between the students and other researchers, every summer we help plan and participate in a weekly seminar series, "Toolik Talking Shop" during which researchers give short presentations about current or recent investigations in the Toolik region. At the end of the summer we work with TFS to organize a poster session for REU students to show off and to “defend” their summer projects to an interested and friendly audience. In addition, since 2005, each summer we have included 4-8 undergraduate students in a group research project to monitor the recovery from a small tundra wildfire near Toolik Lake. Overall, most of our REU students have gone on to graduate school and often they are included as authors on publications. Graduate students, and occasionally REU students, are invited to our annual winter meeting in Woods Hole to present their results, interact with their peers and colleagues, and to participate in planning for the following summer's research.

4. *Outreach to federal, state, and local management agencies*: Much of the research done at Toolik Lake is directly relevant to the problems of managing the huge expanse of publicly owned, wild land on the North Slope of Alaska. We provide regular briefings for BLM, ANWR, DNR, Alaska Fish and Game, and North Slope Borough officials; usually during visits to their offices in Anchorage, Fairbanks, and Utqiaġvik, as well as tours of our research sites at Toolik Lake. We work particularly closely with BLM, Alaska Fish and Game, and with the North Slope Borough in association with the annual permitting process for our research. The Alaska Fish and Game office has used our data and advice in the past to set angling policies and fish catch regulations. Our contacts with the North Slope Borough have increased in frequency lately as our research increasingly involves helicopter travel through areas where subsistence hunting takes place. We invite representatives from these agencies to attend our winter meeting in Woods Hole, to learn about our latest results and plans. For the past several years, Toolik Field Station has also invited representatives of these agencies to speak at the weekly “Toolik Talking Shop” evening seminars for Toolik scientists and students, helping to make this a two-way channel of communication.

5. *National and International Research Planning and Organization:* We continue our long-term participation in a wide range of national and international research planning and oversight organizations.

In the past 5 years this has included participation in the steering or advisory committees for the NSF-funded SEARCH project (the Study of Environmental Arctic Change), ISAC (International Study of Arctic Change), and the ACIA (Arctic Climate Impacts Assessment), and we will continue to help with the long-term management and organization of the University of Alaska's Toolik Field Station by serving on the TFS Steering Committee and the Advisory Committee for the TFS Environmental Data Center (EDC). The planning activities are particularly important in development of broader scientific impacts of our research, and for applications of understanding developed from our research at the PanArctic, continental, and global scales.

Anticipated changes, 2017-2023: Overall, we think that our education and outreach initiatives are diverse, responsive, and inclusive and we expect to continue all components in 2019-2023. One change we anticipate is the new collaboration with the Utqiaġvik Schools (discussed above under *ARC-LTER Schoolyard program*).

The main need is to continue working to secure independent sources of funding for each of these components. Each year that they are available, we apply for RET funding from NSF and we have been able to raise money from the *Friends of the MBL* to help send a Falmouth, MA teacher to Toolik to participate in our Schoolyard program.

8. PROJECT MANAGEMENT, BUDGET, SITE MANAGEMENT

Overall management structure: Arctic LTER research spans a broad spectrum of researcher backgrounds, skills, and interests. For efficiency and to promote effective planning we have organized into four groups, each focused on major components of the landscape, i.e., terrestrial, streams, lakes, and “landscape interactions”. This structure has proved highly effective for planning and project management, especially for major manipulations of lakes, streams, and tundra.

An Executive Committee (EC) consisting of the lead PI (currently Rastetter), representatives of each research group (currently Gough [terrestrial], Bowden [streams], Budy [lakes], and Kling [landscape interactions]), plus three additional ARC researchers (currently Giblin, Crump, and Griffin) meets several times a year: at least once in the fall (usually by conference call), once in person during a winter plenary meeting of all project personnel and collaborators, in person during the summer field season (with available members), and at other times as necessary. The purpose of the fall meeting is to review the previous summer's work, review the current state of the project's budget, and begin discussion of any changes in priorities, funding allocations, or new opportunities that might emerge in the coming year. At the fall meeting we also set the agenda and choose a theme for the winter meeting. The day before the winter meeting, the EC meets to review the agenda, consolidate priorities, and discuss any pressing issues related to the project. During this winter meeting, each of the four focus groups meet to review the past year’s science accomplishments, discuss group priorities, finalize plans for the upcoming summer research season, and assess requirements for Toolik user-days and helicopter time. We then meet in plenary to reconcile variable needs or overlaps in plans, user-day allotments, and helicopter time among the four research groups. Throughout the year, the EC responds to requests for information or collaboration, prepares annual reports and other communications, and interacts with the LTER Network office and with NSF. At least one member of the EC plus a researcher selected at large from among the ARC LTER collaborators attends every LTER Network Science Council meeting.

Critical project personnel include the four full-time, senior research assistants (SRA) associated with each of the four research groups plus a part-time assistant who work with the PI (Laundre [terrestrial], Iannucci [streams], White [lakes], Dobkowski [landscape interactions], and Kwiatkowski [modeling]). These assistants work with the EC and the four research group leaders to do most of the day-to-day project management and coordination; they also serve as information managers working with the lead PI within each group. Laundre is the project's senior Information Manager, coordinates with the other SRAs, and represents the ARC LTER information management interests with the LTER network.

Budget: Our approach to budgeting is practical and intended to maximize our ability to maintain core experiments and data collection while supporting extensive collaborations with individual investigators and other projects. Most of the project's core budget ($1,127,000 per year) is divided equally among the four major research groups: Terrestrial, Streams, Lakes, and Landscape Interactions. Each of these groups receives support for one full-time Senior Research Assistant, one Summer Field Assistant, and one month of PI salary for that group's representative on the EC. Each group also receives a supplies and travel budget. Smaller amounts are retained in the core budget to cover costs of our annual meeting in Woods Hole, education activities (Schoolyard and REU support), and core Information Management tasks. In the current funding cycle, we have also set aside about $10,000-15,000 per year to promote collaborations and each year we make available $5,000-10,000 to support site-level and network-level synthesis activities.

Additional activities and expenses are covered using annual supplemental funds when available. The uses of those funds are determined each year by NSF. Decisions about what we apply for are prioritized by the EC.

Field site management: Most of the land used by the Arctic LTER for research (Fig. 1) is managed by the US Bureau of Land Management (BLM), from whom we are required to seek permits for our sampling activities and equipment installations. Additional permits are required by the Alaska Department of Fish and Game for research on fish, and by the State of Alaska and the North Slope Borough when working on their land. We work with these agencies to ensure that the permitting process runs smoothly.

Toolik Field Station (TFS) is a facility of the Institute of Arctic Biology of the University of Alaska Fairbanks (UAF); it operates under lease of its land from BLM (only the 34-acre camp itself is covered). The labs, dorms, kitchen, and other buildings at TFS are owned by either NSF or UAF, and most of the funding for TFS operations comes through a cooperative agreement between UAF and NSF's Office of Polar Programs (OPP). Most of the rest of the funding also comes from NSF-OPP when projects with NSF support, including the Arctic LTER, receive logistics support for room, board, and laboratory costs based on the number of "user-days" at TFS. LTER scientists work closely with TFS management to ensure that research needs are met and to avoid conflicts among projects. During the summer a "Chief Scientist" meets daily with camp management to discuss immediate issues, and each summer general meetings are held with all camp personnel invited. LTER scientists also attend annual winter planning meetings as members of the TFS Steering Committee; M.S. Bret-Harte, an ARC LTER scientist at the University of Alaska, is the Scientific Director of TFS.

Collaborating projects, diversity, and interactions with LTER and other Networks: Opportunities for collaboration were a primary consideration in designing the ARC LTER research, especially its long-term experiments and monitoring. Collaborating projects include those that work directly on LTER sites and experiments, and projects that use TFS facilities or collaborate on synthesis papers. All collaborating investigators (PI-level researchers who contribute to the project in various ways), research assistants, postdocs, and students are invited to the ARC-LTER winter meeting in Woods Hole. Each year we also invite to the meeting several potential collaborators as well as agency representatives (e.g., NSF, BLM). This meeting includes presentations by each of the four focus-group leaders on the past-year's results, plus science talks and a poster session by other LTER personnel and collaborators.

Often the LTER project will encourage a particular interaction by inviting visitors to work at Toolik Lake and supplying a small amount of travel and logistics funds, in anticipation of their eventually obtaining independent funding (examples include current projects led by R. Cory and G. Kling, by B. Nielsen, by L. Gough and R. Rowe, and by D. Emerson and W. Bowden, all of which began with small amounts of travel and logistics funding provided by ARC LTER). The ARC LTER project has also been successful in attracting young investigators by encouraging those who were trained at Toolik Lake as postdocs and graduate students to return as investigators with their own funding (e.g., George Kling, Syndonia Bret-Harte, Laura Gough, Natalie Boelman, Byron Crump, Rose Cory, Jennie McLaren, and Mike Weintraub).

ARC LTER collaborators are strongly encouraged to pursue cross-site and network-level collaborations; these are supported with supplemental and core project funds. Examples include within-ARC synthesis projects like our comparison of tundra, stream, and lake response to fertilization (Gough et al. 2016, Moore et al. in prep); other examples include LTER Network collaborations and reviews (e.g., Smith et al. 2015; Christie et al. 2015, Hobbie et al. et al. 2017; Rastetter et al. *submitted Ecosphere*; Rastetter project NSF 1651722).

Anticipated changes, 2013-2017: Our management system has worked well since 1987 and we plan no major changes. There is, however, one shorter-term and one ongoing management issue we face. In the next three years we will rotate some of the project leadership: several of the EC members including the Lead PI have been with the project for decades and will retire in the next 6-12 years. We must begin to plan now for these transitions. We have already identified a new PI for the next renewal (K. Griffin). Under his guidance, we will begin to identify people to replace retiring members of the EC. Second, we must continue to attract new investigators with new skills and interests to the project, not only as retirement replacements but also to ensure continued intellectual vitality and growth. We will address this management issue in the following ways, which we have been using successfully for many years. First, we will continue to rotate participation in the EC by inviting less-senior investigators to participate in EC meetings and, when possible, Network meetings such as the annual SC meetings. Second, to continue to attract new investigators, each year we will support travel to Toolik Lake and to our winter meeting for 1-3 investigators with new or complementary skills and research interests.

A third key management issue is how to improve coordination and collaboration with other projects and groups based at TFS, and with TFS itself. There is a need to anticipate interactions with major monitoring and experimental networks such as NEON and AON, both of which will be active at Toolik Lake in the next decade and will be collecting and storing long-term data sets. This is a major scientific opportunity, as well as a risk of conflicts, overlaps, and inefficiencies. However we have been working closely with NEON personnel at the local and regional levels, and several of our PIs and collaborators have past, current, or pending AON funding. Finally, we extend invitations to our annual ARC LTER meeting for new projects near Toolik in order to help coordination and potential build collaborations (e.g., in 2019 N. Jelinski who leads a DOE-funded soil project attended our annual meeting).

9. INFORMATION MANAGEMENT AND TECHNOLOGY

Overall Strategy and Structure: Information management in the Arctic LTER has two principal aims. The first is to maximize data ***access*** both within the project and to other researchers. We try to maximize data access by rapidly adding new datasets to the database (usually before publication) and by making all the datasets available for downloading with the only restrictions as outlined under the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/). The second aim is to optimize data ***usability*** and ***integration*** for within-site synthesis and modeling, regional and long-term scaling, and multisite or global comparisons and syntheses. Careful planning at the research design stage is required to ensure that any single set of measurements is easily linked to other measurements; typically, this includes working closely with collaborating projects so that their work on LTER sites and experiments is optimally integrated.

The structure of our information management system parallels the overall structure of the project, with four major components to the ARC LTER information system linked to the terrestrial, landscape interactions, streams, and lakes research components. A Senior Research Assistant (SRA), Jim Laundre, is the overall project information manager with responsibility for overseeing the integrity of the ARC information system. Information management is a primary responsibility of the four full-time SRAs associated with each of the core research components. While each of the four core SRAs maintains the data in their area, all are in frequent communication on overall data compatibility and metadata standards (currently two work at the MBL in Woods Hole, one is at University of Michigan, and one at University of Vermont). Each SRA is deeply involved in the actual research design, day-to-day management, and data collection within their area. The four SRAs work closely in the field with investigators, technicians, and students to ensure quality control and appropriate documentation. Overall guidance is provided by the ARC Executive Committee while Laundre attends the LTER Network Information Manager's video teleconferences and meetings and makes sure we are kept up to date and compatible with Network data standards.

Each year at our annual winter meeting in Woods Hole we review the status of the information system and ways of improving its accessibility and ease of use. At this meeting, we focus on the upcoming summer season and on how to design our research for optimum integration of diverse datasets. All project personnel including postdocs, graduate students, and occasional REU students participate in these discussions. See http://arc-lter.ecosystems.mbl.edu/information-managment-arctic-lter for details.

Availability of Datasets: Datasets of the Arctic LTER project are available from either the Arctic LTER web site (http://arc-lter.ecosystems.mbl.edu/data-catalog) or the Environmental Data Initiative (EDI) data portal (https://portal.edirepository.org). Because EDI is a member node of DataONE they are also available through DataONE's search page (https://www.dataone.org/find-data). We ask only that datasets be properly cited and that NSF and the ARC LTER be acknowledged in any papers published. Data from the large-scale experiments and from routine monitoring are available online as soon as the data are checked for quality and, where necessary, transformed for presentation in standard units and scales. Many datasets, such as weather observations, stream flow and data that do not require a great deal of post-collection chemical or other analysis, are available within 6 months of collection. Other data, particularly from samples requiring chemical analysis in our home laboratories, might take up to two years before they appear on-line. Collaborating projects can and often do contribute their datasets to our online database and if required these datasets can be replicated to the NFS's Arctic Data Center. ARC LTER also participates in the LTER Network's "ClimDB," "HydroDB," and the new community survey data, "ecocomDP". These centralized databases provide access to meteorological, hydrological, and community survey data from all the LTER sites

Format of Datasets: Investigators, technicians, and students who collect the data are responsible for data analysis, quality control, and documentation. This ensures that the data are checked and documented by those most familiar with the data. While investigators might use any software for their own data entry and analysis, we expect that all documentation and datasets that are submitted conform to the required ARC LTER formats. The metadata and data can be submitted using ARC LTER's Excel based metadata form. Comments are used extensively throughout the sheet to aid in filling out the metadata. Data validation lists are used to created drop down lists for units, measurement scale, and number types. For researchers who do not use Excel, a rich text form is available with the data being submitted as comma delimited ASCII. Researchers are encouraged to include the metadata worksheet in their Excel workbooks to facilitate documentation. The worksheet was designed to be easily moved or copied. Submitted files are checked for conformance by the four SRAs. An Excel macro is used to check the metadata for completeness and inclusion of LTER vocabulary terms. Once files are accepted, they are placed in the appropriate data directories and content created using the Arctic LTER web management system based on the Drupal Environmental Information Management System (DEIMS). The xml files generated from DEIMS conform to the LTER network's "EML Best practices" and can then be uploaded to the EDI data portal.

General site information and publications: General information about the ARC LTER project is provided on our web site (http://arc-lter.ecosystems.mbl.edu) including site descriptions, past proposals and other documents, a site bibliography including citations for publications based on project research, educational opportunities, contact information for site personnel, and links to related sites. This information is updated once a year or whenever major changes occur.

Toolik Field Station Environmental Monitoring Program: The Arctic LTER and its precursor projects have maintained an environmental monitoring program at Toolik Lake since 1975, including basic weather data as well as stream and lake observations. These data have always been made available to other projects and to Toolik Field Station (TFS) management but, as the number and diversity of projects at TFS have grown, it has become clear that it would be more appropriate for TFS to maintain these observations and make them available via the TFS web site. Increased support for TFS from NSF-OPP has also made it possible for TFS to make additional observations that the ARC LTER cannot afford by itself.

To accommodate these changes, since September 2006 TFS has gradually assumed responsibility for maintenance and data management of the main Toolik weather station, which LTER has been supporting since 1987. The ARC LTER project is still responsible for collection and management of weather and other data collected from experimental plots and as part of LTER research. Toolik Field Station weather data is available from the TFS web site (http://toolik.alaska.edu/edc/index.php). The TFS Environmental Data Center (EDC) have additional components including plant phenological monitoring, bird observations, and other year-round observations of weather and natural history that cannot be made by LTER personnel who are not year-round residents.

Geographic Information Systems, Mapping, and Remote Sensing: Geographic information from the Toolik Lake region is extensive, detailed, and linked to several key global and regional databases. Because much of this first-class information system was developed with funding independent from the ARC LTER project, we have focused our efforts on insuring access to this valuable database and on optimizing its usability for our needs. Where appropriate, we have contributed some funds and personnel support to guarantee this access and usability.

- The *Circumpolar Geobotanical Atlas*, developed by Dr. Donald (Skip) Walker and colleagues at the Alaska Geobotany Center, University of Alaska (http://www.arcticatlas.org), features a nested, hierarchical series of maps of arctic ecosystems at scales ranging from 1:10 (1 m2) to 1:7,500,000 (the entire Arctic), with multiple data layers at each scale including vegetation, soils, hydrology, topography, glacial geology, permafrost, NDVI, and other variables. Much of the development of this hierarchical system is based on original work done by Walker and colleagues at Toolik Lake and Imnavait Creek, with multilayer maps of these areas at 1:10, 1:500 (1 km2), 1:5000 (25 km2), and of the Kuparuk River basin at 1:25,000 and 1:250,000.
- The *Toolik Field Station GIS and Remote Sensing* (http://toolik.alaska.edu/gis/) was developed with support from NSF-Office of Polar Programs to help manage and support research based at the Field Station including LTER research. This GIS is maintained by a full-time GIS and Remote Sensing Manager and includes a multilayer GIS based largely on the Geobotanical Atlas data described above, combined with landownership information, roads and pipelines, and disturbances (e.g., Fig. 1). Particularly important for our purposes is a detailed map of research sites including all the LTER experimental plots and sample locations in the upper Kuparuk region. The GIS includes a map of Inupiaq place names with annotations of historic use of the land by the Inupiaq people, along with a dictionary of plant and animal names and common words.

Anticipated changes, 2019-2022: Several changes are planned to our overall Information Management strategy and practices.

- We currently use Drupal 7 (DEIMS 7) with custom Excel scripts to check and parse metadata/data and to create the xml needed for uploading datasets to the EDI data portal. Efforts at several LTER sites are underway to migrate DEIMS 7 to Drupal 8. This migration will seek to improve metadata creation by simplifying content creation and export. In addition, EDI is developing several R based tools for metadata checking and parsing into xml. We will explore ways to use and contribute to these two efforts to provide a simpler and more streamlined system for metadata entry, parsing and uploading to the EDI data portal.

- We also plan to continue organizing and consolidate current data sets and make available older “legacy” data sets. We have started to use R scripts to QAC and analyze multi-year datasets and will continue to develop and expand this approach.
- Many collaborating projects might choose or are required to use other data repositories (e.g., Arctic Data Center, GenBank). Although these repositories are searchable through DataONE it is a challenge to identify Arctic LTER supported data. We will be exploring ways of using keywords and grant numbers with a custom DataONE search to identify Arctic LTER data across multiple data repository.

10. CURRENT CHALLENGES AND CHANGES FROM PROPOSAL

Conceptual Framework: Our conceptual framework, built around the concepts of biogeochemical and community openness and connectivity was designed to help us compare the responses of three very different types of ecosystems – terrestrial, streams, and lakes – to disturbances like climate warming and permafrost thaw (press) and wild fire and thermokarst erosion (pulse). The biogeochemical concepts have helped us understand, for example, how vegetation in terrestrial ecosystems can quickly recover from wildfire despite relatively closed nutrient cycles by mining the large residual stores of soil nutrients, but the soil will take millennia to recover their lost nutrient stocks. Streams, in contrast, respond quickly to increased nutrient supply from thermokarst erosion and recover quickly, but cannot retain those nutrients once the elevated supply stops. Lakes appear to be somewhere in between and recover from disturbance-related nutrient inputs moderately rapidly biogeochemically (~3-5 years).

The concept of community openness is more multifaceted than we had originally recognized. For example, both the tundra plant community on land and the animal communities of isolated lakes (i.e., without stream connections to other lakes) are relatively closed. However, the mechanisms of closure are very different. In the plant community the closure is maintained by competitive exclusion of recruits. In the lake community the closure is maintained by the lake’s isolation (no surface inflows or outflow). Are there commonalties between these two very different forms of community closure that can served as a means of comparing how these very different ecosystems respond to climate or acute disturbance? We are still assessing this question.

Another issue with the concept of community openness is that it applies more readily to components of the community rather than to the whole community. For example, in terrestrial tundra we recognize the closure of the plant community as an important property of the ecosystem affecting how it responds to disturbance. However, the animal community is open and is much more strongly connected with the surrounding landscape than are the plants. Similarly, the lakes are open with respect to the seasonal grayling migration but are less open to the movement of char, burbot, or lake trout. In addition, a large proportion of the grayling diet includes terrestrial insects, thereby connecting them strongly to terrestrial ecosystems; in contrast, the diets of char, burbot, and trout are almost exclusively aquatic. These properties clearly have implications for how the individual ecosystems respond to disturbance but complicate the use of the concept of openness when comparing the responses of terrestrial, stream, and lake ecosystems. We anticipate that the concept of community openness will continue to evolve as we gain new information and apply it to compare the responses of terrestrial, stream, and lake ecosystems to disturbance.

Graduate Student Organization: We maintain a graduate student representative to the LTER network (currently it is Adrianna Trusiak from the University of Michigan). However, we have had challenges maintaining an active and self-organized ARC LTER graduate student group, because the students are geographically dispersed among many schools around the country, and because the time they are in the field at Toolik varies, the only time that they can readily meet in person is at the winter meeting in Woods Hole. To help stimulate a more active graduate student organization, we propose to (1) have biannual reports from the graduate students to the Executive Committee (EC), organized by our ARC LTER graduate student representative, and (2) include the graduate student representative in at least part of our Executive Committee (EC) meeting prior to the ARC LTER winter meeting and in our EC conference call in the fall. At these meetings, this graduate student representative will be able to provide detail on the reports from our graduate student group or answer questions that the EC might have on how to improve the educational and research environment for our graduate students associated with our LTER and with the LTER network.

11. ARCTIC LTER PUBLICATIONS. A list of publications since the start of the ARC LTER in 1987 is available at the ARC LTER web site, http://arc-lter.ecosystems.mbl.edu/biblio.

Summary	Since Dec. 2016	Since 1975
Total Journal Articles	**64**	**650**
Number of unique journals	44	150
Contributing authors	712	1418
Total Books	**0**	**7**
Total Book Chapters	**1**	**96**
Total Student Works	**6**	**126**
PhD theses	5	42
Masters theses	1	69
Senior honor theses	0	15
Number of universities and colleges	5	36
Journal	Since Dec. 2016	Since 1975
Ecology	2	39
Global Change Biology	5	32
Hydrobiologia	0	30
Limnology and Oceanography	2	24
Oecologia	1	21
Ambio	1	20
Canadian Journal of Fisheries and Aquatic Sciences	1	19
Journal of Ecology	0	18
Freshwater Biology	1	18
Ecosystems	2	15
Ecological Applications	1	14
Arctic, Antarctic, and Alpine Research	0	14
BioScience	0	13
Geophysical Research Letters	3	12
Journal of the North American Benthological Society	0	11
Science	1	10
Ecological Monographs	1	10
Oikos	2	10
Applied and Environmental Microbiology	0	9
Journal of Geophysical Research: Atmospheres	0	9
Journal of Geophysical Research: Biogeosciences	0	9
Global Biogeochemical Cycles	1	9
New Phytologist	1	8
Arctic	0	8
Vereinigung Verhandlungen International Limnologie	0	8
Biogeochemistry	0	8
Nature	0	8
Water Resources Research	3	7
Environmental Research Letters	2	7
Proceedings of the National Academy of Sciences	2	7
Hydrological Processes	0	7
Soil Biology and Biochemistry	1	6
Biogeosciences	0	6
Arctic and Alpine Research	0	6
Journal of Plankton Research	0	6

Ecology Letters	1	6
Ecology and Evolution	4	5
Holarctic Ecology	0	5
Environmental Science and Technology	0	5
Ecological Modelling	1	5
Ecosphere	1	5
Frontiers in Microbiology	0	5
Other journals with fewer than 5 ARC papers since 1975	21	156
Total	**64**	**650**

12. CITATIONS

Abbott, B. W., G. Gruau, J. P. Zarnetske, F. Moatar, L. Barbe, Z. Thomas, O. Fovet, T. Kolbe, S. Gu, A.-C. Pierson-Wickmann, P. Davy, and G. Pinay. 2018. Unexpected spatial stability of water chemistry in headwater stream networks. Ecology Letters 21:296-308.

Adams, HE, BC Crump, and GW Kling. 2014. Metacommunity dynamics of bacteria in a freshwa-ter lake; the role of species sorting and mass effects. Frontiers in Aquatic Microbiology 5(82):1-10. doi: 10.3389/fmicb.2014.00082

Adams, H. E., B. C. Crump, and G. W. Kling. 2015. Isolating the effects of storm events on arctic aquatic bacteria: temperature, nutrients, and community composition as controls on bacterial productivity. Frontiers in Aquatic Microbiology doi: 10.3389/fmicb.2015.00250

Asmus, A., A. Koltz, J. McLaren, G. Shaver, and L. Gough. 2018. Long-term nutrient addition alters arthropod community composition but does not increase total biomass or abundance. Oikos 127: 460–471, 2018 doi: 10.1111/oik.04398

Atkin, OK, KJ Bloomfield, PB Reich, et al. 2015. Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. New Phytologist 206: 614-636 doi 10.1111/nph.13253

Biggs, J., N. Ewald, A. Valentini, C. Gaboriaud, T. Dejean, R. A. Griffiths, J. Foster, J. W. Wilkinson, A. Arnell, P. Brotherton, P. Williams, and F. Dunn. 2015. Using eDNA to develop a national citizen science-based monitoring programme for the great crested newt (Triturus cristatus). Biological Conservation 183:19-28.

Bowden, WB, MN Gooseff, A Balser, A Green, BJ Peterson, and J Bradford. 2008. Sediment and nutrient delivery from thermokarst features in the foothills of the North Slope, Alaska: Potential impacts on headwater stream ecosystems. Journal of Geophysical Research 113: G02026, doi:10.1029/2007JG000470

Bret-Harte MS, MC Mack, GR Shaver, DC Huebner, M Johnston, C Mojica, C Pizano and JA Reiskind. 2013. The response of Arctic vegetation and soils following an unusually severe tundra fire Philos. Trans. R. Soc. B 368 20120490

Budy, P, and C Lueke. 2014. Understanding how lake populations of arctic char are structured and function with special consideration of the potential effects of climate change: a multi-faceted approach. Oecologia 176:81-94.

Budy, P. , A. Giblin, G. Kling, D. White, and C. Luecke. *In review*. Understanding the indirect effects of climate change on pristine arctic lakes and char; delayed, multi-trophic level response and recovery to a long-term, low-level fertilization experiment. *Submitted to* Ecology.

Bushaw, KL, RG Zepp, MA Tarr, D Schulz-Jander, RA Bourbonniere, RE Hodson, WL Miller, DA Bronk, and MA Moran. 1996. Photochemical release of biologically available nitrogen from aquatic dissolved organic matter. Nature 381:404-407.

Chapin, FS, III, GR Shaver, AE Giblin, KG Nadelhoffer, and JA Laundre. 1995. Respons-es of arctic tundra to experimental and observed changes in climate. Ecology 76:694-711.

Cherry, JE, SJ Dery, Y Cheng, M Stieglitz, AS Jacobs, and F Pan. 2014. Climate and hydrometeorology of the Toolik Lake region and the Kuparuk River basin: Past, present, and future. Pages 21-60 in Hobbie, JE, and GW Kling (eds), Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams and Lakes. Oxford University Press, New York, NY, USA.

Christie, KS, JP Bryant, L Gough, VT Ravolainen, RW Ruess, and KD Tape. 2015. The role of vertebrate herbivores in regulating shurp expansion in the Arctic: a synthesis. BioScience 65: 1123-1133.

Cory, R. M., B. C. Crump, J. A. Dobkowski, and G. W. Kling. 2013. Surface exposure to sunlight stimulates CO2 release from permafrost soil carbon in the Arctic. Proc. National Academy of Sciences 110:3429-3434, doi/10.1073/pnas.1214104110. 10.1073/pnas.1214104110

Cory, R. M., C. P. Ward, B. C. Crump, and G. W. Kling. 2014. Sunlight controls water column processing of carbon in arctic fresh waters. Science 345:925-928. *doi: 10.1126/science.1253119*

Cory, R. M., K.H. Harrold, B. T. Neilson, and G.W. Kling. 2015. Controls on dissolved organic matter (DOM) degradation in a headwater stream: the influence of photochemical and hydrological conditions in determining light-limitation or substrate-limitation of photo-degradation. Biogeosciences 12:6669-6685. *doi:10.5194/bg-12-6669-2015*

Crump, B. C., H. E. Adams, J. E. Hobbie, and G. W. Kling. 2007. Biogeography of bacterioplankton in lakes and streams of an Arctic tundra catchment. Ecology 88:1365-1378.

Crump, B. C., L. A. Amaral-Zettler, and G. W. Kling. 2012. Microbial diversity in arctic freshwaters is structured by inoculation of microbes from soils. The ISME Journal 2012:1-11. doi:10.1038/ismej.2012.9

Curasi, SR, TC Parker, AV Rocha, ML Moody, J Tang, and N Fetcher. 2019. Differential resposes of ecotypes to climate in a ubiquitous arctic sedge: implications for future ecosystem C cycling. New Phytologist doi 10.1111/nph.15790

Daniels, WC, GW Kling, and AE Giblin. 2015. Benthic community metabolism in deep and shallow arctic lakes during 13 years of whole-lake fertilization. Limnology and Oceanography 60: 1604-1618.

Dornelas, M, LH Antao, F Moyes, et al. 2017. BioTIME: A database of biodiversity time series for the Anthropocene. Global Ecol Biogeogr doi 10.1111/geb.12729

Evans, NT, BP Olds, MA Renshaw, CR Turner, Y Li, CL Jerde, AR Mahon, ME Pfrender, GA Lamberti, and DM Lodge. 2016. Quantification of mesocosm fish and amphibian species diversity via envi-ronmental DNA metabarcoding. Molecular Ecology 16:29-41

Gettel, G.M., A.E. Giblin, R.W. Howarth. 2007. The effects of grazing by the snail Lymnaea elodes on benthic N-fixation and primary production in oligotrophic arctic lakes. Limnol. Oceanogr. 52: 2398-2409.

Gough, L, GR Shaver, J Carrol, DL Royer, and JA Laundre. 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. J Ecology 88: 54-66.

Gough, L, ND Bettez, KA Slavik, WB Bowden, AE Giblin, GW Kling, JA Laundre, and GR Shaver. 2016. Effects of long-term nutrient additions on arctic tundra, stream, and lake ecosystems: beyond NPP. Oecologia 182:653-665.

Hamilton, TD. 2003. Glacial Geology of the Toolik Lake and Upper Kuparuk River Regions. Biological Papers of the University of Alaska # 26, Institute of Arctic Biology, Fairbanks AK, USA.

Harms, T. K., J. W. Edmonds, H. Genet, I. F. Creed, D. Aldred, A. Balser, and J. B. Jones. 2016. Catchment influence on nitrate and dissolved organic matter in Alaskan streams across a latitudinal gradient. Journal of Geophysical Research-Biogeosciences 121:350-369.

Hershey, A. E., W. B. Bowden, L. A. Deegan, J. E. Hobbie, B. J. Peterson, G. W. Kipphut, G. W. Kling, M. A. Lock, R. W. Merritt, M. C. Miller, J. R. Vestal, and J. A. Schuldt. 1997. The Kuparuk River: A long-term study of biological and chemical processes in an arctic river. Pages 107-130 in A. Milner and M. W. Oswood, editors. Freshwaters of Alaska. Springer-Verlag, NY.

Hobbie, J. E., G. R. Shaver, E. R. Rastetter, J. E. Cherry, S. J. Goetz, K. C. Guay, W. A. Gould, and G. W. Kling. 2017. Multiple ecosystem responses to climate change at a Low Arctic and a High Arctic long-term research site. Ambio 46: S160–S173, *doi: 10.1007/s13280-016-0870-x.*

Hobbie, JE, and GW Kling (eds). 2014. Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams and Lakes. Oxford University Press, New York, NY, USA.

Hu, FS, PE Higuera, J Walsh, WL Chapman, PA Duffy, LB Brubaker, and ML Chipman. 2010. Tundra burning in Alaska: Linkages to climatic change and sea-ice extent. J Geophys. Res. 115: G04002

Jiang, Y, EB Rastetter, AV Rocha, AR Pearce, BL Kwiatkowski, GR Shaver. 2015. Modeling Carbon-Nutrient interactions during the early recovery of tundra after fire.. Ecological Applications 25:1640-1652.

Jiang, Y, EB Rastetter, GR Shaver, AV Rocha, Q Zhuang, and BL Kwiatkowsk. 2017. Modeling long-term changes in tundra carbon balance following wildfire, climate change, and potential nutrient addition. Ecological Applications 27:105-117

Jiang, Y, AV Rocha, EB Rastetter, GR Shaver, U Mishra, Q Zhuang, BL Kwaiatkowski. 2016. C-N-P interactions control climate driven changes in regional patterns of C storage on the North Slope of Alaska. Landscape Ecol. 31: 195-213. DOI 10.1007/s10980-15-0266-5

Judd, K. E. and G. W. Kling. 2002. Production and export of dissolved C in arctic tundra mesocosms: the roles of vegetation and water flow. Biogeochemistry 60:213-234.

Keller, K., J. D. Blum, and G. W. Kling. 2010. Stream geochemistry as an indicator of increasing thaw depth in an arctic watershed. Chemical Geology 273:76-81.

Kelly, R. 2016. Making environmental DNA count. Molecular Ecology Resources. 16:10–12.

Khosh, M. S., J. W. McClelland, A. D. Jacobson, T. A. Douglas, A. J. Barker, and G. O. Lehn. 2017. Seasonality of dissolved nitrogen from spring melt to fall freezeup in Alaskan Arctic tundra and mountain streams. Journal of Geophysical Research-Biogeosciences 122:1718-1737.

Kling, GW, HE Adams, ND Bettez, WB Bowden, BC Crump, AE Giblin, KE Judd, K Keller, GW Kipphut, EB Rastetter, GR Shaver, and M Stieglitz. 2014. Land-water interactions. Pages 143-172 in Hobbie, JE, and GW Kling (eds), Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams and Lakes. Oxford University Press, New York, NY, USA.

Kling, GW, GW Kipphut, MM Miller, and WJ O'Brien. 2000. Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. Freshwater Biol. 43: 477-497.

Klobucar, S. L., T. W. Rodgers, and P. Budy. 2017. At the forefront: evidence of the applicability of using environmental DNA to quantify the abundance of fish populations in natural lentic waters with additional sampling considerations. Canadian Journal of Fisheries and Aquatic Sciences 74:2030-2034.

Klobucar, SL, JW Gaeta, and P Budy. 2018. A changing menu in a changing climate: Using experimental and long-term data to predict invertebrate prey biomass and availability in lakes of arctic Alaska. Freshwater Biology DOI: 10.1111/fwb.13162

Klobucar, S.L., and P. Budy. *In review.* Assessing the abiotic and biotic factors that structure lake food webs with populations of arctic char (*Salvelinus alpinus)* in arctic Alaska. *Submitted to* Oecologia.

Klobucar, S.L., J.A. Rick, E.G. Mandeville, C.E. Wagner, and P. Budy. In prep. Investigating the morphological and genetic diversity of arctic char (*Salvelinus alpinus)* populations in distinct groups of foothill lakes in arctic Alaska. To be submitted to Ecology & Evolution

Koltz, AM, Asmus, AA, Gough, L, Pressler, Y, Shaver, G, and JC Moore. Aboveground and belowground consumer communities display parallel functional responses to unprecedented tundra fire. in prep

Lynch, LM, MB Machmuller, MF Cotrufo, EA Paul, and MD Wallenstein. 2018. Tracking the fate of fresh carbon in the Arctictundra: Will shrub expansion alter responses of soil organic matter to warming?Soil Biology & Biochemistry,120, 134–144. https://doi.org/10.1016/j.soilbio.2018.02.002

Machmuller, M., L. Lynch, S. Mosier, G.R. Shaver, F. Calderon, L. Gough, J.R. McLaren, E. Paul, M.N. Weintraub, M.F. Cotrufo, and M.D. Wallenstein. In prep. Plant-soil-microbe interactions lead to the recovery of Arctic soil C stocks after long-term nutrient fertilization.

Mack MC, EAG Schuur, MS Bret-Harte, GR Shaver GR, and FS Chapin. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431:440-3.

McGraw, JB, JB Turner, S Souther, CC Bennington, MC Vavrek, GR Shaver, and N Fetcher. 2015. Northward displacement of optimal climate conditions for ecotypes of Eriophorum vaginatum L. across a latitudinal gradient in Alaska. Global Change Biol 21:3827-3835.

Moore, J.C., P. Budy, L. Gough, A. Huryn, A. Koltz, S.M. Parker, Y. Pressler, G.R. Shaver, and S. Simpson. In Prep. The Different Responses of Arctic Terrestrial and Aquatic Food Webs to Long-term Nutrient Additions

Myers-Smith, IH, BC Forbes, M Wilmking, et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts, and research priorities. Envirn Res Let 6: 045509 doi 10.1088/1748-9326/6/4/045509

Neilson, B. T., M. B. Cardenas, M. T. O’Connor, M. T. Rasmussen, T. V. King, G. W. Kling. 2018. Groundwater Flow and Exchange Across the Land Surface Explain Carbon Export Patterns in Continuous Permafrost Watersheds. Geophysical Research Letters 45(15):7596-7605. *doi: 10.1029/2018GL078140*

O'Brien, WJ, C Buchanan, JF Haney. 1979. Arctic Zooplankton Community Structure: Exceptions to Some General Rules. Arctic 32:237-247.

Pearce, AR, EB Rastetter, WB Bowden, MC Mack, Y Jiang, and BL Kwiatkowski. 2015. Recovery of arctic tundra from thermal erosion disturbance is constrained by nutrient accumulation: a modeling analysis. Ecological Applications 25:1271-1289.

Peterson, B. J., J. E. Hobbie, A. E. Hershey, M. A. Lock, T. E. Ford, J. R. Vestal, V. L. McKinley, M. A. J. Hullar, M. C. Miller, R. M. Ventullo, and a. G. S. Volk. 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. Science 229:1383-1386.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Feibig, V. McKinley, M. C. Miller, J. R. Vestal, R. Venutllo, and G. Volk. 1993. Biological response of a tundra river to fertilization. Ecology 74(3):653-672.

Peterson, BJ, JE Hobbie, TL Corliss, and K Kriet. 1983. A continuous-flow periphyton bioassay: Tests of nutrient limitation in a tundra stream. Limnol. Oceanogr.28: 583-591

Rastetter , EB, GW Kling, L Gough, WB Bowcen, A Giblin, P Budy, and GR Shaver. In Prep. Role of biogeochemical openness in the response of ecosystems to climate chagne and disturbance

Rastetter, E, M Ohman, K Elliott, J Rehage, V Rivera-Monroy, R Boucek, E Castañeda-Moya, T Danielson, L Gough, P Groffman, CR Jackson, C Miniat, G Shaver. Submitted. Future Trajectories for Ecosystems in the U.S. Long-Term Ecological Research Network: The Importance of Time Lags. Ecosphere.

Rees, H. C., B. C. Maddison, D. J. Middleditch, J. R. M. Patmore, and K. C. Gough. 2014. REVIEW The detection of aquatic animal species using environmental DNA - a review of eDNA as a survey tool in ecology. Journal of Applied Ecology 51:1450-1459.

Rocha, AV, B Blakely, Y Jiang, K Wright, and S Curasi. In Prep. Is arctic greening consistent with the ecology of tundra? Lessons from an ecologically informed mass balance model.

Rodgers, T., J.R. Olson, S.L. Klobucar, and K.E. Mock. 2017. Quantitative PCR assays for detection of five Alaskan fish species: *Lota lota*, *Salvelinus alpinus*, *Salvelinus malma*, *Thymallus arcticus*, and *Cottus cognatus* from environmental DNA. Conservation Genetics Resources. doi: 10.1007/s12686-017-0883-1

Romanovsky, V.E., S.L. Smith, and H.H. Christiansen. 2010. Permafrost thermal state in the polar northern hemisphere during the International Polar Year 2007–2009: A synthesis. Permafrost and Periglacial Processes 21: 106–116.

Roslin, T, B Hardwick, V Novotny, et al. 2017. Higher predation risk for insect prey at low latitudes and elevations. Science356:742-744.

Shaver, GR, and FS Chapin III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: Nutrient accumulation and growth. Ecology 61:662-675.

Shaver, GR, EB Rastetter, V Salmon, LE Street, MJ van de Weg, A Rocha, MT van Wijk, and M Williams. 2013. Pan Arctic modelling of net ecosystem exchange of CO2. Philosophical Transactions of the Royal Society B 368: 20120485 http://dx.doi.org/10.1098/rstb.2012.0485

Shaver, GR, JA Laundre, MS Bret-Harte FA Chapin III, JA Mercado-Diaz, AE Giblin, L Gough, WA Gould, SE Hobbie, GW Kling, MC Mack, JC Moore, KJ Nadelhoffer, EB Rastetter, and JP Schimel. 2014. Terrestrial ecosystems at Toolik Lake Alaska. Pages 90-142 in Hobbie, JE, and GW Kling (eds), Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams and Lakes. Oxford University Press, New York, NY, USA.

Shaver, GR, LE Street, EB Rastetter, MT van Wijk, and M Williams. 2007. Functional convergence in regulation of net CO2 flux in heterogeneous tundra landscapes in Alaska and Sweden. Journal of Ecology 95:802-817.

Shaver, GR, MS Bret-Harte, MH Jones, J Johnstone, L Gough, J Laundre, FS Chapin III. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. Ecology 82: 3163-3181.

Shaver, GS, JA Laundre, MS Bret-Harte, FS Chapin III, JA Mercado-Diaz, AE Giblin, L Gough, WA Gould, SE Hobbie, GW Kling, MC Mack, JC Moore, KJ Nadelhoffer, EB Rastetter, and JP Schimel. 2014. Terrestrial ecosystems at Toolik Lake. pp 90-142 in JE Hobbie and GW Kling (eds) Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams, and lakes. Oxford University Press, New York, New York, USA

Sistla, SA, JC Moore, RT Simpson, L Gough, GR Shaver, and JP Schimel. 2013. Long-term warm-ing restructures Arctic tundra without changing net soil carbon storage Nature 497 615-618

Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term response of the Kuparuk River ecosystem to phosphorus fertilization. Ecology 85:939-954.

Smith, EM, and R Benner. 2005. Photochemical transformations of riverine dissolved organic matter: Ef-fects on estuarine bacterial metabolism and nutrient demand. Aquat. Microb. Ecol. 40: 37–50.

Smith, MD, KJ La Pierre, SL Collins, AK Knapp, KL Gross, JE Barrett, SD Frey, L Gough, RJ Miller, JT Morris, LE Rustad, and J Yarie. 2015. Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. Oecologia DOI 10.1007/s00442-015-3230-9

Snyder, L., and W. B. Bowden. 2014. Nutrient dynamics in an oligotrophic arctic stream monitored in situ by wet chemistry methods. Water Resources Research 50:2039-2049.

Street, LE, GR Shaver, EB Rastetter, MT van Wijk, BA Kaye, and M Williams. 2012. Incident radiation and the allocation of nitrogen within arctic plant canopies: Implications for predicting gross primary productivity. Global Change Biology 18: 2838-2852.

Thomsen, P. F., J. Kielgast, L. L. Iversen, P. R. Moller, M. Rasmussen, and E. Willerslev. 2012. Detection of a Diverse Marine Fish Fauna Using Environmental DNA from Seawater Samples. Plos One 7.

Vähätalo, A, and R Zepp. 2005. Photochemical mineralization of dissolved organic nitrogen to ammoni-um in the Baltic Sea. Environ. Sci. Technol. 39: 6985–6992.

Walker, DA, TD Hamilton, HA Maier, CA Munger, and MK Raynolds. 2014. Glacial history and long-term ecology in the Toolik Lake region. Pages 61-80 in Hobbie, JE, and GW Kling (eds), Alaska’s Changing Arctic: Ecological Consequences for Tundra, Streams and Lakes. Oxford University Press, New York, NY, USA.

Williams, M. and E. B. Rastetter. 1999. Vegetation characteristics and primary productivity along an arctic transect: implications for scaling up. Journal of Ecology. 87: 885-898

Wollheim, W. M., B. J. Peterson, L. A. Deegan, J. E. Hobbie, B. Hooker, W. B. Bowden, K. J. Edwardson, D. B. Arscott, A. E. Hershsey, and J. Finlay. 2001. Influence of stream size on ammonium amd suspended particulate nitrogen processing. Limnology and Oceanography 46:1-13

Zarnetske, J. P., M. Bouda, B. W. Abbott, J. Saiers, and P. A. Raymond. 2018. Generality of Hydrologic Transport Limitation of Watershed Organic Carbon Flux Across Ecoregions of the United States. Geophysical Research Letters 45:11,702-711,711.

Zarnetske, P.L., M.C. Urban, D.K. Skelly, P. Budy, and S.L. Klobucar. *In prep.* Do climatic changes or biotic interactions explain the condition of Arctic freshwater fishes over 30 years? *To be submitted to* Global Change Biology

13. APPENDIX: Tables of (1) Major field sites, (2) Core monitoring and process studies, (3) long-term, whole-ecosystem manipulations, and (4) Current cooperating projects.

Table 1. Sampling sites of Arctic LTER research. For details of location and description see Fig. 1 and http://ecosystems.mbl.edu/ARC/.

Core study watersheds and watershed-scale comparisons used to integrate the LTER	
Toolik Inlet Watershed	A 48 km2 watershed of streams and lakes that forms the largest input of water and materials into Toolik Lake, located on the 10-60,000 yr aged surface
Upper Kuparuk Watershed	146 km2 watershed predominantly underlain by older Sagavanirktok-aged surfaces (~300,000 yr), extreme headwaters on 60,000 yr aged surface
Imnavait Watershed	2.2 km2 watershed with weir on primary stream and weir on one of many distinct water tracks; >300,000 yr surface. Long-term 15N tracer experiment
South River Watershed	115 km2 watershed of varying burn severity within 1000 km2 Anaktuvuk River Burn (mostly >300,000 yr aged surface)
Core disturbance sites	
Anaktuvuk River Burn	Multiple sites on 1000 km2 2007 burn including numerous whole catchments of varying burn severity and thermokarst activity
Atigun River Burn	18 ha 2004 burn monitored yearly by REU students
TLNRA Thermokarsts	Various thermokarst features within and near the Toolik Lake Natural Research Area (TLNRA), including gully thermokarsts (Toolik River, I-minus-2) and thaw slumps (lakes NE-14 and I-minus-1, and Imnavait Creek).
"Valley of Thermokarsts"	Numerous active layer detachments in 96 km2 sub-watershed of 2007 AR Burn
Terrestrial ecology and ecosystem comparisons	
Toolik Lake area including Toolik Inlet watershed	Multiple sites on Itkillik I and Itkillik II aged surfaces (10,000-60,000 yr old), including moist acidic and nonacidic tundras, wet sedge tundra, riparian tundra, and dry heath
Imnavait Creek	Toposequences on Sagavanirktok-age surface (~300,000 yr), ranging from dry heath to wet sedge and riparian shrub communities. 15N tracer experiment
Anaktuvuk River Burn	Multiple sites on areas of varying burn severity including South River watershed

Table 1 continued

Stream ecology and ecosystem comparisons	
Upper Kuparuk River	4th order, clear-water tundra stream; 25 km in length from origins to Dalton Hwy. crossing (146 km2 area); draining surfaces 60,000 to 300,000 yr old.
Oksrukuyik Creek	3rd order, clear-water tundra stream; 12 km in length (73.5 km2 area); tributary of the Sagavanirktok River. Headwaters in Itkillik 1 (~60,000) surface and mid- reaches in ~300,000 yr old Sagavanirktok 1 surface
South River, North River	Streams within Anaktuvuk River Burn
Trevor Creek	3rd order, moderate rock flour, mountain stream; 9 km in length, 42 km^2 area; tributary to the Atigun River.
Survey streams	Multiple streams in mountains and foothills representing Mountain, Glacier, Tundra and Spring stream types.
Lakes ecology and ecosystem comparisons	
Toolik Lake	25 m deep, 1.5 km2, ultra-oligotrophic, receives inputs of Toolik Inlet watershed
Survey lakes, Toolik Inlet series	Multiple lakes differing in geologic setting, area, depth, and trophic structure including fish
Experimental and Control Lakes	Paired Shallow and Deep lakes including controls (Fog-2, Fog-4), fertilized (E-5, E-6) and recovering lakes (N-1, N-2)
NE-14	Active glacial thermokarst on shore of 24 ha lake
Perched, Horn, Dimple Lakes	Shallow and deep lakes with/without fish in Anaktuvuk River Burn. Perched and Dimple lakes in South River watershed
Landscape Interactions and hillslope and catchment processes	
Tussock Watershed	1 ha watershed with a primary stream and weir located on South shore of Toolik Lake, ~60,000-100,000 yr aged surface
Imnavait Watershed	Long-term 15N tracer experiment, water-track hydrology and biogeochemistry, hillslope studies of water, C, N transport and cycling
Toolik Inlet Watershed (the “I-Series”)	A series of streams and lakes that form the largest input of water and materials into Toolik Lake, located on the 10,000 yr surface
South/North River and Dimple Watersheds	Watersheds of varying area and burn severity within the 1000 km2 Anaktuvuk River Burn

Table 2. Core monitoring and process studies to be carried out by the ARC LTER personnel. Detailed protocols and methods at: http://ecosystems.mbl.edu/arc/Datatable.html.

Location	**Type of measurement**	**frequency**
Climate, C, N, Energy Budgets, and Hydrology of LTER Core Watersheds		
Toolik Lake, Toolik Inlet, surrounding Landscape	Main climate station and several satellite stations, atmospheric deposition monitoring, inlet stream gauge, lake temperature, water level, and irradiance measures (aboveground and in the lake)	Daily, weekly, or continuous using data loggers; 3-6x per summer for nutrients; occasional early- and late- season visits
Upper Kuparuk Watershed, Upper Oksrukuyik Creek, Trevor Creek	Stream gauge, temperature at Dalton Highway crossing	as above
Imnavait Creek	Climate Station, stream weir, and multiple soil temp/moisture data loggers, 3 eddy flux towers along hillslope	as above
Anaktuvuk River Burn	Multiple stream gauges and autosamplers, in South and North River watersheds, data loggers and 3 eddy flux towers in South River watershed	as above
Terrestrial ecology and biogeochemistry		
Permanent plots along Dalton Highway and control plots of long-term experiments at Toolik Lake	Vegetation growth and flowering	Annual flower counts, seasonal phenological observations in some years
Control and treatment plots of long term experiments at Toolik Lake; occasional resampling of older plots for long term changes	Vegetation NPP, C and N uptake, soil C and N stocks	Weekly NDVI measurements in control and treatment plots every year; plant community composition sampled every year; major biomass harvests each year; sites depend on collaborating projects
Long term plots in contrasting vegetation/soils at Toolik Lake	N mineralization, thaw depth	Annually at approximately the same time

Table 2 continued		
Anaktuvuk River Burn sites	Disturbance effects on vegetation, soils	Biomass, NPP harvests in collaboration with Rocha LTREB grant; C and N stocks
Stream ecology and biogeochemistry		
Kuparuk River and Oksrukuyik Creek	Transport in river, pelagic/benthic linkages, flow, temperature, conductivity, alkalinity, SRP, TDP, PP, NO3, NH4, TDN, PON, DOC, POC, chlorophyll in seston and on rocks, insects, moss cover, fish (young, adult)	3-4x per summer for nutrients, chlorophyll, moss, insects and fish; continuous measurement of stream metabolism
Kuparuk River and tributaries	Macroinvertebrate life cycles, seasonality	Seasonal sampling of invertebrate life cycles and growth rates
Kuparuk River and tributaries	Fish habitats and growth, changes in seasonality	Seasonal sampling of growth rates, habitats, and food sources
Anaktuvuk Burn and TLRNA thermokarst sites. and surveys of other stream types.	Disturbance effects on stream communities, chemistry. Flow, temperature, conductivity, alkalinity, SRP, TDP, PP, NO3, NH4, TDN, PON, DOC, POC, chlorophyll in seston and on rocks, insects, moss cover, fish (young, adult)	1-3 times per summer with collaborating projects
Lake ecology and biogeochemistry		
Monitoring of Toolik Lake Main Station	In situ profiling of temperature, conductivity, pH, PAR, chlorophyll, and water transparency. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity. Monitoring of planktonic communities. Estimation of primary productivity and bacterial production through radioisotope incubation.	Weekly ice off through ice on

Table 2 continued

Monitoring of Toolik Lake Inlet and Outlet	In situ profiling of temperature, conductivity, and pH. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity.	Weekly ice off through ice on
Monitoring of Sentinel Lakes NE9B, NE12, S6, S7, S11, Fog 2, Fog 4, I1, I2, I3, I4, I5, I6HW, I6, I7, I8 ISwamp, LTER 346, and LTER 347.	In situ profiling of temperature, conductivity, pH, PAR, chlorophyll, and water transparency. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity. Monitoring of planktonic, and benthic invertebrate communities, and selected LTER fish communities.	1-2x per every other year
Monitoring of Disturbance (fire, thermokarst) Recovery Lakes (Dimple, Horn, Perched Lake in Anaktuvuk Burn and thermokarst lake LTER 345 and Lake NE14)	In situ profiling of temperature, conductivity, pH, PAR, chlorophyll, and water transparency. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity. Monitoring of planktonic communities and selected fish communities.	Lake LTER 345 2x per year. NE14 1x per every other year
Monitoring of recovery in Nutrient Enrichment Lakes (low level addition) Lake E5 and Lake E6	In situ profiling of temperature, conductivity, pH, PAR, chlorophyll, and water transparency. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity. Monitoring of planktonic and fish communities. Estimation of primary productivity and bacterial production through radioisotope incubation.	3x per year

Table 2 continued		
Monitoring of recovery in Nutrient Enrichment Lakes (low level addition) Lake N1 and N2	In situ profiling of temperature, conductivity, pH, PAR, chlorophyll, and water transparency. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity. Monitoring of planktonic communities.	1x per every other year
Monitoring of New Warming Experiment Lake Fog 1, Lake Fog 2, and Lake Fog 3	In situ profiling of temperature, conductivity, pH, PAR, chlorophyll, and water transparency. Laboratory analysis chlorophyll-a, organic and inorganic fractions of carbon, nitrogen, and phosphorus, major dissolved cations and anions, and alkalinity. Monitoring of planktonic, benthic invertebrate, and fish communities. Monitoring of metrological parameters. Estimation of primary productivity and bacterial production through radioisotope incubation.	Bimonthly ice off through ice on
Linkage between stream inflow and lakes Toolik Lake and Toolik Inlet series	Chemistry, primary and bacterial production, and thermal structure measurements at times of wind or rain events	Weekly for chemistry, prim prods. Continuous for temperature Event-based for chemistry and production
Dimple, Horn, Perched Lake in Anaktuvuk Burn, Lake NE-14	Disturbance effects on lake communities and biogeochemistry	1-3x per year in with collaborating projects
Landscape Interactions		
Tussock watershed and Imnavait Creek.	Soil water chemistry and transfer to primary streams. Soil water and stream nutrients and organic matter to estimate production in soils and flux out of primary catchments and "water tracks" (sites of occasional surface water flow)	3x per year for soils at ca. 30 sites; Weekly plus event-based for stream chemistry.
Toolik Inlet series of lakes and streams; I-Series of connected lakes and streams flowing into Toolik	Water inorganic and organic chemistry, primary and bacterial production, chla to determine interactions of aquatic systems across the landscape	3x/year sampling of 11 lake and 24 stream sites

Table 2 continued		
Effects of long-term (press) disturbance	Tussock Watershed thaw grid and Imnavait basin thaw grid.	ca. 100 sites at each location, 2 surveys per year.

Table 3. Core long-term whole ecosystem experimental manipulations.

Sites	Experimental treatment	Principal measurements	Status & sampling
Terrestrial			
5 contrasting vegetation types at Toolik Lake	Fertilizer, warming, shading experiments	Vegetation greenness (NDVI), NPP, biomass, soil C/N/P stocks and turnover, plant and soil communities	Started 1980-89; Continue treatments except now monitoring recovery of experiments begun in 1981
Moist acidic and heath tundra, Toolik	Herbivore exclosure x fertilizer addition	As above	Started 1996; continue treatments; harvest with collaborating projects TBD
Moist acidic tundra, Toolik	Species removal x fertilizer addition	As above	Started 1997; continue treatments; harvest with collaborating projects TBD
Moist acidic tundra, Toolik	Multilevel NxP factorial fertilizer addition	As above	Started 2006; continue treatments; NDVI weekly each summer; harvest with collaborating projects planned for 2020
Streams			
Kuparuk River	Seasonal constant phosphate addition to 0.3 µM level final concentration	GPP, respiration, nutrient cycling, autotrophic communities, macroinvertebrate communities and production, fish ecology	Started 1979, continue sampling 3- 4 x per summer. Experimental fertilization stopped in 2017. Now monitoring recovery.
Kuparuk River	New moss re-establishment experiment in previously-fertilized recovery reach	GPP, respiration, nutrient cycling, autotrophic communities, macroinvertebrate communities and production, fish ecology	Start 2011; sampling 2-3 x per year

Table 3 continued			
Lakes			
Lakes Fog1,2,3, and 5	Experimental lake warming, add heat continuously with 3 warming units	All trophic levels from bacteria to fish, including benthic and pelagic production, and physiochecmial measurements	2016 = pre-manipulation sampling, 4x per year
Lakes E-5, E-6 (control lakes Fog-2, Fog-4)	Nutrient addition once per week to increase nutrient loadings by 50%	Alkalinity, nutrients, DOM, chlorophyll, zooplankton in seepage and drainage lakes; Regional fish survey	Started 2000; continue sampling 3x per year; fertilization terminated in 2012; now in "recovery"
Lakes N-1, N-2	Fertilizer treatments discontinued	Monitor recovery as above	1-3x per year, 2011-2016
Landscape Interactions			
Inlet Series of Lakes feeding into Toolik Lake	Closure of Lake I1 and I2 outlets, starting in summer 2020	Chemistry and discharge of outlet streams from Lakes I1 and I2.	Pre-manipulation data since 1991; intensified in 2018.

Table 4. Collaborating projects.

Grant title	**Investigators**	**funding-source**	**start-date**	**end-date**
LTREB: Following the reorganization and resynchronization of biogeochemical cycles after an unprecedented tundra fire	Adrian Rocha, Edward Rastetter	NSF-LTREB	5/1/2016	4/30/2021
Collaborative Research: Quantification of Dominant Heat Fluxes in Streams and Rivers in the Arctic	Bethany Neilson, Doug Kane	NSF - OPP	1/1/2012	12/31/2018
Scaling the Ecology of Soil Carbon.	Bruce Hungate	DOE	8/1/2016	7/31/2019
Falmouth K-12 teachers experience at Toolik	Edward Rastetter	Friends of the MBL	5/1/2017	12/1/2019
Biogeochemical Responses to Variations in Climate and Disturbance in Terrestrial Ecosystems	Edward Rastetter	NSF-DEB	8/15/2017	8/14/2020
LTREB Renewal: Collaborative research: What controls long-term changes in freshwater microbial community composition?	Byron Crump, George Kling	NSF - DEB	1/1/2012	12/31/2018
Advancing InSAR Technology for Monitoring and Prediction of the Hydrologic State of Permafrost Terrain in the Arctic	Ann Chen, Bayani Cardenas, George Kling	NASA	1/1/2018	12/31/2020
Collaborative Research - Coupled biological and photochemical degradation of dissolved organic carbon in the Arctic	Byron Crump, Rose Cory, George Kling	NSF - DEB	1/1/2018	12/31/2021
LiDAR, passive spectral, and ecophysiological approaches to link Forest Tundra Ecotone structure and function	Jan Eitel, Lee Vierling, Natalie Boelman, Kevin Griffin	NASA	1/1/2015	12/31/2019
Collaborative Research: Research Opportunity Award: Temperature Optima for photosynthesis in *Eriophorum vaginatum*: a foundation species of tussuck tundra	Jessica Schedlbauer	NSF-GEO	1/19/2016	12/31/2017

Table 4 continued				
Nitrogen cycling feedbacks between snow and shrubs in a warming Arctic	Marion Bret-Harte, Michelle Mack, Roger Ruess	NSF-DEB	1/8/2016	31/7/2019
Collaborative Research: Carbon, Water, and Energy Balance of the Arctic Landscape at Flagship Observatories in Alaska and Siberia	Marion Bret-Harte, George Kling, Edward Rastetter	NSF-OPP	3/15/2016	2/29/2020
Collaborative Research: Adaptability of a key Arctic freshwater species to climate change	Mark Urban	NSF-OPP	1/1/2015	12/31/2017
CAREER: Microbial Allocation of Assimilated Carbon: Interactions between Temperature, Substrate Quality, and Microbial Physiology Determine Efficiency of Arctic Soil Carbon Cycling	Matthew Wallenstein	NSF OPP	7/1/2013	6/30/2019
Testing the influence of long-term ecological change on evolutionary responses in zooplankton	Matthew Walsh	NSF-DEB	8/1/2015	7/31/2018
Collaborative Research: Arctic Oases - How does the delayed release of winter discharge from aufeis affect the ecosystem structure and function of rivers	Michael Gooseff Alex Huryn	NSF-ANS	3/15/2016	2/29/2020
Collaborative Research: Local Adaptation in a Dominant Arctic Tundra Sedge (Eriophorum Vaginatum) and its Effects on Ecosystem Response in a Changing Climate	Michael Moody, Jianwu Tang, Ned Fetcher	NSF-GEO	1/1/2015	12/31/2017
Climate warming and disturbance regimes in the far north.	Michelle Mack	NCEAS	1/8/2009	30/6/2010
Collaborative Research: The roles of plant roots, mycorrhizal fungi and uptake of deep nitrogen in the permafrost carbon feedback to warming climate	Michelle Mack, Lee Taylor, Dave McGuire, Helene Genet	NSF-PLR	1/6/2015	31/5/2018
Increasing fire severity and the loss of legacy carbon from forest and tundra ecosystems of Northwestern North America	Michelle Mack	NASA	1/8/2015	31/7/2019

Table 4 continued

Collaborative Research: Adding animals to the equation: linking herbivore impacts on carbon cycling in northern Alaska	Natalie Boelman, Laura Gough, Jennie McLaren, Rebecca Rowe, Edward Rastetter, Kevin Griffin	NSF-OPP/ARCSS	10/1/2019	9/30/2021
Collaborative Research: An exploration of the direct and indirect effects of climatic warming on arctic lake ecosystems.	Phaedra Budy, Byron Crump, Anne Giblin	NSF-OPP	7/15/2016	6/30/2021
Iron and reactive oxygen species in the oxidation and fate of dissolved organic matter	Rose Cory	NSF - CAREER	1/1/2015	12/31/2019
Science Theme Proposal. “Interactions of iron and organic matter as controls on the fate of permafrost carbon in the Arctic”	Rose Cory	DOE – EMSL	1/1/2016	12/31/2018
Dimensions: Collaborative Research: Community genomic drivers of moss microbiome assembly and function in rapidly changing Alaskan ecosystems	SA McDaniel	NSF-DEB	1/8/2015	31/7/2020
EAGER SitS: Collaborative Research: Projecting Arctic soil and ecosystem responses to warming using SCAMPS: A stoichiometrically coupled, acclimating microbe-plant-soil model	Seeta Sistla, Edward Rastetter	NSF-OPP	9/1/2018	8/31/2020
Assessing the Effects of Climate Change on the Net Metabolism and Carbon Cycling of Arctic Lakes	Soren Brothers	Utah State University (Seed Grant)	1/1/2019	12/31/2019
Winter respiration in the Arctic: Constraining current and future estimates of CO2 emissions during the non-growing season	Susan Natali	NASA	10/1/2015	9/31/2019
NNA: Collaborative Research: Interactions of the Microbial Iron and Methane Cycles in the Tundra Ecosystem	William B Bowden, David Emerson	NSF-DEB	10/1/2018	9/30/2021

Table 4 continued

Collaborative Research: Stream Consumers and Lotic Ecosystem Rates (SCALER): Scaling from Centimeters to Continents	William B Bowden, Michael Flinn	NSF-Macrosystems	10/1/2011	8/31/2017
Collaborative research: reconciling conflicting Arctic temperature and fire reconstructions using multi-proxy records from lake sediments north of the Brooks Range, Alaska	Yonsong Huang	NSF-OPP	7/1/2015	7/1/2018