

2012-01-01

Implications Of Decade Time Scale Arctic Plant Community Change On Ecosystem Function

Mark Jason Lara

University of Texas at El Paso, mjlara@miners.utep.edu

Follow this and additional works at: https://digitalcommons.utep.edu/open_etd



Part of the [Biogeochemistry Commons](#), [Climate Commons](#), [Ecology and Evolutionary Biology Commons](#), and the [Environmental Indicators and Impact Assessment Commons](#)

Recommended Citation

Lara, Mark Jason, "Implications Of Decade Time Scale Arctic Plant Community Change On Ecosystem Function" (2012). *Open Access Theses & Dissertations*. 1861.

https://digitalcommons.utep.edu/open_etd/1861

This is brought to you for free and open access by DigitalCommons@UTEP. It has been accepted for inclusion in Open Access Theses & Dissertations by an authorized administrator of DigitalCommons@UTEP. For more information, please contact lweber@utep.edu.

IMPLICATIONS OF DECADE TIME SCALE ARCTIC PLANT COMMUNITY
CHANGE ON ECOSYSTEM FUNCTION

MARK JASON LARA

Department of Biological Sciences

APPROVED:

Craig E. Tweedie, Ph.D., Chair

Steven F. Oberbauer, Ph.D.

Vanessa L. Lougheed, Ph.D.

Elizabeth J. Walsh, Ph.D.

Benjamin C. Flores, Ph.D.
Dean of the Graduate School

Copyright
by
Mark J. Lara
2012

IMPLICATIONS OF DECADE TIME SCALE ARCTIC PLANT COMMUNITY
CHANGE ON ECOSYSTEM FUNCTION

by

MARK JASON LARA, B.Sc.

DISSERTATION

Presented to the Faculty of the Graduate School of

The University of Texas at El Paso

in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences

THE UNIVERSITY OF TEXAS AT EL PASO

December 2012

Acknowledgements

No monumental task can be completed alone. I would like to extend my deepest and sincerest gratitude to the many people who helped me throughout the various challenges that seemed to emerge far too often:

First and foremost I would like to thank my advisor, mentor, and editor, Dr. Craig E. Tweedie, who showed me the path to achieve greatness. Dr. Tweedie made countless opportunities available for interested-hard working students to join his research group. His excitement and passion for scientific advancement, was contagious, transferring to myself and many others. Dr. Tweedie has been among my top 5 most influential people in my life thus far, and for this I am extremely grateful. I would also like to thank many others that had a close hand in my success: My committee members, Vanessa L. Lougheed, Steven F. Oberbauer, Elizabeth J. Walsh, for their time and feedback; David R. Johnson for countless draft revisions, statistical advice, and the voice of scientific reason; David H. Lin for teaching, trouble shooting, and being around to help simplify my seemingly complex ideas; Sandra Villarreal for being my BTF partner/friend to help me keep my sanity when times got hard; Jerald Brady for software development potentially reducing my data processing time by a minimum of 3 months, and for all our philosophical conversations; Ryan Cody for hours GIS support, I.T. support, and help in the field; Santonu Goswami and Paulo Olivas for trouble shooting and assistance with the Unispec DC and the LICOR 6200. I would also like to thank Mayra Melendez, Stephanie Robinson, Ana Garcia, and Cristina Subt, for countless tedious hours of biomass sorting. I am also extremely grateful to the PIs from UTEP's NSF funded GK-12 program, Vanessa L. Lougheed, Aaron Velasco, William (Bill) Robertson, and Cynthia Ramirez. I was funded by this program during the final year of my Ph.D., and during this time I learned a great deal about teaching, leadership, and mentorship from the PIs, fellows, and teachers.

I would also like to thank my family, for their love and support throughout my time at UTEP. Our competitive nature has pushed me to chase my dreams and each day I find myself a little bit closer to the prize. Lastly, I am extremely blessed to be married to the wonderful Melissa M. Lara that loves

and supports me, perhaps more importantly, puts up with all the late nights and canceled dates for the sake of work. You are truly my missing piece.

This project was funded through support from the National Science Foundation, Office of Polar Programs (grant no. ANS-0732885) and the Cyber-Share Center of Excellence, (grant no. HRD-0734825). We thank the Ukpęvik Iñupiat Corporation (UIC) for land access; and the Barrow Arctic Science Consortium (BASC) for logistical support. Any opinions, findings, conclusions, or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

Abstract

Almost half the global soil organic carbon pool is found in northern high latitudes. The majority of this soil carbon is stored in a greenhouse inert state within permafrost. As pronounced warming of high northern latitudes ensues, there is a strong likelihood that this substantial soil organic carbon pool will be mobilized to the atmosphere where it is likely to positively enhance greenhouse warming. Modeling studies suggest this positive feedback could alter future climate states of the Arctic and the globe, and affect how humans may need to adapt to climate change. Accordingly, understanding the patterns and controls and the fate and transport of carbon in arctic terrestrial ecosystems has become well recognized as a research priority.

This dissertation focuses on improving knowledge of decade-time scale plant community change and its impact on ecosystem function (i.e. biogeochemical cycling, and energy balance) in select sites throughout the North American Arctic. The studies presented largely take advantage of historic research activities conducted between the late 1950's and mid-1970s that have been resampled to assess change in ecosystem structure (i.e. makeup of plant species and abundance) and ecosystem function. The overarching goal of this dissertation is to determine how ecosystem function has changed in central Baffin Island, Canada, and in northern Alaska near Barrow in response to changes in climate, herbivory, nutrient availability, and plant community change over the past 30-60 years.

In collaboration with Dr. Patrick J. Webber, this International Polar Year Back to the Future (BTF) project's primary objective was to determine how structure and function of high latitude arctic terrestrial ecosystems have changed over the past 25 or more years. At two sites, Baffin Island Canada, and Barrow Alaska, we used newly developed multivariate-geostatistical analytical procedure to assess change in ecosystem function over time. At our site in central Baffin Island, the greatest change in ecosystem function was noted for plant communities with high soil moisture. For example, two pond margin communities: *Campylium-Aulacomnium*-moss meadows and *Eriophorum-Pleuropogon* wetlands increased in biomass by 178% and 46%, while NDVI increased 35% and 16%, respectively. Soil moisture was found to decrease in *Carex* stands wet meadows and *Campylium-Aulacomnium*-moss meadows by 30% and 24%, respectively. Other changes were heterogeneous and largely plant

community specific. Similarly, in Barrow Alaska, the greatest change in ecosystem function was found for aquatic and wet plant communities, where productivity varied and soil moisture increased along with methane flux over time. Interestingly, our functional models appeared to be responsive to years with high lemming populations, which were found to decrease albedo and NDVI, while increasing methane fluxes for both aquatic *Carex* graminoid and wet graminoid tundra. Further, moist and dry communities which decreased in soil moisture between 1972-2010 appeared more stable through time, with little change found in structure and function.

During the summer of 2010, a range of ecosystem functional properties were measured in replicate 2 x 2 m herbivore exclusion plots, and adjacent control plots established in wet, moist, and dry land cover types (LCTs) near Barrow, Alaska in 1959. We sought to determine the functional implications of long-term lemming exclusion in wet, moist and dry LCTs, and extrapolated results to the landscape scale. We found herbivore effects to vary between LCTs and the strongest differences between exclosures and control plots were found in wet graminoid tundra. Herbivore exclusion in wet tundra increased albedo (+10%), but decreased thaw depth (-37%), saturated soil layer (-28%), normalized difference vegetation index (-20%), methane flux ($-23\text{mgC m}^{-2} \text{ day}^{-1}$), and increased loss of CO_2 to the atmosphere through increased net ecosystem exchange ($+1.75\text{gC m}^{-2} \text{ day}^{-1}$). Further, lemming exclusion decreased saturated soil layer (-47%) for moist, and decreased thaw depth (-20%) for dry LCTs, while no other significant effects were detected in these LCTs. Measurements of ecosystem function for grazed (control) and ungrazed (exclosure) states were extrapolated over the Barrow Peninsula (421 km^2) using a high spatial resolution land cover map. In the presence of lemmings, tundra maintained a historically accurate peak growing season carbon sink at $-219 \text{ tonnesCeq day}^{-1}$, respectively, while the modeled ungrazed tundra state was estimated to function as a small source $+8 \text{ tonnesCeq day}^{-1}$. Thus, a shift in lemming herbivory has the capacity to dramatically alter ecosystem function at plot to landscape scales and should be regarded as a more important component of the changing Arctic System than what has been the case in the past.

The concluding study of this dissertation was motivated by recent evidence suggesting the extent of aquatic tundra near Barrow, Alaska dominated by *Arctophila fulva*, has increased over the past half-

century, which also appears to be concurrent with increases in nitrogen (N) and phosphorus (P) in aquatic ecosystems in the same area. This study examined the response of ecosystem carbon dioxide (CO₂) and methane (CH₄) flux from *A. fulva* dominated tundra under elevated N and P levels. We extracted monoliths from pond margin aquatic tundra near Barrow, dominated by *A. fulva* and placed these in a continuous flux monitoring system, that controlled environmental conditions (light, air temperature, water table height) at 3 nutrient levels (control: 0.0 mgN L⁻¹, 0.0 mgP L⁻¹, low: 1.5 mgN L⁻¹, 0.6 mgP L⁻¹, and high: 7.5 mgN L⁻¹, 3.0 mgP L⁻¹). In response to the high nutrient treatment, we found *A. fulva* biomass and steady state CH₄ emission (SE) to increase with increased *A. fulva* tiller biomass which acts as gas conduits from the soil to the air. Contrary to expectations, GEE decreased as vascular plant biomass increased. The increase in canopy thickness via biomass growth and a reduction in light use efficiency is likely to be related to this reduction in photosynthetic capacity and carbon sink strength. There were no differences in CO₂ and CH₄ flux between control and low nutrient treatments. No differences in gas ebullition (GE) among nutrient treatments were found, however, a negative relationship between GE and biomass was documented ($R^2 = 0.34$, $p < 0.001$), which to our knowledge is the first time a correlation between vegetation leaf biomass and GE has been recorded. Collectively, short-term experimental results suggest *A. fulva* biomass, CO₂ and CH₄ fluxes in aquatic habitats have likely been altered by high levels of fertilization, which supports long-term field based observations and provides substantial functional implications for future aquatic vegetation change in the Barrow area, and potentially tundra elsewhere in the Arctic.

Table of Contents

Acknowledgements.....	iv
Abstract.....	vi
Table of Contents.....	ix
List of Tables	xi
List of Figures.....	xiv
Chapter 1: Introduction.....	1
1.1 Rationale for this dissertation	1
1.2 Study Area	8
1.3 Current research challenges	9
1.4 Structure of this Dissertation	11
Chapter 2: How has ecosystem function changed over the past half-century at a recently-deglaciated site in the Canadian High Arctic.....	13
2.1 Abstract.....	13
2.2 Introduction.....	14
2.3 Methods	16
2.4 Results.....	20
2.4.1 Climate reconstruction.....	20
2.5 Discussion.....	28
2.6 Conclusion	32
Chapter 3: Estimated Change in Tundra Ecosystem Function from 1972 to 2010 near Barrow, Alaska	33
3.1 Abstract.....	33
3.2 Introduction.....	33
3.3 Methods	35
3.4 Results.....	38
3.5 Discussion.....	43
Chapter 4: 50+ years of Lemming Exclusion Alters Ecosystem Function in Alaskan Coastal Plain Tundra.....	50
4.1 Abstract.....	50
4.2 Introduction.....	51

4.3	Methods	53
4.4	Results.....	56
4.5	Discussion.....	60
Chapter 5: Response of ecosystem CO ₂ and CH ₄ flux to nutrient increase in <i>Arctophila fulva</i> aquatic tundra		67
5.1	Abstract.....	67
5.2	Introduction.....	67
5.3	Methods	70
5.4	Results.....	75
5.5	Discussion.....	81
5.6	Conclusion	85
Chapter 6: General Discussion		86
6.1	Recapitulation of Objectives.....	88
6.2	Synthesis	92
6.3	Considerations for Future Research.....	93
References.....		96
Biographical Sketch.....		107

List of Tables

Table 1: Publication status of the chapters presented in this dissertation.....	12
Table 2: Estimates of mean July Temperatures (T) and Summer Warmth Index (SWI) for the Lewis River site.....	21
Table 3: Main effects for repeated measures MANOVAs for modeled functional attributes between 1964 and 2009 and among plant communities. Numerator degrees of freedom (df) for time, community, and time x community were 1, 8, and 8 respectively, while denominator df were 70. Bolded and italicized values represent significant change at $\alpha < 0.05$; < 0.1	25
Table 4: Percent change of functional values between 1964 and 2009 for all plant communities. Bolded and italicized values represent significant change at $\alpha < 0.05$; < 0.1	26
Table 5: Estimated functional values for 1964 and 2009 for all plant communities. Bolded and italicized values represent significant change at $\alpha < 0.05$; < 0.1 . Units: Biomass (gdw m^{-2}), GEE ($\text{gCm}^{-2}\text{day}^{-1}$), NDVI (reflectance index), Albedo (%), VWC (ratio of mass/unit vol).....	26
Table 6: Sensitivity of net ecosystem exchange (NEE) to modeled changes in temperature ($+2^{\circ}\text{C}$), NDVI (dry: +14%, moist: +13%, wet: +16%), and VWC (dry: -2%, moist: -10%, wet: -22%) between 1964-2009. NEE is presented as change for peak season $\text{gC m}^{-2}\text{day}^{-1}$ and percent. Modeled NEE for dry, moist, wet, and all (combined) for 2009 were 0.2, 0.63, 1.99, and 0.45 $\text{gCm}^{-2}\text{day}^{-1}$, respectively.	27
Table 7: Results of MANOVA tests that determined if each functional attribute varied significantly between sampling dates and plant communities. Significant time*community effects indicate that either an ecosystem functional attribute and/or at least one plant community changed over time. A significant time effect indicates that a minimum of one community changed function over time. Time*community (Numerator DF = 18, Denominator DF = 880.13), Time (Numerator DF = 3, Denominator DF = 311).	41

Table 8: Above ground plant biomass (grams dry weight m ⁻²) for four plant communities harvested near peak growing season in 2010 and 1972. Communities PAG and CAG were lumped in 1972 and have been treated the same way for data reported from 2010.	43
Table 9: Change in functional attributes for each plant community and sampling period derived from Tukey's HSD tests. Arrows indicate a significant increase/decrease ($P \leq 0.05$). "Total", refers to the count of all significant changes for a given time interval/ plant community.	46
Table 10: F-statistics from a two-factor ANOVA of ten functional attributes using land-cover types (LCT; df= 2), control/exclosure plots (EX/CT; df= 1), and an interaction (EX/CT*LCT; df= 2) as main effects. Significant differences are bolded ($\alpha < 0.1^\dagger$, $\alpha < 0.05^*$, and $\alpha < 0.01^{**}$).	57
Table 11: Spatial extrapolation of Albedo (kiloWatts day ⁻¹) and Carbon (NEE, CH ₄ , GWP, tonnes C day ⁻¹) fluxes across the Barrow Peninsula (420.6 km ² , respectively) using Land Cover Types (LCTs) dry, moist, and wet for lemming presence (Present) and lemming absence (Absent). We estimated functional metrics to 1 km ² area, by determining the relative proportion of all LCTs across the region and used plot level m ² values for extrapolation. Positive carbon flux values indicate loss from the ecosystem and negative values indicate uptake to the ecosystem. .	65
Table 12: Main effects for two-way ANOVAs on experimental period means of the CO ₂ flux components (net ecosystem exchange: NEE, gross ecosystem exchange: GEE, ecosystem respiration: RE, and biomass normalized gross ecosystem exchange: nGEE.	77
Table 13: Main effects for two-way ANOVAs on experimental period means of the CH ₄ flux components (total emission: TE, steady emission: SE, gas ebullition: GE, and biomass normalized steady emission: nSE.	79
Table 14: Mean (± 1 S.D.) of calculations for CH ₄ , CO ₂ , and GWP. Using CO ₂ equivalence (100yr time horizon; CH ₄ =23 x CO ₂ ; IPCC 2004; 2007) GWP is calculated using SE +NEE and TE + NEE to determine the warming potential using different metrics of CH ₄ fluxes. Negative	

values represent carbon uptake, while positive represent carbon loss to the atmosphere (i.e.	
positive warming feedback).....	83

List of Figures

Figure 1: Circumpolar Arctic permafrost distribution map (Brown et al. 1997).....	3
Figure 2: Repeat photography of a recently deglaciaded landscape near the Lewis Glacier in North-central Baffin Island, Canada, taken on the 10 Aug. 1963 by P.J. Webber and on 9 Aug. 2009 by C.E. Tweedie.	9
Figure 3: North American arctic map displaying both study sites: central Baffin Island, Canada (green square) and Barrow, Alaska (red square). Light blue line represents the Arctic Circle at 66.5°N latitude. Map credit ARMAP.org.	11
Figure 4: Satellite image of Baffin Island, overlaid with the difference in summer temperatures between the decade 2001-2010 and the preceding three decades. Black circle indicates the approximate location of our study site. Image produced using interactive web mapping provided by the NOAA/ESRL Physical Sciences Division, Boulder Colorado (http://www.esrl.noaa.gov/psd/).	17
Figure 5: NMS 3-axis ordination for plant communities 1964 (open circle) and 2009 (closed circle); communities are arranged from dry (dark red) to wet (dark blue). Regression trees elucidate the most important functional attributes that are associated with axes 1, 2, and 3. See section 2.4.2 for detailed axis descriptions.	22
Figure 6: Surface models of ecosystem function variables derived by interpolating (kriging) measured values for 54 functional plots within NMS ordination space. Colors for surface models represent high (red) to low (blue) values for each functional variable and plant communities are presented along a soil moisture gradient from dry (dark red circles) to wet (dark blue circles). Open and closed circles represent NMS axis scores for plant communities sampled in 1964 and 2009 respectively. R values represent how accurately kriged surfaces correspond to the distribution of measured functional plot values over a two-dimensional	

NMS. Units: Biomass (gdw m ⁻²), GEE (gC m ⁻² day ⁻¹), NDVI (reflectance index), Albedo (%), VWC (ratio of mass/unit vol).	23
---	----

Figure 7: Regression analyses of measured (non-destructive) versus modeled (from surface models produced over NMS analyses) ecosystem functional values. Each data point on panels, VWC (a), NDVI (b), and Albedo (c) represent 30, 10, and 10 field data points collected from historic sites, presented with error bars. Dotted line represents a 1:1 line.	24
---	----

Figure 8: Repeat photography representing four communities in the study area. Photos in the left column were taken in 1964 and the right column 2009. Photographs were taken within less than one calendar week difference. Panel (a-d) are represented by communities Graminoid wetlands, Forb meadows, Herb barren, and Cryptogam barren.	30
---	----

Figure 9: Spatial coverage of the functional plots in ordination space (Figure. 9A, green squares, n = 42) with resampled historic plots (Figure, 9B, black triangles, n = 1320). Historic plots that were outside the approximate range of the functional plots in ordination space were omitted from the model (Figure. 9C, omitted sites highlighted by red arrows).	38
---	----

Figure 10: Models of soil volumetric water content (VWC – top), water band index (WBI - middle), and normalized difference vegetation index (NDVI - bottom) derived from field measurements and modeled NMS surface maps (VWC: $R^2 = 0.69$, $P < 0.0001$, WBI: $R^2 =$ 0.39 , $P < 0.0001$, NDVI: $R^2 = 0.31$, $P < 0.0001$, respectively). Trend-lines are represented by the solid line, while the dotted line represents a one-to-one relationship.....	40
---	----

Figure 11: Surface maps of functional attributes (VWC, WTH, WBI, Albedo, NDVI, CH ₄ , NEE, GEE, R _E , and GWP ₁₀₀ .) overlaid by mean plot NMS axis scores for each plant community. Surface maps were created by kriging values for attributes derived for functional plots within NMS ordination space.	44
--	----

Figure 12: Mean values of each functional attribute, sampling year, and plant community. A= VWC %, B= WTH cm, C= WBI index, D= Albedo %, E= NDVI index, F= CH ₄ mgCm ⁻² day ⁻¹ , G= NEE gCm ⁻² day ⁻¹ , H= GEE gCm ⁻² day ⁻¹ , I= R _E gCm ⁻² day ⁻¹ , J= = GWP ₁₀₀ equivalents of gCm ⁻² day ⁻¹ .NEE Positive GWP ₁₀₀ values indicate decreased warming potential.....	48
Figure 13: Barrow field sites were located within the International Tundra Experiment (ITEX) dry and wet sites, and near the western extent of the International Biological Program (IBP) historical site. Dry, moist, and wet LCTs are represented as triangles, squares, and circles. Left map is a quickbird image from 2008 and the right is the vegetation map developed by Tweedie et al. (submitted) representing the following LCTs: aquatic (red), wet (dark green), moist (light green), dry (yellow), and open water (blue).....	54
Figure 14: Mean (±1S.E.) of peak season thaw depth (TD), saturated soil layer (SSL), Normalized Difference Vegetation Index (NDVI), and Albedo for lemming enclosure (white) and control plots (black) in three land cover types (dry, moist, and wet tundra) near Barrow Alaska. Asterisks signify significant difference (tukey's HSD) at $P \leq 0.05$ between enclosures and control plots. Letters indicate differences among LCTs.....	57
Figure 15: Means (±1S.E.) of peak season Gross Ecosystem Photosynthesis (GEE), Ecosystem Respiration (R _E),Net Ecosystem Exchange (NEE), and Methane flux (CH ₄) for lemming enclosures (white) and control plots (black) among three land cover types in the coastal tundra near Barrow Alaska. Asterisk signifies significant difference (Tukey's HSD) at $p \leq 0.05$ between enclosures and control plots. Letters indicate differences among LCTs.....	59
Figure 16: Mean (±1S.E.) of peak season tundra land cover type for enclosure (white bar) and control plots (black bar) for Global Warming Potential (GWP ₁₀₀) integrated over a 100 year time horizon. Positive values indicate a positive warming potential while negative values a	

negative warming potential. Asterisk signifies significant difference (tukey's HSD) at $p \leq 0.05$ between exclosures and control plots. Letters indicate differences among LCTs.....	59
Figure 17: Schematic representation of functional changes observed in response to herbivore exclusion within wet land cover types (LCTs).	61
Figure 18: Up-scaled albedo and carbon (NEE, CH ₄ , and GWP) across the 421km ² Barrow Peninsula. Values for albedo are represented by a light to dark orange gradient, where the lighter values portray the most reflective land surfaces. Maps for NEE, CH ₄ , and GWP are visualized with a green to red gradient, where green and red values indicate sink and source activity, respectively. See Table 11 for estimates.....	63
Figure 19: Schematic of the continuous flux monitoring setup. Outside air is pumped into the system at a rate of 13.2 L min ⁻¹ , humidified, and passed through plexiglass chambers containing monoliths at a rate of 1.2 L min ⁻¹ . Solenoid valves controlled by a computer allow sequential chamber sampling with an INNOVA 1312 photoacoustic trace gas analyzer. An empty chamber was used as a control for gas flux calibrations with the outside air.....	72
Figure 20: Biomass estimates of <i>A. fulva</i> from Pre-treatment (Week 1-4) and Fertilization periods (Week 5-9). Error bars indicate ± 1 S.D. The vertical line indicates the start of fertilization during week 5.	76
Figure 21: Methane flux was found to increase linearly with <i>Arctophila fulva</i> above ground biomass under both field and experimental conditions. Closed diamonds represent CH ₄ steady emission (SE) fluxes from field based measurements near Barrow, Alaska, while open diamonds represent SE collected from laboratory experimentations.	78
Figure 22:CH ₄ gas ebullition (GE) decreased with increasing <i>A. fulva</i> above ground tiller biomass. Note: logarithmic scale for y-axis.....	80

Figure 23: Experimental period (Pre-treatment, Fertilization, Biomass removal) effects on CH₄ (left panels: TE, SE, GE) and CO₂ fluxes (right panels: NEE, GEE, RE). Error bars indicate ± 1 S.E. Letter differences indicate significant differences among experimental periods81

Chapter 1: Introduction

1.1 RATIONALE FOR THIS DISSERTATION

As a result of human activities, atmospheric carbon dioxide, methane, and other greenhouse gases have markedly increased since 1750, and now far exceed pre-industrial values determined from ice cores (IPCC 2007). It is now well-established that anthropogenic greenhouse gas emissions have increased global temperatures and that a series of climate change impacts within the Earth System are either already in motion, or are likely as a result (IPCC 2007). Northern high latitude ecosystems have experienced a greater rise in air temperatures relative to other regions on the globe and the the past 10 years (i.e. 1999-2008) appear to have been warmer than the previous 2000 years (Kaufman et al. 2009).

The future state and fate of the substantial arctic soil organic carbon pool is particularly concerning given current rates of warming at high northern latitudes (Tarnocai 2009, Hollesen et al. 2011). Arctic land masses are relatively small and have low primary productivity and standing plant biomass relative to the size of the arctic carbon pool (Zimov et al. 2006, Schuur et al. 2008, Tarnocai et al. 2009), suggesting that if this is lost soil carbon will not re-accumulate to the same extent in the near future. This potential loss of soil carbon may have strong global consequences if there is a reduction in carbon uptake capacity in arctic terrestrial ecosystems or a transfer of greenhouse inert soil carbon to a greenhouse active state through the loss of soil carbon to the atmosphere as CO₂ or CH₄ (Schuur et al. 2009). If the Arctic shifts from a long-term sink for atmospheric carbon to a source, (Oechel et al. 1993, Oechel et al. 2000, Natali et al. 2011) there will be increased pressure on other biomes for mitigating the subsequent increase in atmospheric greenhouse gases.

To understand the future state of the Arctic and Earth Systems, improved understanding of key terrestrial ecosystem processes over decade-time scales are needed (Luo et al. 2011). Unfortunately, there are few places in the Arctic where sustained environmental monitoring of terrestrial ecosystem properties and processes has occurred. One of the only ways to attain knowledge of decade time scale change in these systems is to revisit and resample historic research sites to assess likely ecosystem structural and functional change. Long term studies have been found to be highly important, as short

term vegetation changes are poor predictors of long term trends (Hill and Henry 2011, Kapfer et al. 2012). This dissertation addresses several challenges limiting understanding of decade time scale change in terrestrial ecosystem biogeochemical cycling in the Arctic that to date have been difficult to address due to the lack of historical data and sustained monitoring, and novel statistical analyses that link ecosystem structure and function. This study is a contribution to the International Polar Year (IPY) Back to the Future (BTF) project, formulated to revisit and resample old (>25 yrs) arctic tundra vegetation research sites and assess patterns and implications of long-term changes (Callaghan et al. 2011).

1.1.1 Arctic Ecosystems

The spatial domain of the Arctic has been defined in many ways, and the appropriate definition largely depends on the particular context being considered. The Arctic can be defined by the following: 66.5 °N latitude, north of the Arctic Circle, maximum monthly air temperature below 10 °C (Koppen 1931), southern most boundary of discontinuous permafrost (McGuire et al. 2006), or perhaps the most ecologically relevant - the region north of the boreal forest tundra-taiga ecotone where tundra typically begins (Callaghan et al. 2002). The area of tundra north of the boreal forest (i.e. not alpine tundra) is estimated to cover more than 12 million km² and is bounded by the Arctic Ocean to the north (Chapin et al. 2005), and acknowledges arctic tundra has comprising a suite of ecosystems with specific ecosystem functions.

Though climate varies markedly across the Arctic, it is generally characterized by low mean annual temperatures, low annual precipitation, low solar insolation, and short summer growing seasons for plants. . Much of the Arctic is underlain by continuous permafrost and the depth of seasonally thawed soil is shallow and typically between 25-73 cm (Hinkel and Nelson 2003). Permafrost soils or soils frozen more than two years, vary in continuity across the circumpolar Arctic, which are represented by continuous, discontinuous, sporadic, and isolated patches (Figure 1). The depth of seasonally thawed permafrost, vary between 0-300cm (Tarnocai et al. 2009). In addition, the majority of Arctic tundra (80%) is located within 100km of the Arctic Ocean coastline and therefore has a strong maritime influence (Walker et al. 2005). For example, a recent circumpolar remote sensing study links

diminishing Arctic sea ice cover with increased summer land-surface temperatures and vegetation productivity (Bhatt et al. 2010).

In addition, tundra soils are generally nutrient poor due to slow decomposition and turnover (Hobbie and Chapin 1996).

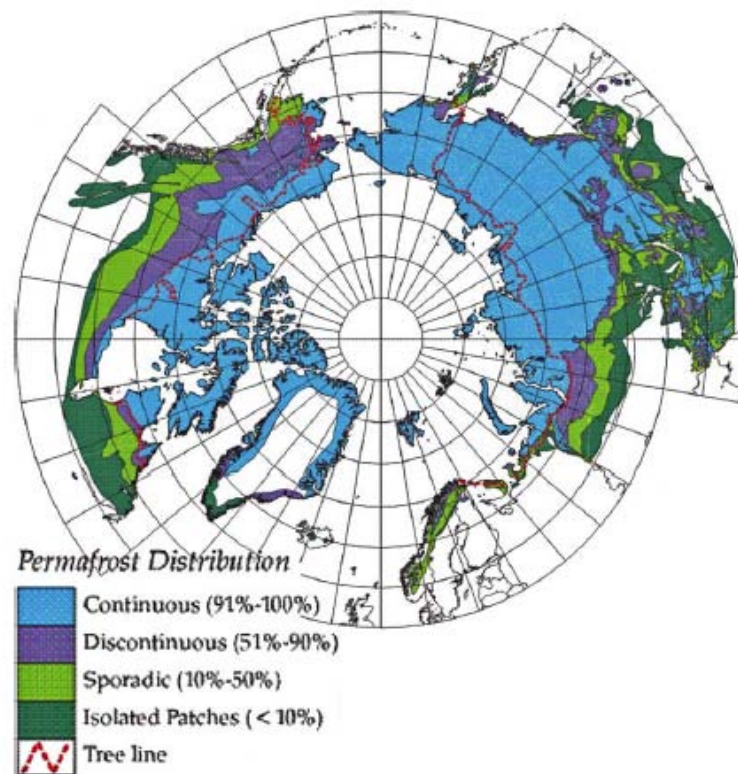


Figure 1: Circumpolar Arctic permafrost distribution map (Brown et al. 1997).

Geomorphologic processes, driven by seasonal thawing and freezing cycles, shape the landscape of the arctic tundra. Ice wedges are prominent in coastal tundra of the Alaskan Arctic, and often form polygonal shapes resulting in “polygonized” tundra. The presence of permafrost generally restricts drainage and relatively subtle changes in topography can dramatically affect soil moisture, and thus vegetation type (Webber 1978; Hodkinson et al. 1999). Thus, tundra landscapes can have high spatial heterogeneity in vegetation cover due to small variability in microtopography (Muller et al. 1999). This phenomenon presents a significant challenge to remote sensing (Stow et al. 2004), and modeling (Sitch et al. 2007) studies as different vegetation types respond differentially to seasonal and environmental change (Lara et al. 2012, Lin et al. 2012). Adequately addressing heterogeneity of tundra landscapes in ecological scaling studies is an ongoing challenge (Stoy et al. 2009). Key to addressing such a challenge

is a advancement in understanding of factors controlling ecosystem land-atmosphere carbon exchange, and an improved knowledge of how ecosystem function will be affected by climate change (namely warming) and other ecosystem interactions such as with herbivores. These are reviewed below.

1.1.2 Ecosystem carbon exchange

Northern ecosystems have accumulated vast amounts of soil carbon over the last millennia and are estimated at approximately 1672 Pg carbon, which cumulatively amount to half of the global soil organic carbon pool (Tarnocai et al. 2009). Soil organic carbon appears to have accumulated in Arctic tundra ecosystems at a rate of $15\text{--}30\text{gC m}^{-2} \text{ y}^{-1}$ (Gorham 1991, Turunen et al. 2002), the majority of which is now stored in permafrost. Tundra vegetation takes up atmospheric carbon dioxide (CO_2) through gross ecosystem exchange (GEE). Carbon dioxide is released back to the atmosphere, via heterotrophic and autotrophic respiration, collectively referred to as ecosystem respiration (R_E). The net ecosystem exchange (NEE) constitutes the sum of these two counteracting fluxes. Separately, from CO_2 exchange, methane (CH_4) is primarily produced in waterlogged (anaerobic) subsurface environments, by methanogens. Methane produced by methanogens can be oxidized by methanotrophs in aerobic conditions (Whalen 2005). Thus, biogenic methane fluxes are typically positive (source of methane to the atmosphere) in waterlogged soils, and negative (methane diffuses from the atmosphere to the soil) in relatively dry landcover types where soils are still moist enough to support methanotrophs. Methane is an important greenhouse gas because it has approximately 25 times the global warming potential of CO_2 , over a 100 year time horizon (IPCC 2007). High latitude tundra ecosystems have long functioned as a carbon sink as a result of low decomposition caused mostly by waterlogged soils with low temperatures (Clymo 1984).

The net exchange of CH_4 from tundra is best understood from the balance between production (methanogenesis) and consumption (methanotrophy). Temperature strongly affects metabolic rates of methanogens (Conrad 1989) and fermentative processes that generate acetate and H_2 (Kotsyurbenko 2005). Acetate and H_2 are both used by methanogens as substrate in decomposition and CH_4 production. Furthermore, soil water and permafrost thaw depth influence methane production, as these properties alter soil temperature and redox status. Aerobic layers (containing methanotrophic bacteria) that overlie

zones of production may consume CH₄ prior to release (Whalen (Whalen and Reeburgh 1990). The impact of methanotrophy on net CH₄ emission depends strongly on the mode of transport that CH₄ takes to the atmosphere. Diffusive CH₄ transport through deeper soils of anaerobic regions to the atmosphere is associated with the highest rates of methanotrophy (Whalen and Reeburgh, 1990). In contrast, plants can conduct CH₄ from deeper, anoxic zones to the atmosphere through gas conducting tissues called, “aerenchyma”, bypassing methanotrophic oxic layers (Bartlett et al. 1992, Torn and Chapin 1993, King et al. 1998, Juutinen et al. 2003). Further, CH₄ ebullition or bubbling is thought to have very little associated methanotrophy because the bubbles move quickly from anoxic zones to the atmosphere (Walter et al. 2006).

1.1.3 Response of Tundra Ecosystems to Warming

Tundra ecosystems appear to play a key role in global carbon cycling because of the large carbon store (Section 1.1.2) contained in permafrost and the strong potential for changes in carbon storage to occur with warming (Schuur et al. 2008; 2009). The balance in land-atmosphere carbon exchange controlled by the positive effects warming has on tundra plant productivity relative to increased respiratory losses in response to warming will determine the extent and direction and magnitude of change to the arctic carbon store (Shaver et al. 2000). Warming may increase microbial decomposition rates and organic substrate availability as permafrost warms and thaws (Aerts et al. 2006, Natali et al. 2011), although, respiratory losses may be offset by warming mediated increases in plant biomass (Hudson and Henry 2009, Hill and Henry 2011). A meta-analysis by (Rustad et al. 2001) found warming to increase soil R_E by 20% and nitrogen mineralization by 46%. Moreover, warming and thawing permafrost soils may release plant available nitrogen into a nitrogen limited ecosystem (Keuper et al. 2012), which may have strong effects on ecosystem function (Chapter 5).

A growing body of evidence indicates the Arctic is becoming more productive (Jia et al. 2009; Bhatt et al. 2010, Epstein et al. 2012, Reynolds et al. 2012). Decade time scale change analyses of derived greening trends (i.e. NDVI: normalized difference vegetation index) show increases across much of the circumpolar Arctic (Bhatt et al. 2010), suggesting increased carbon uptake capacity by

tundra vegetation (Epstein et al. 2012, Raynolds et al. 2012). It appears these changes correspond to pronounced warming (Euskirchen et al. 2006), and/or increased shrub growth (Myers-Smith et al. 2011, Elmendorf et al. 2012). In addition, findings suggest the greatest changes in magnitude to be in the Canadian High Arctic (Jia et al. 2009, Bhatt et al. 2010), where vegetation is also known to have become more productive (Cadieux et al. 2008, Hudson and Henry 2009, Hill and Henry 2011, Frasier et al. 2011).

Warmer temperatures may be also associated with changes in ecosystem water balance in both aquatic and terrestrial systems via increased evaporation, evapotranspiration, and altered precipitation patterns (IPCC 2007). Aquatic tundra ecosystems are sensitive to climate changes due to the direct effects of warming on water temperature, thermal stratification, and the duration of ice cover. While indirectly related to warming by increased water runoff and nutrient and/or dissolved organic carbon inputs to aquatic ecosystems (Wrona et al. 2006). In addition, many regions across the north American Arctic are found to be drying, as satellite observations find the total cover of water across Canada to have decreased by approximately 6700km² between 2000-09 where the most dramatic water loss was reported for Arctic regions (Carroll et al. 2011). These observations are in line with the disappearance of ponds (Smol and Douglas 2007) and lakes (Smith et al. 2005, Avis et al. 2011).

A variety of analyses in terrestrial ecosystems have indicated that many Arctic landscapes are drying (Smith et al. 2005, Riordan et al. 2006). A recent study on the north slope of Alaska estimated landscape level displacement of wet and moist tundra by drier land cover types (Lin et al. 2012), which suggests dramatic change in ecosystem function. In addition, process-based models indicate the direction of warming related climatic feedbacks to the climate system depends largely on landscape wetness and dryness. An increase in landscape dryness for example, can promote greater release of CO₂ to the atmosphere through enhanced decomposition. (McGuire et al. 2009). A reduction of anaerobic water bodies capable of producing CH₄ (e.g. Section 1.1.2). Indirect consequences of drier tundra ecosystems, have led to increased large-scale fire disturbances. For example, in 2007 the Anaktuvuk river fire burned 1,039 km² of the Alaskan north slope, making it the largest fire on record for the tundra biome. Mack et al. (2011) estimated $2,016 \pm 435$ gC m⁻² was lost for the entire burned area, which

amounts to a release of 2.1 Pentagrams (e.g. 1Pentagram = 1Billion metric tons) of carbon lost to the atmosphere. This is similar to the net annual sink strength for all arctic tundra landscapes over the last 25 years.

1.1.4 Response of Tundra to Herbivory

In addition to tundra responses to warming (Section 1.1.3) the structure and function of arctic tundra is affected herbivore grazing (Batzli 1980). Grazing can be influenced by climate through shifts in the temporal availability, quality, and quantity of the herbivore diet (Wookey et al. 2009). Though, there has been disagreement regarding the importance of grazing herbivores in tundra systems (Zimov et al. 1995a), the potential for grazers to cause shifts in vegetation composition has recently been well established (Moen and Danell 2003, Van der Wal and Brooker 2004, Brathen et al. 2007), the effects on ecosystem function remain poorly studied except for few exceptions (Sjogersten et al. 2008, 2012). Arctic herbivores (i.e. lemmings, voles, geese, and caribou) may place top-down constraints on primary productivity through selective foraging (Tape et al. 2010) and indirectly through disturbance (Van der Wal et al. 2001, Villarreal et al. 2012), alteration of plant succession rates (Speed et al. 2010), competition (Olofsson et al. 2002), facilitation of shrub encroachment (Sturm et al. 2005, Olofsson et al. 2009), and through the alteration of soil nutrient status (Olofsson et al. 2004, Van der Wal et al. 2004).

Two species of lemming occur in the Northern Alaska, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). The brown lemming, however, is more abundant and prefers lower wetter habitats than the collared lemming (Batzli et al. 1983, Duchesne et al. 2011). The brown lemming is capable of large cyclic population outbreaks increasing their density 150-250% during population high years. High lemming populations decimate the vegetation to such an extent that herbivore populations begin to starve and the population crashes. Plant productivity is substantially lowered as removed as a result by as much as 90% in some areas (Schultz 1964). With the thinning of plant canopies, more solar radiation reaches the soil surface, which warms the soil and the depth of thaw increases (Batzli and Pitelka 1975, Ng and Miller 1977). These responses following high lemming years were the foundation of the Nutrient Recovery Hypothesis (Schultz 1964). Fluctuations in lemming/vole populations have been observed remotely to alter NDVI patterns (Olofsson et al. 2012), suggesting

microtine rodents may directly alter arctic ecosystem function, however the intrinsic natural functional effects of herbivores on the coastal tundra remains to be thoroughly explored.

1.2 STUDY AREA

This study was completed at two primary locations – Baffin Island in the Canadian High Arctic and near Barrow, Alaska. A description of these study sites follow.

1.2.1 Baffin Island, Canada

The study site on Baffin Island was located near the northwest margin of the Barnes Ice Cap (70° 24' N, -74° 49' W), within close proximity to the Lewis Glacier, central Baffin Island, within Bioclimate Subzone C (North American High Arctic: (Walker et al. 2005)). The nearest permanent weather stations are located at Dewar Lakes and Clyde River, 106 km south of the Barnes Ice Cap at an elevation of 518 and 27 m, respectively. Climate data from these weather stations show that between 1971 and 2000 mean daily temperatures in summer (JJA) were approximately 2.96°C and -26.6°C in winter (DJF). Average annual precipitation is approximately 282 mm, with rainfall and snowfall comprising 115 mm, and snowfall 166 cm, respectively (www.climate.weatheroffice.gc.ca/climate_normals). The interior of North-central Baffin Island is a broad plateau of primarily Precambrian rock, dominated by a vast upland surface, approximately 600 m above sea level (Ives 1963). The landscape contains massive rounded hills that rise 100 to 150 m, but can reach elevations up to 900 m. Valleys are present and generally very broad, with relief in the upland valleys being commonly less than 100 m.

The Barnes Ice Cap is the last contiguous remnant of the Laurentide Ice Sheet (Dyke 1987), and is retreating at an average rate of 3-15 m yr⁻¹ (Armenakis 2008). The Lewis Glacier is retreating at approximately 25 m yr⁻¹ (Jacobs et al. 1993). As a result of this retreat most of the land surfaces within our study site are within this proglacial chronosequence and less than 500 years old (Andrews 1964). Glacial moraines in proximity to the west side of the ice cap are evidence of glacial expansion within the last 200-500 years (Andrews 1964). Photographic evidence from 1963 and 2009, taken within 2 calendar

days of one another during the growing season, shows snow banks, and snow packs to have disappeared (Figure 2). Vegetation across the Lewis Valley is described in detail in Section 2.3.1.



Figure 2: Repeat photography of a recently deglaciated landscape near the Lewis Glacier in North-central Baffin Island, Canada, taken on the 10 Aug. 1963 by P.J. Webber and on 9 Aug. 2009 by C.E. Tweedie.

1.2.2 Barrow Alaska, USA

Historically, the town of Barrow, Alaska has hosted an active scientific research program since the early 1970s. This research history includes the former International Biological Program (IBP) research site (71°17'N, 156°41'W) established in 1971 and the International Tundra Experiment (ITEX) research site (71°18'N, 156°44'W) established in 1994. Mean annual temperature, precipitation, and snowfall are -12 °C, 11 cm, and 69 cm respectively (1971-2000; NCDC <http://cdo.ncdc.noaa.gov/climatenormals/clim20/state-pdf/ak.pdf>). The landscape has a low relief best characterized as poorly drained polygonized tundra (Brown et.al 1980). Maximum depth of thaw ranges from 30 to 90 cm (Nelson et al. 1998, Hinkel and Nelson 2003) and the snow-free period is variable in length but generally begins in early June and lasts until early September (Brown 1980). The tundra of the study site is composed of a variety of vegetation types that were classified by Villarreal et al. (2012) and are described in detail in Section 3.3.1.

1.3 CURRENT RESEARCH CHALLENGES

Due to the absence of long-term monitoring, assessing change in ecosystem structure and function over decade-time scales is challenging in arctic ecosystems. However, several studies have demonstrated the benefits of rediscovering and resampling old research sites throughout the Arctic to

assess change over time. Such studies have documented increases in shoot height and leaf size (Hudson et al. 2011), increased in reproductive output in shrubs and graminoids (van Wijk et al. 2004, Hollister and Flaherty 2010, Klady et al. 2011), increases in above ground biomass (Hudson and Henry 2009, Hill and Henry 2011) and shifts in ecosystem carbon balance (Oechel et al. 1993, Oechel et al. 2000, Malmer et al. 2005, Johansson et al. 2006, McGuire et al. 2010). To date, few of these resampling studies have coupled change detection of ecosystem structure to ecosystem functional attributes over decade-time scales. Widespread warming and greening has been documented in arctic landscapes over the last 30 years using large-scale low-resolution satellite remote sensing (Bhatt et al. 2010). However, the lack of ground-based observations currently constrains our ability to understand the implications and drivers of these changes in most arctic terrestrial ecosystems (Callaghan et al. 2005).

Improved understanding of key terrestrial ecosystem processes over decade-time scales are needed to understand the future state and fate of the Arctic and Earth Systems (Luo et al. 2011). For arctic terrestrial ecosystems, ecosystem structure appears to be strongly coupled to ecosystem function, including biogeochemical cycling (Symstad et al. 2003, Callaghan et al. 2004, Hooper et al. 2005). Several key studies, however, highlight associations between plant functional types and species composition and nutrient cycling (Hobbie 1992, Hobbie et al. 2002, Edwards and Jefferies 2010), surface albedo (Chapin et al. 2005), net primary production (Webber 1978, Chapin et al. 1995), and trace gas emissions of CO₂ and CH₄ (Joabsson and Christensen 2001, Strom and Christensen 2007).

1.3.1 Goals and objectives

The overarching goal of this dissertation is to determine how ecosystem, community, and species function has changed in central Baffin Island Canada (Figure 3) and northern Alaska near Barrow (Figure 3) over 25+ years. This project aims to address several of the most urgent research challenges through the following objectives:

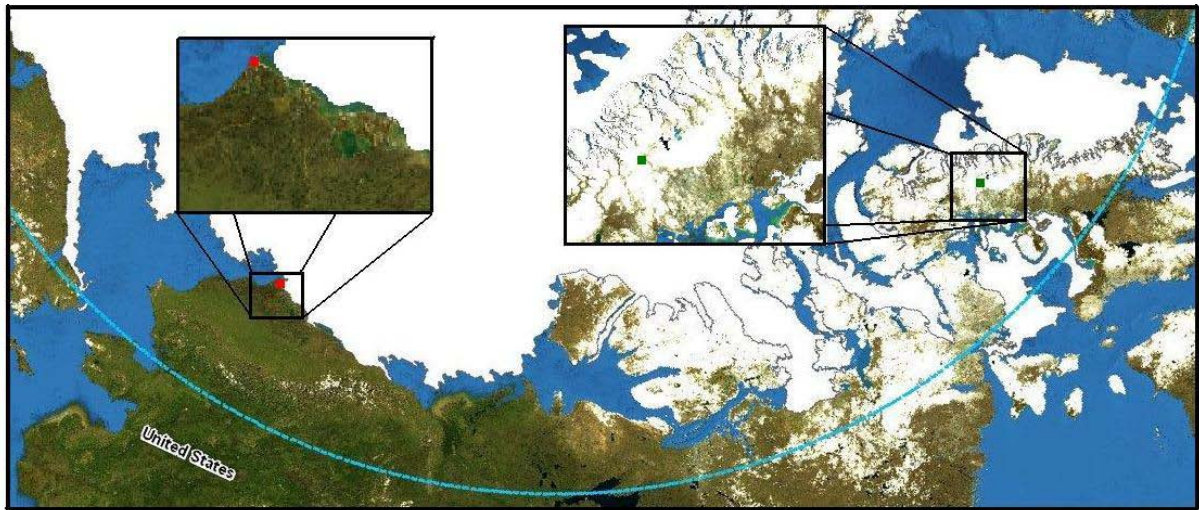


Figure 3: North American arctic map displaying both study sites: central Baffin Island, Canada (green square) and Barrow, Alaska (red square). Light blue line represents the Arctic Circle at 66.5°N latitude. Map credit ARMAP.org.

Barrow Island, Canada

- 1) Determine how plant community change between 1964 and 2009 in a recently deglaciated high arctic landscape has resulted in changes to ecosystem productivity, soil moisture, and albedo

Barrow Alaska, USA

- 2) Determine how plant community change between 1972 and 2010 has likely changed ecosystem function
- 3) Assess the functional implications of 60 years of herbivore exclusion on ecosystem function
- 4) Determine how the pond macrophyte, *Arctophila fulva* and other ecosystem properties respond to elevated levels of N and P

1.4 STRUCTURE OF THIS DISSERTATION

This dissertation is composed of six chapters. Four chapters have been written for publication in internationally peer-reviewed journals. The publication status of each chapter including title, authors, target journal, and submission information is listed in Table 1. The author of this dissertation is the lead author and principle analyst for each paper. In addition to work presented here, the author of this

dissertation has contributed to the recent International Tundra Experiment (ITEX) synthesis (Elmendorf et al. 2012), Back to the Future (BTF) synthesis (Callaghan et al. 2011), a paper assessing plant community change at Barrow Alaska (Villarreal et al. 2012), and community response to long-term herbivore exclusion (Johnson et al. 2011).

Table 1: Publication status of the chapters presented in this dissertation

Status of the chapters presented in this dissertation	
1	Introduction M.J. Lara No submission intended
2	How has ecosystem function changed over the past half-century at a recently deglaciated site in the Canadian High Arctic M.J. Lara, S. Villarreal, D.R. Johnson, P.J. Webber, J.D. Jacobs, C.E. Tweedie Global Change Biology To be submitted for publication
3	Estimated Change in Tundra Ecosystem Function from 1972 to 2010 near Barrow, Alaska M.J. Lara, S. Villarreal, D.R. Johnson, R.D. Hollister, P.J. Webber, C.E. Tweedie <i>Environmental Research Letters</i> 7:015507, doi:10.1088/1748-9326/7/1/015507
4	50+ years of Lemming Exclusion Alters Ecosystem Function in Alaskan Coastal Plain Tundra M.J. Lara, D.R. Johnson, C.E. Tweedie <i>Journal of Ecology</i> To be submitted for publication
5	Response of ecosystem CO ₂ and CH ₄ flux to nutrient increase in <i>Arctophila fulva</i> aquatic tundra M.J. Lara, D.H. Lin, D.R. Johnson, V.L. Loughheed, C.E. Tweedie Arctic Antarctic and Alpine Research To be submitted for publication
6	General Discussion M.J. Lara No submission intended

Chapter 2: How has ecosystem function changed over the past half-century at a recently-deglaciated site in the Canadian High Arctic

2.1 ABSTRACT

Remote sensing evidence suggests the Canadian High Arctic has undergone dramatic greening since the 1980s. To date, there have been few ground-based long-term (>25 years) studies to confirm satellite observations and few studies have examined the potential ecological causes and implications of satellite-derived greening in the High Arctic. In 2009 as a contribution to the International Polar Year-Back to the Future (BTF) project (IPY endorsed project No. 512), we resampled sites established in 1964 to characterize plant community assemblages near the northern limit of the Barnes Ice Cap, north-central Baffin Island, Canada. A combination of plant community change analyses and field based ecosystem function measurements (CO₂ exchange, normalized difference vegetation index, surface albedo, and soil moisture) were used to determine ecosystem functional change between 1964-2009 using a multivariate-geospatial modeling technique. Regional climate spanning the past 50 years was also reconstructed showing a sustained trend of warmer and wetter summers. Generally, the greatest ecosystem functional change was associated with plant communities restricted to high soil moisture conditions. These included two pond margin communities: *Campylium-Aulacomnium*-moss meadows and *Eriophorum-Pleuropogon* wetlands increased in biomass by an estimated 178% and 46% respectively, while NDVI increased by an estimated 35% and 16%, respectively. Further, we found soil moisture to decrease in *Carex stans* wet meadows and *Campylium-Aulacomnium*-moss meadows by 30% and 24%, respectively. Other changes appeared to be community specific. The *Saxifraga oppositifolia*-Cryptogamic crust community that is commonly found on dry rocky exposed sites increased in NDVI, which appears to be related to increased cover of the rock lichen *Alectoria minuscula*. Additionally, the driest plant communities: *Poa-Papaver* barren and *Cassiope-Sphenolobus* snowbed, were the most resistant to change, and no change in productivity, albedo, or VWC were found for these plant communities. We attribute changes to warmer summer temperatures, a loss of snow banks that served as a sustained water source for the majority of the summer snow free period, plant succession following deglaciation, and lake drainage over the past few thousand years. This study

highlights the importance of revisiting, resampling, and archiving data associated with historical sites that are suitable for the assessment of long-term vegetation change in the Arctic.

2.2 INTRODUCTION

Climate warming is expected to be most pronounced in the Arctic (IPCC 2007), and may have major ecological repercussions (Post et al. 2009). Decade-time scale satellite and aerial observations of change indicate wide spread greening (i.e. NDVI: normalized difference vegetation index) across much of the circumpolar Arctic (Bhatt et al. 2010), suggesting increased atmospheric CO₂ uptake potential and storage by tundra vegetation. Bhatt et al. (2010) also found the highest percent change (1982-2008) in landscape greening to be in the Canadian High Arctic, which appears to be corroborated by Frasier et al. (2011), who reported extensive greening in northern Canada since the 1980s. Repeat sampling of dry heath (1981-2008) and wet sedge communities (1980-2005) found increases in above ground plant biomass at Ellesmere Island (Hudson and Henry 2009, Hill and Henry 2011). In addition, many regions across the North American Arctic have been found to be drying. Water bodies across Canada have been reported to have decreased by approximately 6700km² between 2000 and 2009, where the most dramatic loss was reported for the Arctic (Carroll et al. 2011). This agrees with the disappearance of Arctic ponds (Smol and Douglas 2007) and lakes (Smith et al. 2005, Avis et al. 2011). However, determining how these changes may impact terrestrial ecosystem structure (i.e. plant community composition) and function (i.e. biogeochemical cycling and albedo), remains a key research challenge (Luo et al 2011).

Generally, the High Arctic is characterized by (1) low annual temperature and precipitation, (2) the presence of ice caps, glaciers, semi-permanent snow banks, and (3) relatively barren vegetation (Walker et al. 2005, Euskirchen et al. 2007). Recognizing the magnitude of climatic and environmental change ongoing in the Arctic (ACIA 2005, IPCC 2007), global change research has increasingly focused on assessing how these changes will impact the substantial arctic soil organic carbon pool (Tarnocai et al. 2009; Schuur et al. 2011) and alter the capacity for carbon sequestration (Euskirchen et al. 2006). The balance between carbon losses via ecosystem respiration (R_E) and storage via gross ecosystem productivity (GEE) in the High Arctic are expected to be heavily weighted towards larger storage than loss as temperatures are low, soils are mostly inorganic, and spatial patterns of vegetation productivity

have likely increased since the early 1980s (Jia et al. 2009, Bhatt et al. 2010, Frasier et al. 2011). Warming and glacial retreat occurring in the High Arctic has been dramatic (Abdalati et al. 2004, Briner et al. 2009, Kaufman et al. 2009) and presents an opportunity for plant colonization and succession (Nakatsubo et al. 2010, Yoshitake et al. 2010), which may alter the capacity for terrestrial carbon sequestration. Understanding how landscape level perturbations such as warming, drying, greening, and plant succession will affect ecosystem function is largely unknown (Callaghan et al 2011). Further, several recent studies show that long-term patterns of vegetation change are difficult to predict using only outcomes from short term studies (Kapfer et al. 2012; Hill and Henry 2011), which supports the need for sustained long-term ground based observations to both validate decade-time scale remote sensing trends and modeling predictions, while elucidating drivers/mechanisms associated with ecosystem structural and functional change in the Arctic.

As a companion study to Villarreal et al. (*in prep.*), which describes the 1964-2009 resampling of historical plant community plots in central Baffin Island Canada, we examine how ecosystem structural change has affected ecosystem function. Similar to Lara et al. (2012), our analysis and findings are based on the strict assumption that within ecosystems, i) plant communities change because plant species that comprise these communities change in cover and abundance in response to a variety of environmental changes and/or due to succession (Epstein et al. 2004, Walker et al. 2006, La Puma et al. 2007, Hudson et al. 2011, Villarreal et al. 2012); ii) plant community change can result in changes to ecosystem function (*sensu* Johansson et al. 2006, Oberbauer et al. 2007); and iii) that the relationship between ecosystem structure and function does not change over time when plant communities and environmental conditions do not change. Specifically, we address four questions: 1) what environmental gradients control ecosystem function at the plant community level, 2) how does ecosystem function differ between communities, 3) how has ecosystem function changed from 1964-2009, and 4) to what degree has ecosystem functional change been influenced by warming and/or plant community succession?

2.3 METHODS

2.3.1 Site description

The site used for this study is located near the northwest margin of the Barnes Ice Cap (70° 24' N, -74° 49' W), within close proximity to the Lewis Glacier, central Baffin Island within Bioclimate Subzone C (CAVM 2003). The nearest permanent weather stations and settlements are located at Dewar Lakes and Clyde River, 105 km south and 150 km southeast of the Barnes Ice Cap at an elevation of 518 and 25 m, respectively. Climate data show that the average daily temperature, for 1971-2000 was 2.96 °C in summer (JJA) and -26.6 °C in winter (DJF). Mean annual precipitation was 282 mm, with rainfall comprising 115 mm, and snowfall 166 cm (www.climate.weatheroffice.gc.ca/climate_normals). Within the Lewis Valley, the landscape is characterized by exposed rock and lichens, sparsely vegetated rolling uplands along a proglacial chronosequence of glacial cross valley moraines, former shorelines, and large glacial mineral deposits adjacent to the Isortoq River and its tributaries (CAVM 2003, Webber 1971). Over recent history this region has undergone substantial change. Over the past 40 years, the edge of the Barnes Ice cap has retreated 3-15 m yr⁻¹ and dropped 1 m yr⁻¹ (Armenakis 2008), while the Lewis Glacier has retreated at a rate of 25 m yr⁻¹ between 1960s to 1990s (Jacobs et al. 1993). Repeat photography between 1963 and 2009 (photos acquired within 2 calendar days) show the loss of snow banks and snow packs. Vegetation across the Lewis Valley classifies to nine plant communities. Following the nomenclature of Webber 1971 and listed sequentially along a dry to wet soil moisture gradient, these include *Poa-Papaver* barren (Herb barren), *Cassiope-Sphenolobus* snowbed (*Cassiope* snowbed), *Saxifraga oppositifolia*-cryptogamic crust (Cryptogam barren), *Salix arctica-Alopecurus* meadow (*Salix* meadow), Pioneer lacustrine sediment (Successional meadow), *Luzula confusa*-forb meadow (Forb meadow), *Campylium-Aulacomnium*-moss meadow (Moss meadow), *Carex stans* wet meadow (*Carex* wet meadow), and *Eriophorum-Pleuropogon* wetland (Graminoid wetland). Detailed descriptions of these communities are given in Villarreal et al. (*in prep.*). Thaw depth was difficult to measure in most situations due to the presence of rocks but organic-rich moist-wet low lying surfaces had thaw depths between 60 and 90 cm in mid to late summer 2009.

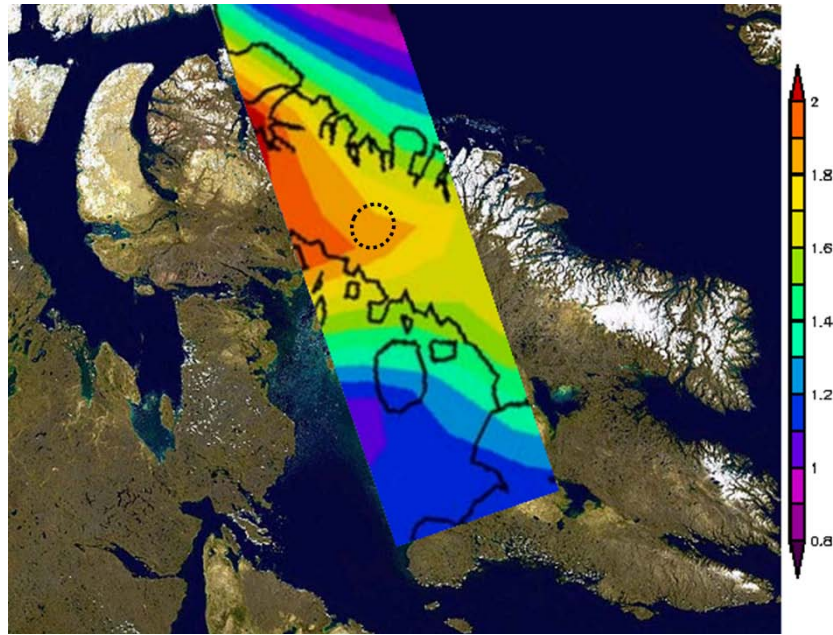


Figure 4: Satellite image of Baffin Island, overlaid with the difference in summer temperatures between the decade 2001-2010 and the preceding three decades. Black circle indicates the approximate location of our study site. Image produced using interactive web mapping provided by the NOAA/ESRL Physical Sciences Division, Boulder Colorado (<http://www.esrl.noaa.gov/psd/>).

2.3.2 Field sampling

During the early 1960s an intensive research effort characterized the geography (Ives and Andrews 1963), local glacial chronology (Andrews 1964), and elements of the plant ecology (Webber 1971) of the study area. Webber (1971) established eighty-two 1 x 10 m sites (here after referred to as “historic sites”) in a range of plant communities representative of the Lewis Valley (Webber 1971). In 2009 seventy-nine of these historic sites were relocated and resampled for species cover and abundance as a component of the International Polar Year – Back to The Future project. A detailed description of plant community change documented through this resampling effort along with the sampling protocols used, are given in Villarreal et al (*in prep.*). This study was coordinated with the 2009 resampling effort and strictly addressed ecosystem functional change.

Climate data were collected using a portable automatic weather station (Hobo AWS, Onset Computer, Bourne, Massachusetts, USA) that was established near the historic plots for the duration of the field study. The AWS measured air temperature (2 m), relative humidity (2 m), soil temperature (-1 cm), barometric pressure (1 m), soil moisture (-10 cm), photosynthetically active radiation (3 m), solar radiation (3 m), and wind speed and direction (3 m) at one minute intervals. To characterize ecosystem

functional attributes of plant communities in the study area, we used a variety of mostly plot level physiological and other sampling techniques. Fifty-four 30 x 30 cm plots (here after called “functional plots”) were established between late July and early August 2009 within the nine plant communities identified by Villarreal et al. (*in prep.*). Where possible, these were established as close as possible to the historic sites. Species cover and abundance were estimated visually for all vascular and non-vascular plant species by the same observers who resampled sites in the study described in Villarreal et al. (*in prep.*). Using a similar approach for estimating plot level land-atmosphere CO₂ fluxes described by Lara et al. (2012), aluminum chamber bases were inserted 5 cm into the soil and left to equilibrate for a minimum of 12 hours. We measured the following functional attributes for each plot: Land-atmosphere CO₂ fluxes were measured using a LI-COR 6200 Photosynthesis System (LI-COR Inc., Lincoln, NB, USA), and four different thicknesses of shade cloth were used to generate ecosystem light response curves (Shaver et al. 2007, Lasslop et al. 2010). Calculation of net ecosystem CO₂ exchange (NEE), ecosystem respiration (R_E), and gross ecosystem exchange (GEE) followed methods of Oberbauer et al. (2007). Above ground biomass was harvested from all functional plots, dried, and sorted to plant functional groups (i.e. graminoid, shrub, herb, etc.). Surface albedo (short-wave reflectance of the surface) was measured using a net radiometer (CNR 2 Kipp and Zonen, Inc.) whereby incoming and outgoing short-wave radiation (310-2800 nm) were measured separately and then used to calculate the percentage of reflected radiation. Soil volumetric water content (VWC) was measured at 12 cm depth using a time domain reflectometer probe (TDR-300 spectrum technologies). Depth of thaw was measured where rocks were not prevalent using protocols described by the Circumpolar Active Layer Monitoring program (CALM, Brown et al. (2000)). Hyperspectral reflectance was measured with a portable PP Systems Dual detector narrowband Unispec DC spectrometer (350-1150 nm) that was used to calculate a normalized difference vegetation index ($NDVI = (R_{IR} - R_{VIS}) / (R_{NIR} + R_{VIS})$); Rouse et al 1974). Repeat photography suggested that the rock lichen (*Alectoria minuscula*) has increased in coverage since the early 1960s. Therefore, we determined if *A. minuscula* may have affected NDVI reflectance patterns. We set up six paired plots measuring 15 x 15 cm on 6 large boulders scanning *A.*

minuscula cover presence and absence. Significance testing for NDVI values was determined by a paired student's t-test.

2.3.3 Climate reconstruction

A 50-year climate reconstruction was developed for the study area by climatologist, J. D. Jacobs from the Memorial University of Newfoundland. Temperature trends are referenced against the North Atlantic Oscillation (NAO), as this climatic phenomenon can influence regional temperatures, and gridded regional datasets (Kalnay et al. 1996) are used to compare site and regional precipitation patterns. The site based climate reconstruction made use of both historic meteorological records collected in the study between 1963-65 (Løken, 1964), 1989-95 (Jacobs et al, 1993), as well as data from the two permanent weather stations in the region (i.e. Dewar Lakes and Clyde River), which have collected data continuously between 1958-2010. Temperature records from the various records were adjusted for station elevation using an average lapse rate of $0.6\text{ }^{\circ}\text{C } 100\text{ m}^{-1}$. We used daily mean air temperatures measured at 2 m above the ground and total precipitation (rainfall plus snowfall expressed as mm water equivalent) to develop a multiple regression. The latter used field data collected between 1963-65 (Løken, 1964), 1989-95 (Jacobs et al, 1993) and time series from the two permanent stations. Using the multiple regression, a 50-year time series was developed for the study area. This time series was used to estimate July temperatures (July T) and the Summer Warmth Index (SWI, defined as the mean temperature sums in each year for the months June, July, August, when mean temperatures are above $0\text{ }^{\circ}\text{C}$) and to determine change trends.

2.3.4 Estimating ecosystem functional change between 1964 and 2009

To determine how plant community change has altered ecosystem function, we use a change analysis, similar to that described by Lara et al. (2012). Plant community structure was derived using a single non-metric multi-dimensional scaling (NMS) ordination of plant cover and abundance data from both historic, resampled (1964, $n=79$; 2009, $n=79$) and functional plots (2009; $n=54$; total NMS plots = 212 plots and 108 species). Ordinations were run in PC-Ord 5.10 (MjM Software Design, Gleneden Beach, OR, USA) set to 'slow and thorough' using Sørensen's similarity coefficient. A series of recursive partitioning analyses (regression trees) were used to explore how NMS axis scores related to

environmental and functional attributes. Using the ‘ordinary kriging’ function in the Geostatistical Analyst extension of ArcGIS 10 (ESRI, Redlands, CA, USA), we created NMS surface projection models for each functional attribute using two-dimensional ordination axes scores from only the functional plots. Surface models were overlaid with both historic and resampled plot axes scores to extract estimates of functional attribute data for each historical and resampled site. To validate this approach, we non-destructively sampled historic sites for NDVI, Albedo, and VWC in 2009. Pearson correlations between modeled and actual (non-destructively) measured values for NDVI, Albedo, and VWC were used to determine the most accurate kriging model used for change analysis. Additionally, we use a net ecosystem exchange (NEE) model developed from field based sampling of 625 plots spanning a variety of land cover types throughout Beringia (Lin 2012), to determine the sensitivity of ecosystem CO₂ flux to potential changes in environmental factors.

Modeled functional change output were analyzed using a repeated measures Multivariate Analysis of Variance (RM-MANOVA) where time (i.e.1964 and 2009) and plant communities were treated as among and within subject factors. Exact F was used to determine if functional attributes varied over time and between plant communities at various time points (time x community). When RM-MANOVA results indicated a significant difference between plant communities and/or over time, univariate ANOVA post hoc tests were used to explore the functional changes over time for each plant community. All functional data were transformed prior to kriging and statistical analyses (Logarithmic: Biomass, GEE, VWC; Arcsine: NDVI, Albedo) to fit the assumptions of normality. Student t-tests, Regression trees, RM-MANOVAs, and correlation analyses were performed in JMP version 10 (SAS, Cary, NC, USA).

2.4 RESULTS

2.4.1 CLIMATE RECONSTRUCTION

July temperatures and SWI in the study area appeared to vary (Table 2) in association with the North Atlantic Oscillation (NAO) index (Hurrell and Deser 2009). The lowest July temperature for the study area occurred during the 1970s, a period of generally low temperatures in the eastern Canadian Arctic that were associated with a persistently positive NAO index. However, underlying this variability

is a clear trend ($0.5\text{ }^{\circ}\text{C decade}^{-1}$, $R^2 = 0.6109$, $p < 0.001$) toward warmer summer periods. In the last three decades, summer conditions at lower elevations at the study site have shifted into the range typical of Bioclimatic Subzone D (Walker et al. 2005), and higher elevation areas as well as areas close to the ice cap, though cooler, likely warmed at the same rate. Large spatial variability precluded extrapolation of precipitation from other stations in the region. Gridded regional datasets (Kalnay et al. 1996) underestimated precipitation, but indicated that summer precipitation was significantly lower during cooler periods (NAO index positive) and higher in warmer periods (NAO index negative). Despite this variation, there was a consistently positive trend in precipitation over the 2000-2010 period.

Table 2: Estimates of mean July Temperatures (T) and Summer Warmth Index (SWI) for the Lewis River site.

Decade	July T	SWI
1961-1970	8.2	20.1
1971-1980	7.2	19.5
1981-1990	9.1	20.8
1991-2000	8.8	20.5
2001-2010	9.9	22

2.4.2 Ecosystem functional change

The NMS ordination of species cover data from both historic sites and functional plots, yielded a three-dimensional solution with a final stress and instability of 18.05 and 0.0005, respectively, after 500 iterations. The proportion of variability explained by the ordination was 68.9% with axis one, two, and three representing 18.8%, 28.2%, and 22.0% of the cumulative variance, respectively. Though a three dimensional ordination was recommended, the patterns and extent of community shifts from 1964 to 2009 in ordination space were similar to the two-dimensional solution reported by Villarreal et al. (*in prep.*) for only the historic plots from which species indicator values were used instead of cover data for reasons explained by Villarreal et al. (*in prep.*).

Variability in axis 1 was best explained by slope (21.5% of axis variation) and measures of productivity and soil moisture (e.g. live/dead biomass, NEE, and VWC, together explained 35.5%). Cumulatively, a regression tree including slope, live/dead biomass, NEE, and VWC accounted for 57% of the variation in axis 1 scores (Figure 5a). Variability along axis 2 was best explained by VWC (55.9%

of axis variation). Additionally, snow cover, NDVI, albedo, and PRI were also important (11.2%, 5.4%, 4.3%, 4.3% of axis variation, respectively) and cumulatively accounted for 81.1% of the variation in axis 2 scores (Figure 5b). Variation in Axis 3 scores were best explained by NDVI (40.2% of axis variation). Additionally, Albedo, Snow cover, live biomass, GEE, LAI, and Surface age (16.1%, 12.7%, 2.9%, 2.8%, 2.8%, of variation explained, respectively), accounted for 81.9% of the variation in axis 3 scores (Figure 5c).

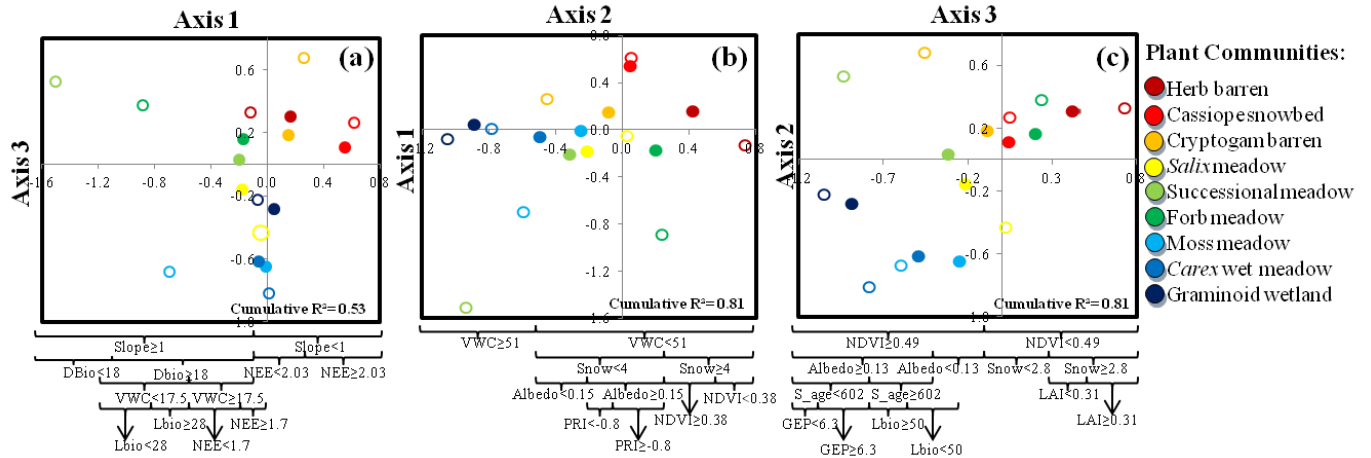


Figure 5: NMS 3-axis ordination for plant communities 1964 (open circle) and 2009 (closed circle); communities are arranged from dry (dark red) to wet (dark blue). Regression trees elucidate the most important functional attributes that are associated with axes 1, 2, and 3. See section 2.4.2 for detailed axis descriptions.

Ecosystem function varied substantially between plant communities and showed strong gradients for productivity, albedo, and soil moisture indices (Figure 6). Because the majority of plant communities are found in dry rocky soils, there was a strong similarity in ecosystem functional variables between plant communities. However, substantial functional differences exist. For example, the most productive communities were also the wettest (i.e. forb, moss, and *Carex* wet meadows) and the least productive community (Cryptogam barren communities) was also the driest. Interestingly, albedo was lowest (e.g. low reflectivity) in plant communities (i.e. Cryptogam barren and successional meadows) with dark cryptogamic soil crust (primarily *Cephaloziella arctica*) and standing water (i.e. *Carex* wet meadows), while the majority of other communities had a similar albedo (Figure 6).

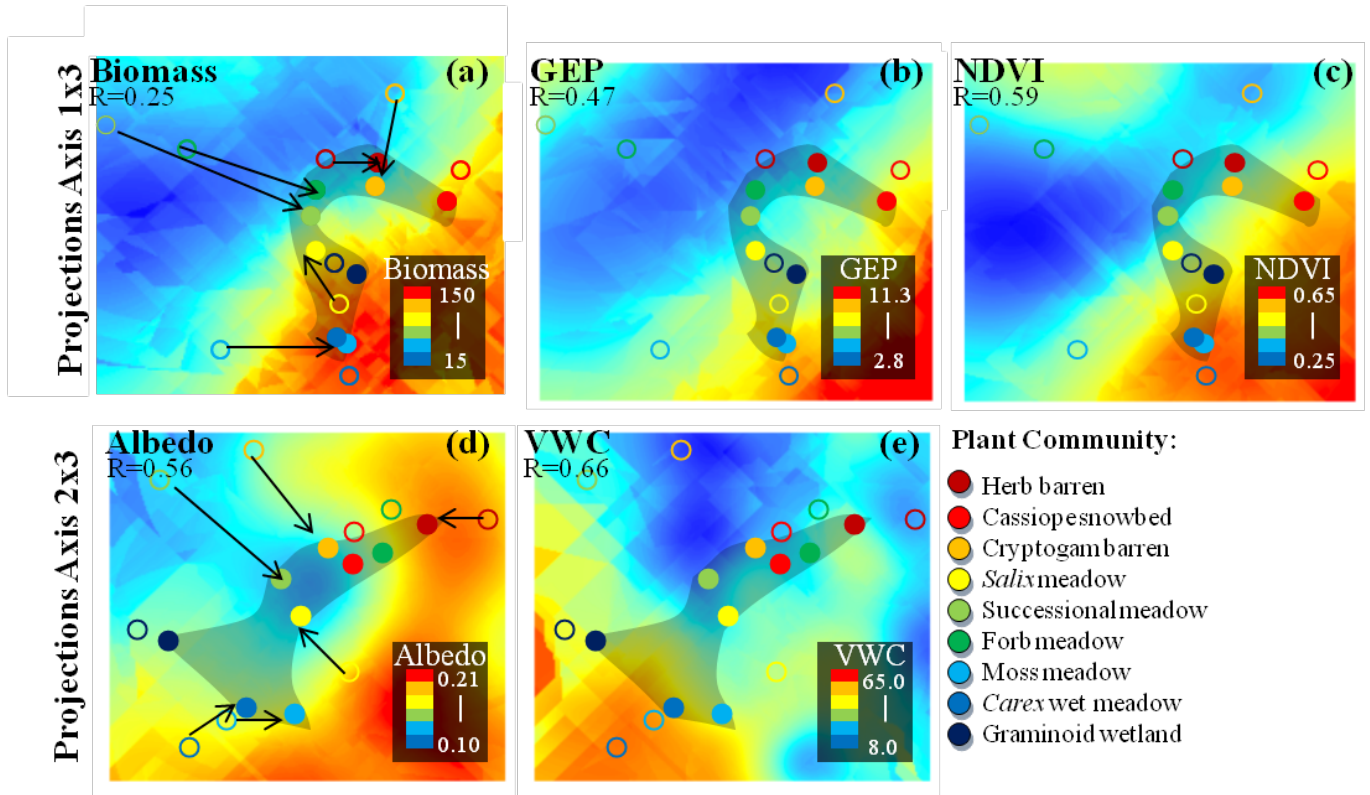


Figure 6: Surface models of ecosystem function variables derived by interpolating (kriging) measured values for 54 functional plots within NMS ordination space. Colors for surface models represent high (red) to low (blue) values for each functional variable and plant communities are presented along a soil moisture gradient from dry (dark red circles) to wet (dark blue circles). Open and closed circles represent NMS axis scores for plant communities sampled in 1964 and 2009 respectively. R values represent how accurately kriged surfaces correspond to the distribution of measured functional plot values over a two-dimensional NMS. Units: Biomass (gdw m^{-2}), GEE ($\text{gC m}^{-2}\text{day}^{-1}$), NDVI (reflectance index), Albedo (%), VWC (ratio of mass/unit vol).

Because the NMS yielded a 3D solution, we produced three surface models (i.e. Axis1 x 2, Axis 1 x 3, Axis 2 x 3) for each functional attribute (Biomass, GEE, NDVI, Albedo, VWC). To determine the single most accurate kriging method for modeling functional attributes, we correlated an independently derived functional attribute dataset for historical sites collected in 2009, with modeled historical site functional values. The highest correlations between actual (non-destructive) measured and modeled functional values for the three surface models were determined to be the best models to assess functional change over time. We found model “Axis 2 x 3” to best represent VWC ($R^2 = 0.78$, $p < 0.001$, Figure 7a) and Albedo ($R^2 = 0.38$, $p < 0.001$, Figure 7c), while model “Axis 1 x 3” best represented NDVI ($R^2 = 0.53$, $p < 0.001$, Figure 7b), thus, we use “Axis 1 x 3” to assess NDVI and other vegetation productivity (i.e. Biomass and GEE) proxies, as strong linear relationships are found between NDVI and GEE

($\text{NDVI} = 1.13(\log[\text{GEE}] \text{m}^{-2}) + 0.15$, $R^2 = 0.45$, $p < 0.001$) and NDVI and Biomass ($\text{NDVI} = 0.92(\log[\text{Live Biomass}] \text{m}^{-2}) + 1.04$, $R^2 = 0.35$, $p < 0.001$).

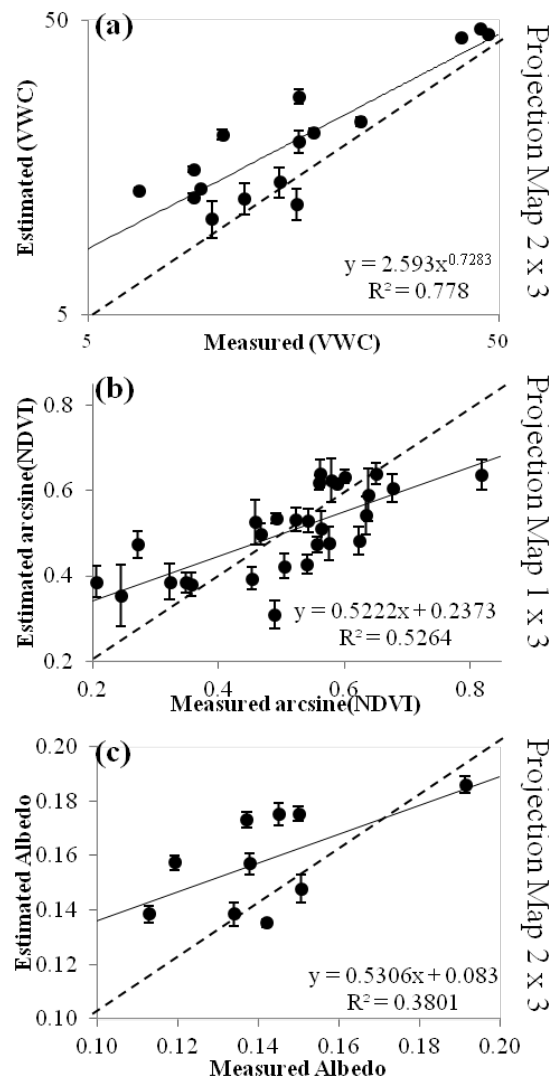


Figure 7: Regression analyses of measured (non-destructive) versus modeled (from surface models produced over NMS analyses) ecosystem functional values. Each data point on panels, VWC (a), NDVI (b), and Albedo (c) represent 30, 10, and 10 field data points collected from historic sites, presented with error bars. Dotted line represents a 1:1 line.

We found community productivity estimates to respond similarly over time and within specific communities. Biomass and NDVI both strongly responded to time, community, and the interaction between time and community (Table 3), while time and the interaction between time and communities did not vary significantly for GEE, but did vary for plant community (Table 3). Post-hoc tests determined that biomass increased from 1964-2009 in Forb meadows (+40.8%) and Graminoid wetlands

(+45.7%), but the greatest increase was found in Moss meadows with an increase of 178% or 70.6 g m⁻² (Table 4; 5). Similarly, NDVI increased in Graminoid wetlands (+28.8%) and in Moss meadows (+34.6%; Table 4). In addition, NDVI increased in the Cryptogam barren community (+18.7%), similar to what would be expected with greater *A. minuscula* presence over time (see below), while NDVI decreased in *Salix* meadows (-9.4%; Table 4). Similar to NDVI, we found GEE to increase (+27.1%) in the Cryptogam barren community and Moss meadows by 28.8% (Table 4). Albedo varied significantly between communities and the interaction between time and community, but not over time (Table 3). Albedo decreased (i.e. became less reflective) in *Salix* meadows, but no other changes over time and in other communities were detected. Unlike albedo, we found VWC to decrease over time ($p = 0.0757$; Table 3; 4), and vary among communities, but no interaction was found between time and community. Moss and *Carex* wet meadows decreased in VWC over time the most at -24.2% and -29.6%, respectively (Table 4).

Table 3: Main effects for repeated measures MANOVAs for modeled functional attributes between 1964 and 2009 and among plant communities. Numerator degrees of freedom (df) for time, community, and time x community were 1, 8, and 8 respectively, while denominator df were 70. Bolded and italicized values represent significant change at $\alpha < 0.05$; < 0.1 .

Multivariate Responses		Exact F	P value
Biomass	Time	8.97	0.0038
	Community	14.64	< 0.0001
	Time x Community	3.38	0.0025
GEE	Time	1.78	0.186
	Community	11.15	< 0.0001
	Time x Community	1.89	<i>0.0749</i>
NDVI	Time	10.08	0.0022
	Community	12.62	< 0.0001
	Time x Community	4.04	0.0005
Albedo	Time	0.13	0.718
	Community	3.35	0.0027
	Time x Community	2.10	0.0468
VWC	Time	3.25	<i>0.0757</i>
	Community	19.85	< 0.0001
	Time x Community	1.51	0.171

Table 4: Percent change of functional values between 1964 and 2009 for all plant communities. Bolded and italicized values represent significant change at $\alpha < 0.05$; < 0.1 .

Community	SMR	Biomass	GEE	NDVI	Albedo	VWC
Herb barren	dry	-1.3	3.6	-3.9	-1.2	1.3
Cassiope snowbed	dry	8.7	2.9	4.9	-0.3	5.9
Cryptogam barren	dry	15.8	27.1	18.7	2.9	-2.0
<i>Salix</i> meadow	dry-mst	-23.4	-7.5	-9.4	-13.8	-0.7
Successional meadow	dry-mst	55.7	-9.2	23.1	14.8	-17.8
Forb meadow	dry-mst	40.8	-1.5	6.8	-6.7	3.0
Moss meadow	mst-wet	178.0	28.8	34.6	5.3	-24.2
<i>Carex</i> wet meadow	wet	-9.4	-7.5	-4.0	-6.2	-29.6
Graminoid wetland	wet	45.7	8.2	15.8	1.9	-11.6

Table 5: Estimated functional values for 1964 and 2009 for all plant communities. Bolded and italicized values represent significant change at $\alpha < 0.05$; < 0.1 . Units: Biomass (gdw m⁻²), GEE (gCm⁻²day⁻¹), NDVI (reflectance index), Albedo (%), VWC (ratio of mass/unit vol).

Community	SMR	Biomass		GEE		NDVI		Albedo		VWC	
		1964	2009	1964	2009	1964	2009	1964	2009	1964	2009
Herb barren	dry	35.6	35.2	3.69	3.82	0.423	0.407	0.176	0.174	16.0	16.2
Cassiope snowbed	dry	60.5	65.8	4.84	4.98	0.476	0.500	0.168	0.168	16.0	16.9
Cryptogam barren	dry	30.2	35.0	3.31	4.20	0.363	0.430	0.150	0.154	14.2	13.9
<i>Salix</i> meadow	dry-mst	69.0	52.8	5.04	4.66	0.513	0.465	0.181	0.156	18.9	18.8
Successional meadow	dry-mst	24.3	37.9	4.22	3.83	0.352	0.433	0.145	0.167	26.8	22.1
Forb meadow	dry-mst	24.8	35.0	3.66	3.61	0.360	0.385	0.177	0.165	16.3	16.8
Moss meadow	mst-wet	39.6	110.2	4.24	5.46	0.429	0.578	0.169	0.178	39.8	30.2
<i>Carex</i> wet meadow	wet	105.9	96.0	6.04	5.59	0.573	0.550	0.178	0.167	44.9	31.6
Graminoid wetland	wet	49.5	72.1	4.60	4.98	0.447	0.517	0.154	0.157	38.5	34.0

To enhance hypothesis generation about past and future ecosystem functional change at the study site, we used an empirical model developed by Lin (2012) to assess likely changes in NEE between 1964-2009 in response to changes in peak season temperature (climate reconstruction) and the change modeled for NDVI and VWC in this study for dry, moist, and wet community soil moisture regimes (SMR; Table 5). The empirical model accounted for 61% ($y = 0.872x - 0.6953$, $p < 0.001$) of the variation in all our 216 modeled flux points in dry, moist, and wet community moisture regimes. Using temperature, NDVI, and VWC estimates for 1964 produced in this study, we determined NEE to have likely increased between 1964 and 2009 for moisture regimes, dry (114%), moist (42%), and wet (24%), reducing carbon uptake capacity. All communities did, however, remain a peak growing season sink for

carbon. We also found the 2 °C increase in temperature modeled for 1964-2009, to have likely resulted in a increase of NEE in dry, moist, and wet communities by 174%, 54%, and 17%, respectively, while modeled increases in NDVI (dry:+14%, moist:+13%, wet:+16%) over the same time interval corresponded to decreases in NEE in dry (-79%), moist (-30%), and wet (-10%) communities (Table 6). Further, modeled decreases in VWC (dry: -2%, moist: -10%, wet: -22%) between 1964-2009 were also estimated to increase NEE in dry (7%), moist (18%), and wet (17%) community moisture regimes. Plant communities within the dry moisture regime were found to be the most sensitive to change when expressed as percentage change (114%) over time, but the greatest absolute change occurred in plant communities associated with wet moisture regimes (0.479 gC m⁻² day⁻¹).

Table 6: Sensitivity of net ecosystem exchange (NEE) to modeled changes in temperature (+2°C), NDVI (dry: +14%, moist: +13%, wet: +16%), and VWC (dry: -2%, moist: -10%, wet: -22%) between 1964-2009. NEE is presented as change for peak season gC m⁻² day⁻¹ and percent. Modeled NEE for dry, moist, wet, and all (combined) for 2009 were 0.2, 0.63, 1.99, and 0.45 gCm⁻²day⁻¹, respectively.

Moisture Regime	Temp	NDVI	VWC	Temp+NDVI	Temp+VWC	Temp+NDVI+VWC
Dry	0.346 174%	+0.158 +79%	0.015 7%	0.182 91%	0.354 178%	0.227 114%
Moist	0.339 54%	+0.185 +30%	0.111 18%	0.154 25%	0.450 72%	0.265 42%
Wet	0.339 17%	+0.201 +10%	0.341 17%	0.138 7%	0.680 34%	0.479 24%
All	0.344 77%	+0.165 +37%	0.062 14%	0.174 39%	0.401 90%	0.257 57%

2.4.3 Rock lichen effects on NDVI

Rock surfaces with the black lichen *A. minuscula* present had approximately 5.9 times higher NDVI relative to bare rock (df=12, p <0.001). The NDVI values for presence and absence of *A. minuscula* were 0.133 and 0.023, respectively. Although *A. minuscula* NDVI values remain low, relative to green vegetation, central Baffin Island is dominated by exposed dry rocky surfaces so increases in *A. minuscula* cover across the landscape as seen in community specific repeat photography (Figure 8c) has the potential to greatly affect remotely sensed NDVI reflectance patterns.

2.5 DISCUSSION

Recent remote sensing evidence (Bhatt et al. 2010) reports landscape level NDVI near Baffin Bay to have increased in magnitude by >70% from 1982-2010, greater than any other region across the circumpolar Arctic. The climate reconstruction for central Baffin Island suggests summer snow free periods have become warmer and possibly wetter over the last 50 years. Modeled functional changes reported here for the Lewis Valley largely corroborate satellite and repeat photographic observations (Figure 8) of change. Generally, the greatest functional changes were found in communities with high VWC, similar to other studies in northern Alaska (Lara et al. 2012), and Beringia (Lin et al. 2012). Results suggest that wet pond margin communities and Moss and *Carex* wet meadow communities underwent the greatest change in VWC, which on average declined by ~25% (Table 4) over the past half-century. Similar drying trends have been noted by Smol and Douglas (2007) on Cape Herschel, Ellesmere Island and Carroll et al. (2011) throughout Canada, but mostly in Arctic regions. Drying trends could be expected with warmer July air temperatures and increased capacity for evapotranspiration in the Lewis Valley (Table 2), but declines in the extent of snow banks could also be related to this (Figure 8b). However, VWC in Graminoid wetlands did not decrease significantly as these areas have a higher water holding capacity and are thus more resistant to change. In line with evidence from repeat photography (Figure 8a), we found Graminoid wetlands and Moss meadows to increase in NDVI and Biomass (46% and 178%, respectively). These results are similar to reports from nearby Bylot and Ellesmere Islands where 84-115% increases wet tundra plant biomass were recorded respectively between 1990 and 2008 (Cadieux et al 2008) and 1980 and 2005 (Hill and Henry 2011). However, the productivity of *Carex* wet meadows does not appear to have increased since 1964 (Biomass: 106g m⁻²; Table 5) and, therefore, could be limited by factors such as nutrient availability, which was not examined in this study. Additionally, we found moist Forb meadow biomass to increase by approximately 10 g m⁻², but this relatively low increase in biomass did not appear to couple with a change in GEE or NDVI. Although, we did not find Successional meadows to change significantly (low sample size), Villarreal et al. (*in prep.*) reports successional plant communities have changed in species composition more than any other plant community. Additionally, Villarreal et al. (*in prep.*) found the dominant shrub *Salix arctica* to decrease dramatically in *Salix* meadow communities between 1964-

2009, which appears to match the decrease in NDVI we documented for the same community. We also found albedo to decrease in *Salix* meadows, possibly because dark soil cryptogamic crusts (mostly *C. arctica*) increased in cover for this plant community (Villarreal et al. *in prep.*). The GEE and NDVI of rocky/exposed Cryptogam barren communities, increased over the study period, which closely resembles observations made with repeat photography that show the cover of *A. minuscula* to increase over time (Figure 8d). The modeled NDVI in this community increased by 0.067 which was interesting as our NDVI rock lichen study showed NDVI to increase by 0.11 when *A. minuscula* was present, suggesting the change in NDVI at the community level may partly be explained by the increase in *A. minuscula* cover. Finally, the relatively dry herb barren and *Cassiope* snowbed communities were found to be the most resistant to change and no change in productivity, albedo, or VWC was found. The lack of long-term change in dry plant communities has also been by other studies in the Arctic (Villarreal et al. 2012, Lin et al. 2012, Lara et al. 2012).

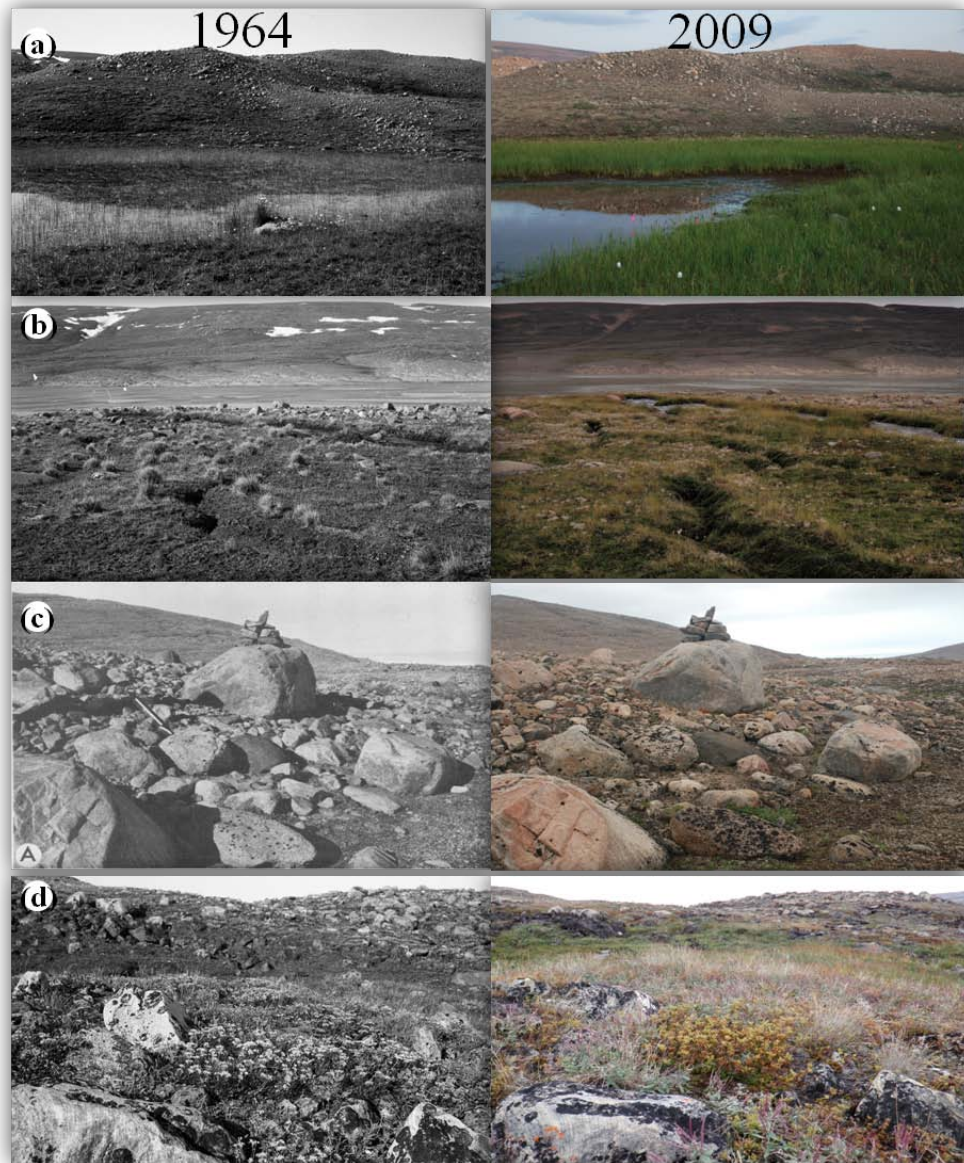


Figure 8: Repeat photography representing four communities in the study area. Photos in the left column were taken in 1964 and the right column 2009. Photographs were taken within less than one calendar week difference. Panel (a-d) are represented by communities Graminoid wetlands, Forb meadows, Herb barren, and Cryptogam barren.

Attributing the modeled change described in this study to climate change and/or successional change is extremely difficult. The use of an NEE ecosystem model developed for the Beringia region (Lin 2012) to detect shifts in land-atmosphere carbon exchange, however, allows for testing the sensitivity of plant communities in our study to temperature and other changes. We found temperature to be a strong control of carbon loss during peak growing season. Results suggest that an increase in air temperature by 2 °C over the past-half century has increased NEE to a greater degree than that offset by

modeled increases in NDVI, and that this shift has likely been driven by increased respiratory losses. In addition to warming, landscape drying appears to have further increased NEE. This modeling effort suggests that dry plant communities experienced the greatest magnitude change (114%) between 1964-2009, and wet plant communities experienced the greatest absolute change ($0.479 \text{ gC m}^{-2} \text{ day}^{-1}$). These findings are particularly striking because dry moisture regimes comprise a relatively large component of the study area and wet were the most functionally dynamic. Though, a variety of recent remote sensing, observational, and experimental studies in the Arctic have documented increased productivity over the past few decades (Bhatt et al. 2010; Myers-Smith et al. 2011; Elmendorf et al. 2012; Epstein et al. 2012), it is important to consider the reciprocal impacts of carbon sequestration/uptake (e.g. greening) as we found warming and drying to exacerbate carbon losses, by reducing the net sink strength in this high arctic ecosystem. In the future, these deglaciated, temperature sensitive regions spanning the high arctic may become of greater significance to elevated atmospheric carbon stocks and to global climate change.

Although we hypothesize potential drivers of functional change (i.e. warming and succession), determining specific drivers with high confidence is difficult in non-experimental studies, where large gaps in time and dynamic interactions between a gamut of environmental factors exist (e.g. climate, cryosphere, hydrology, succession; Luo et al. 2011). However, the modeled functional changes reported in this study are similar to patterns documented by other studies (Bhatt et al. 2010, Hill and Henry 2011, Frasier et al. 2011). Despite the fact that our functional change analysis is calculated using two points in time, and the well-known potential for tundra structure and function to fluctuate inter-annually, results verify change in vegetation greenness and productivity (Bhatt et al. 2010, Hill and Henry 2011), in addition to landscape drying trends documented in Arctic lakes and ponds (Smith et al. 2005, Smol and Douglas 2007, Avis et al. 2011). Importantly, the summer of 2009 was considered to be an abnormally warm year, which may have affected peak season carbon fluxes. However, our analytical modeling approach, conservatively documents functional change only when species composition changes. Therefore, the 2009 abnormally warm year may have only minimally affected change results. Although not ideal, the peak season snap shot sampling approach used in this study is similar to that employed in several other ecosystem assessments (Oberbauer et al. 2007, Lund et al. 2009, Lara et al. 2012,) and

modeling studies (Shaver et al. 2007, Lin et al. *in prep.*), but are unable to estimate seasonal carbon balance due to temporal constraints. In addition the NEE model used for hypothesis generation and sensitivity analysis (Lin 2012) also used snap shot sampling for the Beringia region and was able to effectively predict NEE fluxes from a markedly different arid tundra ecosystem. Our sampling and analytical approach appeared to affectively and conservatively represent functional change despite the absence of long-term functional data and notable variability in climate.

2.6 CONCLUSION

High arctic landscapes have been previously thought to be of little significance with respect to biogeochemical cycling. This study joins a growing suite of evidence that shows that high arctic landscapes are changing dramatically and with regional implications on land-atmosphere feedbacks and biogeochemical cycling. In this study, we show that central Baffin Island is warming and drying during the summer. These changes in climate in association with vegetation succession following deglaciation appear to have resulted in the following landscape changes during the period from 1964-2009: (1) increases in photosynthetic capacity and a general greening of the land surface area, (2) community specific decreases in albedo, thereby increasing surface heat energy absorption, (3) landscape level soil drying, with the highest rates of change observed in wet communities, and (4) despite increases in plant productivity at the community level, the carbon sink strength may have been reduced with increased temperature and soil drying since the 1960s. During this period, dry communities had the greatest magnitude change in NEE and wet communities had the greatest absolute change. This study emphasizes the important need for repeat sampling of historic research sites and their potential to be used to explore long-term change in ecosystem function, which is useful for validating modeling and remotely sensed change observations.

Chapter 3: Estimated Change in Tundra Ecosystem Function from 1972 to 2010 near Barrow, Alaska

3.1 ABSTRACT

How the greening of Arctic landscapes manifests as a change in ecosystem structure and function remains largely unknown. This study investigates the likely implications of plant community change on ecosystem function in tundra near Barrow, Alaska. We use marked plots, established in 1972 and resampled in 1999, 2008, and 2010 to assess plant community change. Ecosystem functional studies were made close to peak growing season in 2010 adjacent to structurally similar marked plots. Measurements included land-atmosphere CH₄ and CO₂ exchange, hyperspectral reflectance, albedo, water table height, soil moisture, and plant species cover and abundance. Species cover and abundance data from marked and destructive plots were analyzed together using non-metric multidimensional scaling (NMS) ordination. NMS axis scores from destructive plots were kriged to create surface plots of ecosystem functional variables in ordination space, from which time series of functional attributes for resampled plots were derived. Generally, the greatest functional changes were found in aquatic and wet plant communities, where productivity varied and soil moisture increased along with methane efflux over time. Further, the least functional changes were found in moist and dry communities which decreased in soil moisture, and appeared more stable through time. Findings suggest that the Barrow landscape could have become less productive and less responsive to change and disturbance over the past few decades. This study is a contribution to the International Polar Year Back to the Future Project (512).

3.2 INTRODUCTION

In the Arctic, shifts in ecosystem function have important implications for predicting the future state of the Arctic System and how these changes may affect the rest of the globe (McGuire et al. 2006, McGuire et al. 2010, Qian et al. 2010). Perhaps of most concern is the future state and fate of the substantial arctic soil organic carbon pool (Tarnocai et al. 2009, Hollesen et al. 2011). Relative to the size of this carbon pool, arctic land masses are relatively small and have low productivity and standing biomass (Zimov et al. 2006, Schuur et al. 2008), suggesting that if this is lost, soil carbon will not re-

accumulate to the same extent in the near future. This scenario has strong global consequences if there is a reduction in carbon uptake capacity and/or a net loss of soil carbon to the atmosphere as CO₂ or CH₄ from arctic landscapes (Schuur et al. 2009). Although time series of satellite-derived normalized difference vegetation indices (NDVI) suggest arctic tundra landscapes have become ‘greener’ over the past three decades (Bhatt et al. 2010), signifying increased carbon uptake potential, changes in ecosystem structure (e.g. plant species composition and abundance) and function (e.g. biogeochemical cycling) associated with these changes remain relatively poorly investigated over similar time frames.

To understand the future state of the Arctic and Earth Systems, improved understanding of key terrestrial ecosystem processes over decade-time scales are needed (Luo et al. 2011). For arctic terrestrial ecosystems, ecosystem structure appears to be strongly coupled to ecosystem functional processes. For example, several key studies highlight associations between plant functional types and species composition and nutrient cycling (Hobbie 1992, Hobbie et al. 2002, Edwards and Jefferies 2010), surface albedo (Chapin et al. 2005), net primary production (Webber 1978, Chapin et al. 1995), and trace gas emissions of CO₂ and CH₄ (Joabsson and Christensen 2001, Strom and Christensen 2007). Based on first principles, these findings suggest that a shift in species composition will likely alter ecosystem function.

For the majority of the Arctic, assessing change in ecosystem structure and function over decade-time scales is challenged by the absence of long-term monitoring. Several recent studies have demonstrated the benefits of resampling old research sites throughout the Arctic to assess change over time (*see* Callaghan et al. 2011). To date, few of these retrospective studies have coupled change detection of ecosystem structure and functional attributes over decade-time scales.

This study is a companion paper to Villarreal et al. 2012, which documents change in arctic terrestrial plant community structure between 1972 and 2010 through repeated resampling of plots established during the International Biological Program (IBP) near Barrow, Alaska. In this study we link functional to structural change reported by Villarreal et al. (2012), and here we solely focus on modeling functional changes in response reported structural change. Our findings are based on the strict assumption that within ecosystems, i) plant communities change because plant species that comprise

these communities change in cover and abundance in response to a gamut of environmental conditions and/or due to succession (Epstein et al. 2004, Walker et al. 2006, La Puma et al. 2007, Hudson et al. 2011, Villarreal submitted), ii) such community change can manifest to affect ecosystem function (*sensu* Johansson et al. 2006, Oberbauer et al. 2007), and iii) that the relationship between ecosystem structure and function does not change over time when plant communities and environmental conditions do not change. This study is a contribution to the International Polar Year – Back to The Future (IPY-BTF) project, which aimed to determine the impacts of arctic plant community change on ecosystem function over decadal time scales by revisiting and resampling historic research sites more than 25 years in age.

3.3 METHODS

3.3.1 Site Description

This study was conducted at the former IBP research site (71°17'N, 156°41'W) near Barrow, Alaska. Mean annual temperature, precipitation, and snowfall are -12 °C, 11 cm, and 69 cm respectively (1971-2000; NCDC <http://cdo.ncdc.noaa.gov/climatenormals/clim20/state-pdf/ak.pdf>). The landscape has a low relief best characterized as poorly drained polygonized tundra (Brown et.al 1980). Maximum depth of thaw ranges from 30 to 40 cm (Nelson et al. 1998, Hinkel and Nelson 2003) and the snow-free period is variable in length but generally begins in early June and lasts until early September (Brown et al. 1980).

The IBP (1967-1974) produced some of the earliest quantitative descriptions of plant community assemblages in the North American Arctic. In 1971, 43 1 x 10 meter sites (here after referred to as “historic sites”) comprised of 10 contiguous 1 m² plots were established in a range of plant communities representative of the coastal tundra in the area. The sites, which are marked with wooden stakes, were first sampled in 1972 (Webber 1978; Webber et al. 1980). Villarreal et al. (2012) determined that these 43 IBP historic sites represent nine plant communities common in the Barrow landscape: aquatic *Carex* graminoid tundra (ACG), creek *Arctophila* graminoid tundra (CAG), pond *Arctophila* graminoid tundra (PAG), seasonally-flooded graminoid tundra (FG), wet graminoid tundra (WG), moist graminoid tundra (MG), dry-moist dwarf shrub graminoid tundra (DMSG), dry dwarf shrub graminoid tundra (DSG), and successional-dry dwarf shrub graminoid tundra (SDSG). Historic data from the IBP were rescued in

1998 and 33 of the sites (330 1 m^2 plots) were relocated and resampled in 1999, 2008 and 2010 using the same protocols for estimating species cover and abundance used in 1972. A detailed description of structural change from this resampling effort is described in Villarreal et al. (2012).

3.3.2 Field Sampling of Functional Attributes

To examine the relationship between plant community structure (species cover and abundance) and ecosystem function, we established 14 sites in close proximity to the historic sites that were resampled. Each site included three 50 cm^2 plots (here after called “functional plots”, $N = 42$). Using a similar approach to other studies that have conducted short-term, plot-level, trace-gas measurements (Shaver et al. 2007, Lund et al. 2009), aluminum chamber bases were inserted 5 cm into the soil and left for a minimum of 12 hours to equilibrate. Species cover and abundance were estimated visually for all vascular and non-vascular plant species in each functional plot (bryophytes were lumped).

The following functional attributes of each plot were measured in early to mid August 2010 close to peak growing season (August 3rd and 15th 2010). Land-atmosphere CO_2 fluxes were measured using a LI-COR 6200 Photosynthesis System (LI-COR Inc., Lincoln, NB, USA), and four different thicknesses of shade cloth from which ecosystem light response curves were generated (Shaver et al. 2007, Lasslop et al. 2010). Calculations of net ecosystem CO_2 exchange (NEE), ecosystem respiration (R_E), and gross ecosystem exchange (GEE) were made following (Oberbauer et al. 2007). Methane (CH_4) flux was measured using a photo-acoustic multi-gas analyzer (INNOVA 1312 AirTech Instruments A/S, Denmark; *sensu* (Lund et al. 2009, Sachs et al. 2010) and processed following (Lund et al. 2009). To evaluate the combined greenhouse warming potential (GWP) of ecosystem CO_2 and CH_4 flux, we converted CH_4 fluxes to CO_2 equivalents assuming a 100 year atmospheric residence time ($\text{GWP}_{100}=23$ for CH_4 (Ramaswamy et al. 2001). Hyperspectral reflectance was measured with a portable PP Systems Dual detector narrowband Unispec DC spectrometer (350-1150 nm) and used to calculate a normalized difference vegetation index ($\text{NDVI} = (R_{\text{IR}} - R_{\text{VIS}}) / (R_{\text{NIR}} + R_{\text{VIS}})$) and water band index ($\text{WBI} = R_{970} / R_{900}$) (Penuelas et al. 1993, Gamon et al. 2006). Surface albedo (short-wave reflectance of the surface) was measured using a net radiometer (CNR 2 Kipp and Zonen, Inc.) by isolating incoming and outgoing short-wave radiation (310-2800 nm) and calculating the percentage of reflected radiation. Soil

volumetric water content (VWC) was measured using a time domain reflectometer probe (TDR-300 spectrum technologies) at 10 cm depth. Depth of thaw was measured using protocols described by the Circumpolar Active Layer Monitoring program (CALM,(Brown 2000)). Water table height (WTH) was measured by drilling a hole to the depth of permafrost into which a 4 cm diameter PVC tube was placed and allowed to equilibrate with water table for 12 hours, after which a ruler was used to determine the height of the water table relative to the depth of thaw (i.e. depth of inundated soil). Aboveground plant biomass was harvested during the period of maximum biomass using the same method applied by (Webber 1978). Climate data were collected using a portable automatic weather station (Hobo AWS, Onset Computer, Bourne, Massachusetts, USA) setup near the historic plots for the duration of the field study. This measured air temperature (2 m), relative humidity (2 m), soil temperature (-1 cm), barometric pressure (1 m), soil moisture (-10 cm), photosynthetically active radiation (3 m), solar radiation (3 m), and wind speed/direction (3 m) at one minute intervals.

3.3.3 Data Analysis

To link the historic plots with the functional plots and assess how change in ecosystem structure has likely affected ecosystem function, we used a single non-metric multi-dimensional scaling (NMS) ordination (McCune 2002) and several geostatistical techniques. The NMS was run in PCOrd 5.10 (MjM Software Design Gleneden Beach, OR, U.S.A.) set to 'slow and thorough' using Sørensen's similarity coefficient. Data included in the NMS comprise species cover from both historic (1972, 1999, 2008 and 2010; n = 1320) and functional plots (2010; n = 42; total n = 1362 plots and 82 species). To derive estimates of functional properties for the historic plots, NMS axis scores for the 42 functional plots were imported to ArcGIS 10 (ESRI, Redlands, California, U.S.A.) as x – y coordinates (Figure 9). For each functional attribute, surface maps were derived using the 'ordinary kriging' function in the Geostatistical Analyst extension of ArcGIS 10. The 1320 historic plots were then overlaid on the surface map derived for each functional attribute to extract a value for each plot, plant community, sampling year combination. Within the NMS, some historic plots fell outside the distribution of the functional plots in ordination space (Figure 9: C) and were not included in further analysis. Although less than 3% of the 1320 historic plots were excluded, the community PAG, which comprised one site and 10 plots,

was omitted as a result. To assess the validity of the interpolative method, VWC, WBI, and NDVI were collected on the historic IBP plots in 2010 and were compared to predicted VWC, WBI, and NDVI values for the corresponding historic plots derived from the kriging models using Pearson's correlation. Data were transformed where necessary to meet the assumptions of normality (VWC – arcsine, WBI, NDVI – natural log).

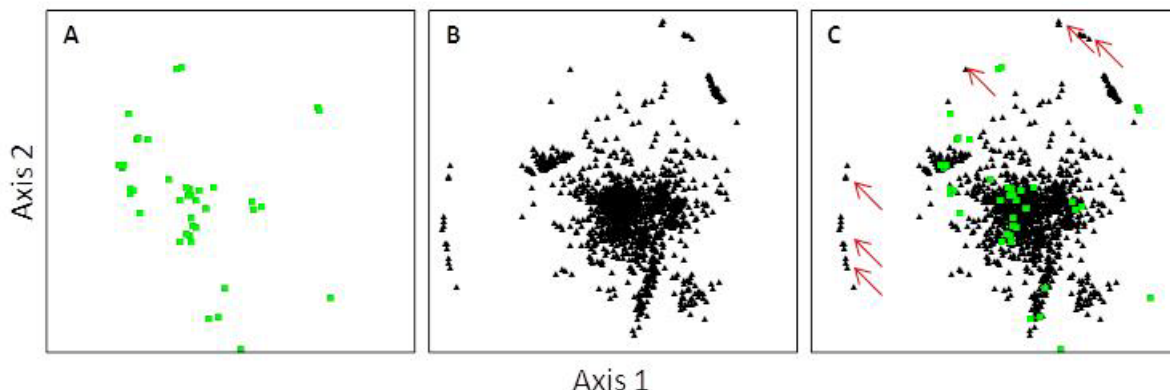


Figure 9: Spatial coverage of the functional plots in ordination space (Figure. 9A, green squares, $n = 42$) with resampled historic plots (Figure, 9B, black triangles, $n = 1320$). Historic plots that were outside the approximate range of the functional plots in ordination space were omitted from the model (Figure. 9C, omitted sites highlighted by red arrows).

To determine if the modeled functional attributes varied among plant communities and between sampling dates, we used a multivariate analysis of variance (MANOVA) for each functional attribute – plant community combination. Modeled values for the functional attributes of each plot were used as the response variable, plant community as the within subject factor, and sampling date as the among subject factor. Wilk's λ was used to determine if each functional attribute varied between sampling dates (time) and among plant communities at various sampling dates (time x community). When MANOVA results indicated a significant difference among plant communities, univariate ANOVA post hoc tests were used to explore the change between resampling dates within each plant community. MANOVA/ANOVAs were performed in JMP version 9 (SAS, Cary, North Carolina, U.S.A).

3.4 RESULTS

3.4.1 Functional Description of Plant Communities

The NMS ordination, using plant community data from the historic plots (Villarreal et al. 2012) and functional plots, yielded a two-dimensional solution with a final stress and instability of 28.1 and

0.007 respectively after 500 iterations. The proportion of the variance explained by the ordination represented 68.8% of the cumulative variance with axis one and two representing 38.1% and 30.7% respectively. Within the NMS, the variability between sampling times for each plant community is similar to that reported by Villarreal et al. (2012), suggesting the addition of the 42 destructive plots affected the ordination very little. Modeled aquatic and wet plant communities were the most functionally dynamic among sampling dates, followed by moist and dry communities which appeared to be more stable and changed little within ordination space between resampling dates. Modeled and actual VWC had a linear relationship (Figure 10; $y = 1.3362x - 0.2397$, $R^2 = 0.69$, $p \leq 0.0001$, $n = 285$), although the relationship slightly under predicted measured values for dry plots and slightly over predicted VWC for wet plots. Correlations between modeled and measured WBI and NDVI were weaker but linear (Figure 10; $y = 0.7853x + 0.0233$, $R^2 = 0.39$, $p \leq 0.0001$, $n = 80$; $y = 1.0201x + 0.0428$, $R^2 = 0.31$, $p \leq 0.0001$, $n = 80$ respectively) and slightly over predicted measured values for both attributes. Although modeled attributes differed from one-to-one relationships, results indicate that derived surface maps were effective at approximating measured functional attributes.

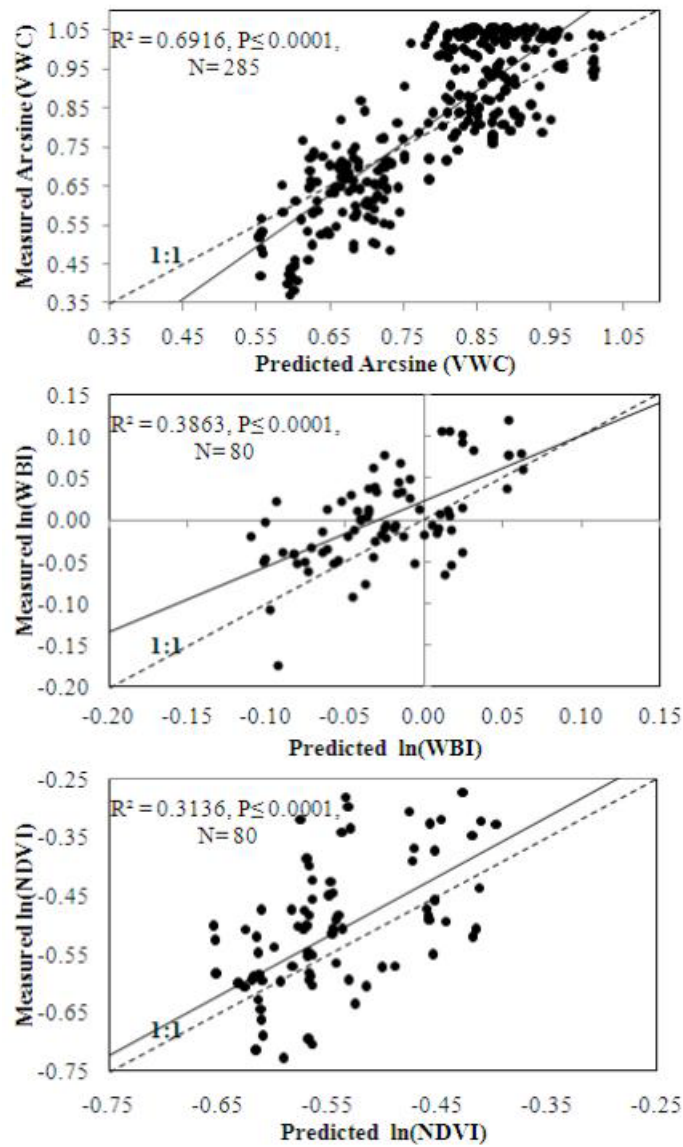


Figure 10: Models of soil volumetric water content (VWC – top), water band index (WBI - middle), and normalized difference vegetation index (NDVI - bottom) derived from field measurements and modeled NMS surface maps (VWC: $R^2 = 0.69$, $P < 0.0001$, WBI: $R^2 = 0.39$, $P < 0.0001$, NDVI: $R^2 = 0.31$, $P < 0.0001$, respectively). Trend-lines are represented by the solid line, while the dotted line represents a one-to-one relationship.

From the surface maps of functional attributes in ordination space (Figure 11), aquatic CAG had the highest VWC and WTH of all plant communities. CAG had the lowest albedo of all plant communities while GEE, R_E , NDVI, and CH_4 emissions were highest. The aquatic-wet community ACG was functionally similar to CAG, although ACG had slightly lower values for all functional attributes except albedo, which was approximately the same. Wet-moist communities FG and WG function similarly to each other; however, FG had a higher NDVI, WBI, albedo, and WTH relative to WG.

Moist-dry communities MG and DMSG overlapped considerably in ordination space, therefore functional characteristics in these communities were similar (Figure 11). DSG was the driest of all plant communities containing a relatively high albedo while GEE, R_E, and CH₄ were low. The modeling approach suggested that dry communities DSG and SDSG functioned markedly similarly; therefore for simplicity and clarity these communities were combined.

3.4.2 Estimation of Ecosystem Functional Change

We found significant time and time-community effects for all ten MANOVAs (Table 7), indicating that at least one plant community in each model varied significantly among historic sampling dates for a given functional attribute (Table 7). Significance tests using Tukey's HSD (Table 9) found ACG, CAG, and WG changed the most between sampling times (≥19 significant changes; Table 9), whereas FG, MG, DMSG, and DSG changed the least (≤5 significant changes; Table 9).

Table 7: Results of MANOVA tests that determined if each functional attribute varied significantly between sampling dates and plant communities. Significant time*community effects indicate that either an ecosystem functional attribute and/or at least one plant community changed over time. A significant time effect indicates that a minimum of one community changed function over time. Time*community (Numerator DF = 18, Denominator DF = 880.13), Time (Numerator DF = 3, Denominator DF = 311).

Functional attribute	Time*community			Time		
	Wilk's λ	Approx.F	Prob>F	F-value	Exact F	Prob>F
NEE	0.64	8.51	**	0.14	14.72	**
GEE	0.55	11.43	**	0.03	2.78	*
CH ₄	0.60	9.81	**	0.20	20.96	**
R _E	0.52	12.63	**	0.36	37.53	**
GWP ₁₀₀	0.66	7.62	**	0.04	3.88	*
Albedo	0.52	12.63	**	0.36	37.53	**
WBI	0.55	11.69	**	0.58	60.25	**
VWC	0.58	10.56	**	0.09	9.42	**
WTH	0.47	15.07	**	0.23	23.47	**
NDVI	0.52	12.51	**	0.49	51.18	**

**= p< 0.001

*= p< 0.05

Estimated soil volumetric water content (VWC) was greater in 2010 for aquatic-wet plant communities CAG and ACG than in 1972, while we found the opposite pattern true for MG (Figure 12a; Table 9). Wet-moist communities FG and WG had considerable inter-sampling variation in VWC

between sampling times but no long-term trend. There was no change in the VWC of dry communities DMSG and DSG. Trends for WTH and WBI followed similar patterns reported for VWC (Figure 12b, 12c; Table 9). Plant communities with high VWC and WTH had the lowest albedo (Figure 12d; Table 9). NDVI was lower in wet-moist communities CAG, ACG, and WG in 2008 than in 1972, while drier communities MG, DMSG, and DSG, did not vary between sampling times (Figure 12e; Table 9).

Methane (CH_4) efflux and NEE was greater in 2008 than 1972 for aquatic-wet communities CAG, ACG, and WG, while moist-dry communities MG, DMSG, and DSG showed no change (Figure 12f, 12g; Table 9). We found GEE in 2010 to be higher for the wet community CAG than in 1972, however the opposite trend was found for ACG and DMSG. No change in GEE was found for WG, MG, and DSG (Figure 12h; Table 9). Ecosystem respiration (R_E) remained relatively constant among sampling dates but was slightly lower in 2010 than 1972 in ACG, MG, and DMSG (Figure 12i; Table 9). Global warming potential (GWP_{100}) indicated decreased forcing potential for WG in 2008 than in 1999 but there was no overall trend spanning the study period (1972-2010, Figure 12j; Table 9). Forcing potential of ACG was higher in 2010 than in 1972 due to decreased GEE, increased CH_4 efflux, and relatively high R_E . No other trends in GWP_{100} were detected.

Peak season biomass of communities PAG, FG, WG, and MG in 1972 and 2010 are reported in Table 8. Biomass data for pond *Arctophila* graminoid tundra (PAG) and creek *Arctophila* graminoid tundra (CAG) were pooled in 2010 to improve inter-comparison with Webber (1978) (Table 8). Total vascular plant biomass increased in communities CAG (+96 g m^{-2} ; 81%) and MG (+44 g m^{-2} ; 70%) and showed little change in FG and WG. Biomass of non-vascular plants generally remained similar for the communities sampled. The biomass of graminoids in aquatic communities CAG increased markedly (+131 g m^{-2} ; 166%), as did the biomass of mosses (+33 g m^{-2} ; 182%), while that of forbs decreased (-35 g m^{-2} ; 88%).

Table 8: Above ground plant biomass (grams dry weight m⁻²) for four plant communities harvested near peak growing season in 2010 and 1972. Communities PAG and CAG were lumped in 1972 and have been treated the same way for data reported from 2010.

Year	Plant Comm.	Gram.	Moss	Shrub	Herb	Lich.	St. dead	Litter	Total vasc.	Total nonvasc.	Photo-active veg.
2010	CAG	210.5	50.9	0.0	4.8	0.0	34.1	46.2	215.3	50.9	266.2
1972	CAG	79.0	18.0	0.0	40.0	0.0	36.0	64.0	119.0	18.0	137.0
2010	FG	69.5	54.8	0.0	0.0	0.0	24.1	8.9	69.5	54.8	124.3
1972	FG	49.0	19.0	1.0	3.0	11.0	51.0	75.0	53.0	30.0	72.0
2010	WG	40.0	39.4	0.0	0.0	0.0	10.9	28.2	40.0	39.4	79.4
1972	WG	43.0	37.0	0.0	2.0	0.0	43.0	47.0	45.0	37.0	82.0
2010	MG	102.9	196.9	0.0	4.1	4.1	61.9	291.9	107.0	201.0	303.9
1972	MG	31.0	244.0	31.0	1.0	55.0	31.0	121.0	63.0	299.0	307.0

Note: Values are the means of harvested biomass representative of specific plant communities during peak growing season during 2010 and 1972 (Webber 1978).

Plant Comm. = plant community, Lich. = Lichen, St.dead = Standing dead, Tot vasc = Total vascular plants, Tot nonvasc = Total nonvascular plants, Photo active veg = Photosynthetically active vegetation, N = Sample size

3.5 DISCUSSION

In this study we sought to infer decade-time scale change in ecosystem function for plant communities that dominate coastal tundra near Barrow, Alaska. Our analytical approach was based on the strict assumption that within ecosystems i) plant communities change because plant species comprising these communities change in cover and abundance in response to altered environmental conditions and/or due to succession (Epstein et al. 2004, Walker et al. 2006, La Puma et al. 2007, Hudson et al. 2011, Villarreal submitted), ii) such community change can manifest to affect ecosystem function (*sensu* (Hooper et al. 2005)), and iii) that the relationship between ecosystem structure and function does not change over time when plant communities and environmental conditions do not change. Independent validation of our approach showed imperfect but adequate results for reconstructing historic ecosystem functional attributes suitable for the development of testable hypotheses of future change, assuming future change trajectories follow the same course as hindcast trends. Other studies using similar assumptions to examine time series trends in ecosystem structure and function include Johansson et al. (2006) who examined the impact of land cover change on ecosystem

function near the Stordalen Mire in subarctic Sweden to assess change in global warming potential over time, and Swann et al (2009), who assesses the potential radiative forcing change due to large vegetation shifts in northern latitude ecosystems.

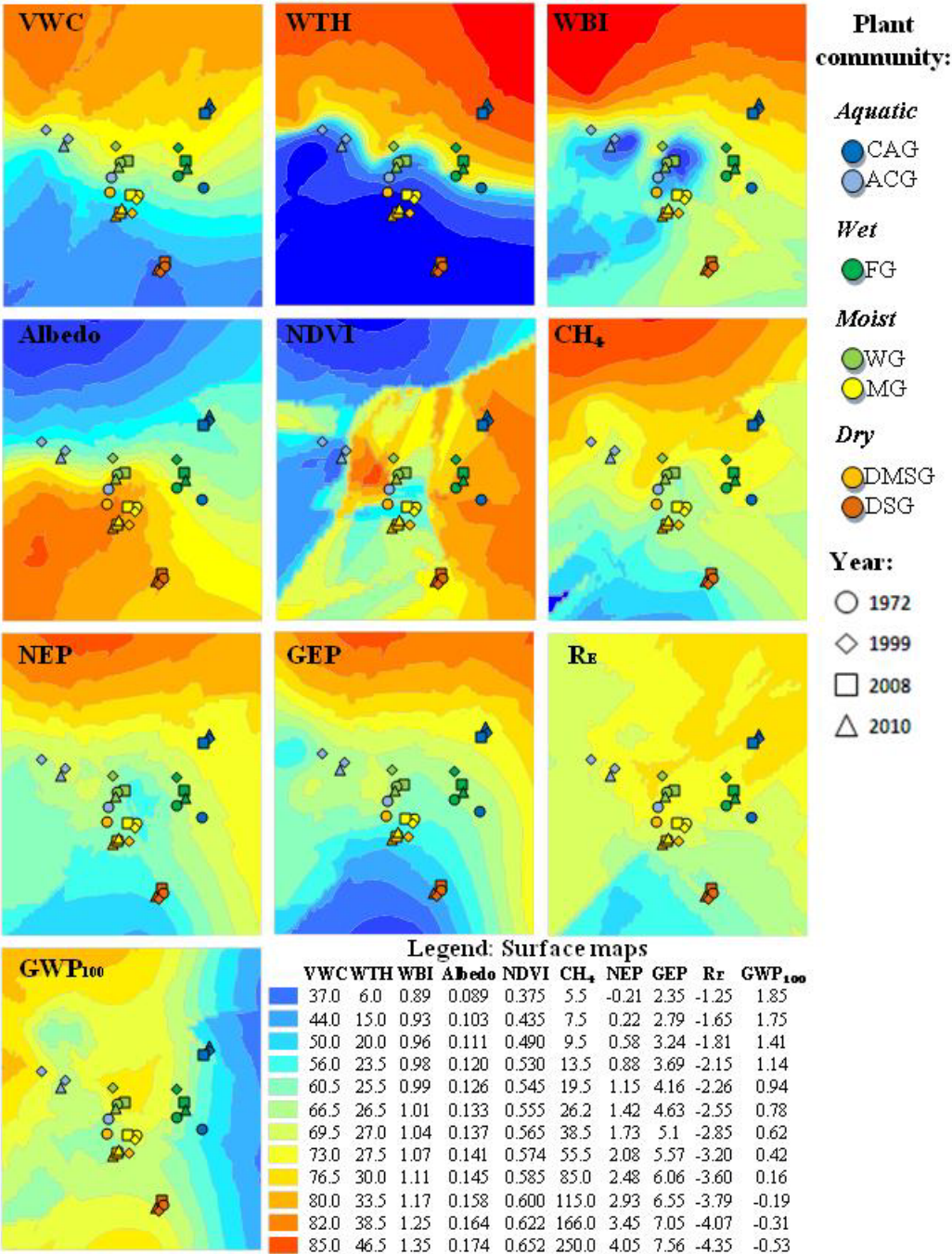


Figure 11: Surface maps of functional attributes (VWC, WTH, WBI, Albedo, NDVI, CH₄, NEE, GEE, R_E, and GWP₁₀₀.) overlaid by mean plot NMS axis scores for each plant community. Surface maps were created by kriging values for attributes derived for functional plots within NMS ordination space.

The ranges of functional attributes modeled in this study are generally within range of that documented by other studies in the area (Webber 1978, Oberbauer et al. 2007, Olivas et al. 2010). The most dramatic changes were observed in wet and especially the aquatic plant community types (Villarreal et al. 2012). These changes are likely to have important implications for ecosystem function as these land cover types comprise approximately 24% of the tundra landscape near Barrow (Tweedie et al. submitted) and, relative to dry and some moist land cover types, are important for surface hydrology and energy balance (Liljedahl et al. 2011), soil thermal properties (Shiklomanov et al. 2010), and trace gas flux – especially methane efflux (Mastepanov et al. 2008, Zona et al. 2009, von Fischer et al. 2010). Based on the relationship between plant community composition and ecosystem function, our study suggests that the soils of these communities have generally become wetter, the water table has increased, albedo and NDVI have decreased, and CH₄ flux and NEE driven mostly by GEE have increased. Overall, however, there appears to have been little change in GWP, except for ACG, which has declined. For most functional attributes modeled for moist and dry plant community types, there has been either little or slight change in an opposite direction to that modeled for the wet and aquatic communities, suggesting the plant communities sampled have become functionally dissimilar over time.

Increases in biomass for communities CAG and MG are similar to trends reported elsewhere in the Arctic over decade-time scales (Hudson and Henry 2009, Hill and Henry 2011), in experimental manipulations such as warming experiments (Hollister and Flaherty 2010), as well as to those projected from ecosystem models (Epstein et al. 2000, Euskirchen et al. 2009). Although these trends match decadal time scale satellite-derived increases in NDVI documented for the region (Bhatt et al. 2010, Jia et al. 2003), they do not always match the trends in NDVI estimated specifically for Barrow. While we cannot adequately explain this trend for some communities, the decrease in NDVI modeled for aquatic plant communities makes sense considering the modeled increase in WTH, which can result in the absorption of light in the infra-red (Goswami et al. 2011), thereby causing a reduction in NDVI. The latter example highlights the challenge of acquiring sensible NDVI measurements for tundra landscapes where WTH fluctuates above and below the ground surface, thereby leading to a potential misinterpretation of a shift in NDVI when the primary change may not be vegetation, but WTH.

Table 9: Change in functional attributes for each plant community and sampling period derived from Tukey's HSD tests. Arrows indicate a significant increase/decrease ($P \leq 0.05$). "Total", refers to the count of all significant changes for a given time interval/ plant community.

Attribute	Time	<i>Aqua</i> CAG	<i>Aqua-wet</i> ACG	<i>Wet</i> FG	<i>Wet-mst</i> WG	<i>Mst</i> MG	<i>Mst-dry</i> DMSG	<i>Dry</i> DSG	Total
NEE	2008-2010	-	↓	-	↓	-	-	-	2
	1999-2008	-	-	-	↑	-	-	-	1
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↑	-	-	-	-	-	-	1
	1972-2008	↑	↑	↑	↑	-	-	-	4
	1972-2010	↑	-	-	-	-	-	-	1
GEE	2008-2010	-	-	-	-	-	-	-	0
	1999-2008	-	-	-	-	-	-	-	0
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↑	-	-	-	-	↓	-	2
	1972-2008	↑	-	↑	-	-	-	-	2
	1972-2010	↑	↓	-	-	-	↓	-	3
CH ₄	2008-2010	-	↓	-	↓	-	-	-	2
	1999-2008	-	↑	-	↑	-	-	-	2
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↑	↑	-	-	-	-	-	2
	1972-2008	↑	↑	-	↑	-	-	-	3
	1972-2010	↑	↑	-	-	-	-	-	2
R _E	2008-2010	-	-	-	-	↓	-	-	1
	1999-2008	-	-	-	-	-	-	-	0
	1999-2010	-	-	-	-	↓	-	-	1
	1972-1999	-	-	-	-	-	↓	-	1
	1972-2008	↑	↓	-	↓	-	↓	-	4
	1972-2010	↑	↓	-	-	↓	↓	-	4
GWP ₁₀₀	2008-2010	-	-	-	-	-	-	-	0
	1999-2008	-	-	-	↑	-	-	-	1
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	-	↓	-	-	-	-	-	1
	1972-2008	-	↓	-	-	-	-	-	1
	1972-2010	-	↓	-	-	-	-	-	1
Albedo	2008-2010	-	↑	-	↑	-	-	-	2
	1999-2008	-	-	-	↓	-	-	-	1
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↓	↓	-	-	-	-	-	2
	1972-2008	-	↓	-	↓	-	-	-	2
	1972-2010	-	↓	-	-	-	-	-	1
WBI	2008-2010	-	↓	-	↓	-	-	-	2
	1999-2008	-	-	-	↑	-	-	-	1
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↑	↑	-	-	-	-	-	2
	1972-2008	↑	↑	-	↑	-	-	-	3
	1972-2010	↑	-	-	-	-	-	-	1
VWC	2008-2010	-	-	-	↓	-	-	-	1
	1999-2008	-	-	-	-	-	-	-	0
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	-	↑	-	-	-	-	-	1
	1972-2008	↑	↑	-	-	-	-	-	2
	1972-2010	↑	↑	-	-	↓	-	-	3
WTH	2008-2010	-	-	-	↓	-	-	-	1
	1999-2008	-	-	-	-	-	-	-	0
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↑	↑	-	-	-	-	-	2

NDVI	1972-2008	↑	↑	↑	-	-	-	-	3
	1972-2010	↑	↑	-	-	-	-	-	2
	2008-2010	-	↑	↑	↑	-	-	-	3
	1999-2008	-	↓	-	↓	-	-	-	2
	1999-2010	-	-	-	-	-	-	-	0
	1972-1999	↓	↓	-	-	-	-	-	2
	1972-2008	↓	↓	-	↓	-	-	-	3
	1972-2010	↓	↓	-	-	-	-	-	2
Total	2008-2010	0	5	1	7	1	0	0	14
	1999-2008	0	2	0	6	0	0	0	8
	1999-2010	0	0	0	0	1	0	0	1
	1972-1999	7	7	0	0	0	2	0	16
	1972-2008	8	9	3	6	0	1	0	27
	1972-2010	8	8	0	0	2	2	0	20
Total		23	31	4	19	4	5	0	86

Attributing change to specific drivers of change is difficult in non-experimental studies where the impacts from a gamut of drivers (e.g. climate and hydrologic change, succession) prevail (Luo et al. 2011). Most of our documented changes match other long-term observations made in the Arctic (Bhatt et al. 2011), as well as those results from both experimental manipulations (Goswami et al. 2011, Hill and Henry 2011) and ecosystem models (Shaver et al. 2007); with the largest changes observed for most functional attributes among 1999, 2008 and 2010. The most obvious explanation for these modeled dynamics is the occurrence of a lemming population outbreak that spanned 2007-2008 (Villarreal et al. 2012). In many instances, there was a greater degree of change over this decadal period than between 1972 and 1999 or 1972 and 2010, highlighting the important role lemmings can play in mediating plant community dynamics and ecosystem function in tundra landscapes (Johnson et al. 2011). Lemmings unequally use habitats depending on seasonal flooding (Batzli 1980), which may explain the different magnitudes of potential impact between plant community types between 2008 and other sampling years.

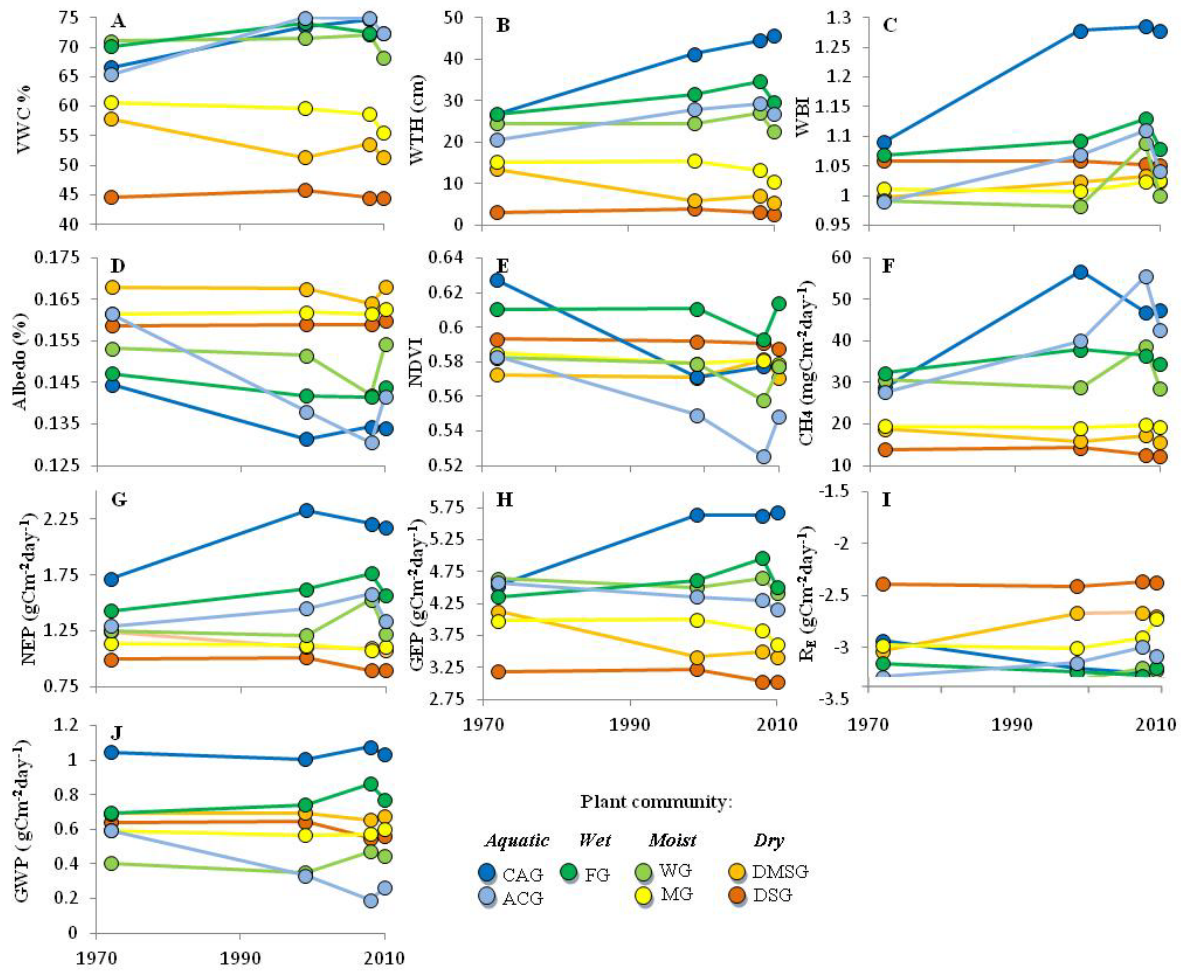


Figure 12: Mean values of each functional attribute, sampling year, and plant community. A= VWC %, B= WTH cm, C= WBI index, D= Albedo %, E= NDVI index, F= CH₄ mgCm⁻²day⁻¹, G= NEE gCm⁻²day⁻¹, H= GEP gCm⁻²day⁻¹, I= R_E gCm⁻²day⁻¹, J= GWP₁₀₀ equivalents of gCm⁻²day⁻¹. NEE Positive GWP₁₀₀ values indicate decreased warming potential.

This study demonstrates that i) different plant communities within a tundra landscape have changed at different rates over decadal time scales - aquatic and wet communities changed more than moist and dry communities, ii) drivers of change are uncertain, however long-term environmental changes and herbivore grazing may largely influence plant community structure and ecosystem function, and iii) changes in plant community composition appear to have altered ecosystem function. This paper demonstrates a novel technique for assessing the functional implications of plant community change and the successful implementation of decade-time scale changes in plant community function. We found the most functionally dynamic plant communities, with respect to change within ordination space, between resampling dates to be aquatic and wet plant communities followed by moist and dry communities which appeared to be more stable and less responsive to change over time. Assessment of the broader scale magnitude and functional implications of plant community change and herbivory in the study area requires further analysis that incorporates land cover change and the scaling of ecosystem functional attributes to the landscape level. Recently, Lin et al. (2012), using multi-temporal classification of aerial and satellite imagery, have suggested that a tundra landscape several kilometers from this study site has dried over the past 60 years with the extent of dry and moist tundra increasing and that of wet tundra decreasing over time. This work is considerably relevant to our work as we show functional change in multiple plant communities over time and Lin et al. (2012) determines the spatial and temporal change in plant communities. Coupling these findings may suggest that the Barrow landscape could have become less productive and less responsive to change and disturbance over the past few decades. Future modeling efforts that incorporate land cover change scenarios, short term and potentially cyclical impacts like lemming outbreaks, and ecosystem functional attributes are required to establish scenarios of future ecosystem states that can serve as hypotheses testable with sustained monitoring.

Chapter 4: 50+ years of Lemming Exclusion Alters Ecosystem Function in Alaskan Coastal Plain Tundra

4.1 ABSTRACT

Mammalian herbivores are well-recognized for their potential to alter tundra plant community composition. The impact of sustained herbivory on ecosystem carbon and energy balance over decade-time scales, however, is poorly understood - mostly because there are so few locations where herbivore exclosures have been maintained over decade-time scales. To determine how long-term lemming exclusion has altered ecosystem function, we measured a range of ecosystem functional properties in replicate 2 x 2 m intact herbivore exclosures and adjacent control plots established in dry, moist and wet land cover types near Barrow, Alaska in 1959. Data were collected at peak growing season in 2010 in conjunction with a companion study that tested for shifts in vegetation composition in the same control and exclosure plots. Herbivore effects varied between land cover types and the strongest differences between exclosure and control plots were found in wet graminoid tundra. Lemming exclusion in wet tundra increased albedo (+10%), but decreased thaw depth (-37%), saturated soil layer (-28%), normalized difference vegetation index (-20%), methane flux ($-23 \text{ mgC m}^{-2} \text{ day}^{-1}$), and increased loss of CO_2 to the atmosphere through net ecosystem exchange ($+1.75 \text{ gC m}^{-2} \text{ day}^{-1}$). Sustained lemming exclusion appears to alter the peak growing season global warming potential (GWP_{100} : integrated over a 100 year time horizon) of wet graminoid tundra from a neutral/slight sink (control) to a net source of carbon to the atmosphere ($+1.15 \text{ gCeq m}^{-2} \text{ day}^{-1}$). Further, lemming exclusion decreased saturated soil layer (-47%) for moist land cover types, and decreased thaw depth (-20%) for dry land cover types, while no other significant effects were found for these land cover types. Measurements of ecosystem function for grazed (control) and ungrazed (exclosure) states were extrapolated over the Barrow Peninsula (421 km^2) using a high spatial resolution land cover map, substantial differences in landscape processes are hypothesized in the sustained absence of herbivores, particularly for the wet tundra landscapes associated with drained thaw lake basins. Across the Barrow Peninsula, we found strong differences between hypothetical ungrazed and grazed states, specifically for albedo ($+3766 \text{ kiloWatts day}^{-1}$), NEE ($+315 \text{ tonnesC day}^{-1}$), CH_4 ($-3.8 \text{ tonnesC day}^{-1}$), and GWP_{100} ($+227 \text{ tonnesC day}^{-1}$). In an ungrazed state, the tundra landscape near Barrow shifted from a substantial sink to a small source. Thus,

a shift in lemming herbivory has the capacity to dramatically alter ecosystem function at plot to landscape scales and should be regarded as a more important component of the changing Arctic System than what has been the case in the past.

4.2 INTRODUCTION

High latitude ecosystems are estimated to contain approximately 1670 Pg of soil carbon, most of which is stored in permafrost soils (Tarnocai et al. 2009) and is twice that currently stored in the atmosphere. Although the potential for climate change to impact arctic soil carbon is well recognized (Schuur et al. 2009, McGuire et al. 2012), the capacity for climate change to alter herbivory is less understood (Wookey et al. 2009). Several studies have shown the potential for herbivores to impact tundra ecosystems (Post and Pedersen 2008, Wookey et al. 2009, Madsen et al. 2011), and have been found to be more influential with respect to long-term vegetation cover and abundance variability in northern Alaska than climate or successional related changes (Villarreal et al. 2012). To understand how recent climate related changes in high Arctic regions impact the future state of the large terrestrial soil carbon store, where higher trophic levels prevail, interactions between ecosystem structure, function, and herbivory must be considered.

Herbivores have been shown to indirectly and directly affect tundra ecosystem function by altering carbon and energy balance. Herbivores can influence nutrient cycling (Olofsson et al. 2004, Van der Wal and Brooker 2004), soil moisture and soil temperature (Zimov et al. 1995b, Van der Wal and Brooker 2004, Gornall et al. 2007), which may all alter decomposition rates affecting soil carbon storage (Mack et al. 2004, Welker et al. 2004). Several studies indicate herbivory can alter above ground biomass and net primary production over small to large spatial scales (Welker et al. 2004, McIntire and Hik 2005) and suppress plant productivity (Sjogersten et al. 2011) associated with short term defoliation events. To date, much of our knowledge of the functional impacts of herbivory has been generated from studies conducted over short time scales (≤ 20 years), and focused on various avian and ungulate plant herbivore interactions (Sjogersten et al. 2008, Post and Pedersen 2008). Relatively little is known regarding the decade-time scale functional impacts, in the absence of sustained herbivore pressure from arvicoline rodents, a dominant herbivore in many arctic landscapes (Batzli 1980, Ims et al. 2011).

However, recent evidence finds landscape NDVI to vary in response to arvicoline rodent activity (Olofsson et al. 2012), suggesting the herbivore effects of voles and lemmings can alter ecosystem function over large spatial scales, but ground based experimental observations are needed to further validate these claims and understand the ecological properties and processes that explain these observations in multiple tundra ecosystems and land cover types (LCTs).

Two species of lemming occur in northern-most Alaska, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*) (Batzli et al. 1980). Notably, the more abundant brown lemming is capable of large cyclic population outbreaks, increasing in density 150-250 % during population high years every three to five years (Batzli et al. 1980). Outbreaks typically result in the decimation of vegetation where as much as 90% of biomass is reduced in some areas (Schultz 1964). The reduction in plant cover and available food biomass to lemmings results in starvation and the lemming population crashes (Batzli 1975). Thus it has been hypothesized that the thinning of plant canopies during high lemming years enables more solar radiation to be absorbed in tundra soils, thereby raising soil temperature and increasing thaw depth (Batzli and Pitelka 1975).

In this study, we examine how 50+ years of lemming exclusion in coastal tundra near Barrow, Alaska has affected peak growing season ecosystem function. This study was implemented in conjunction with a companion study that examined how lemming exclusion affects plant community composition (see Johnson et al. 2011). The study used 12 pairs of lemming exclosure and control plots established in 1959 (Shultz et al. 1969) that remain intact and have effectively excluded lemmings for the past 50+ years. Johnson et al. (2011) found graminoid cover and biomass decreased in wet, moist, and dry tundra LCTs in response to lemming exclusion, while bryophyte cover and biomass increased. Specifically, we address two questions: 1) How has 50+years of lemming exclusion altered plot level peak-season thaw depth (TD), saturated soil layer (SSL), NDVI, surface albedo, carbon dioxide (CO₂) exchange, methane (CH₄) flux, and global warming potential (GWP) in wet, moist and dry LCTs?, and 2) when plot-level results are extrapolated to landscape scales, what is the potential for lemmings to influence ecosystem carbon dynamics and surface reflectivity at the landscape level? This project is a contribution to the International Polar Year-Back to the Future project (Callaghan et al. 2011), which

aimed to determine the impacts of Arctic plant community change on ecosystem structure and function over decadal time scales by revisiting and resampling historic research sites more than 25 years in age.

4.3 METHODS

4.3.1 Site Description

This study was conducted within 5 km of Barrow, Alaska at the northern limit of the Alaskan Arctic Coastal Plain. Mean annual temperature, precipitation, and snowfall are -12 °C, 11 cm, and 69 cm, respectively (NCDC 2005). Air temperature during the 2010 peak season sampling period was within the range of variability recorded during the previous decade. The landscape has a low relief best characterized as poorly drained polygonized tundra (Brown et.al 1980, Liljedahl et al. 2011). Recent plot-level (Villarreal et al. 2012) and remote sensing studies (Tweedie et al. submitted) classify the Barrow landscape into nine distinct plant communities. Plots sampled in this study closely correspond to classes described by Tweedie et al. (submitted) as “seasonally flooded” and “wet graminoid tundra” (wet),” moist” and “dry-moist graminoid tundra” (moist), and “dry-moist” and “dry dwarf shrub graminoid tundra” (dry). Our study sites were situated within close proximity to the International Tundra Experiment (Hollister et al. 2005) and the International Biological Program research sites (Brown et al. 1980).

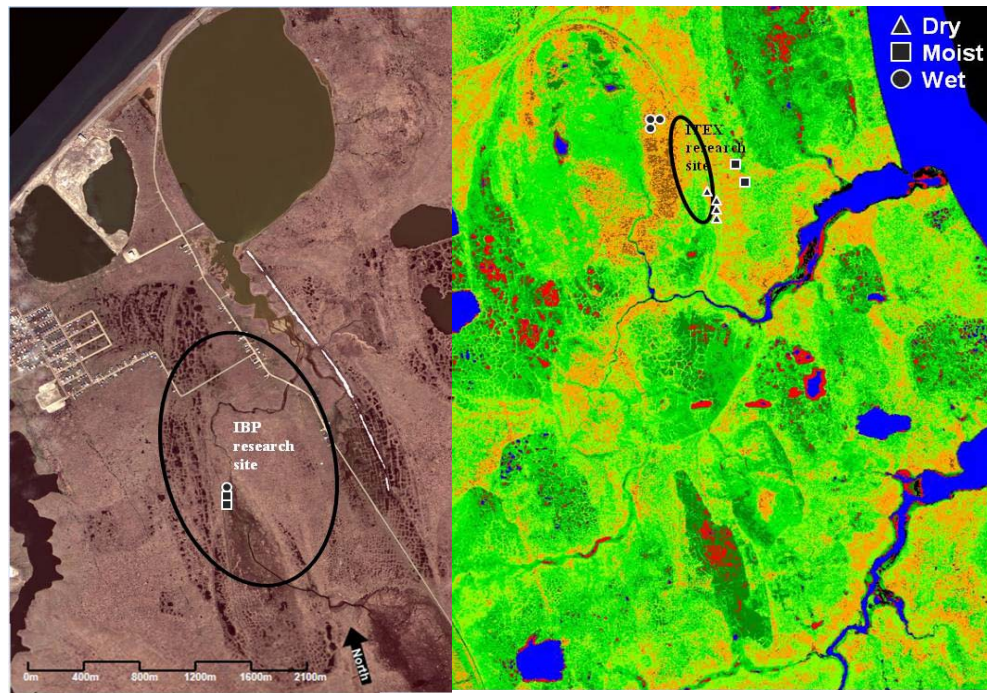


Figure 13: Barrow field sites were located within the International Tundra Experiment (ITEX) dry and wet sites, and near the western extent of the International Biological Program (IBP) historical site. Dry, moist, and wet LCTs are represented as triangles, squares, and circles. Left map is a quickbird image from 2008 and the right is the vegetation map developed by Tweedie et al. (submitted) representing the following LCTs: aquatic (red), wet (dark green), moist (light green), dry (yellow), and open water (blue).

To assess the impact of lemmings on this tundra ecosystem, herbivore exclosures were established during the late 1950s in various plant communities along with paired control plots (Shultz et al. 1969). Twelve of the original 70 pairs of 2 x 2 m exclosures and control plots (N=12, 4 dry, 4 moist, 4 wet) remain intact and have effectively excluded lemmings for the past 50+ years (Johnson et al. 2011). We assigned pairs of plots to wet, moist and dry land cover types following Tweedie et al. (submitted). Using a similar approach to other studies estimating short-term land-atmosphere plot-level trace gas flux (Shaver et al. 2007, Lund et al. 2009, Lara et al. 2012), 30 x 30 cm aluminum chamber bases were inserted 5 cm into the soil of both exclosure and control plots and left for a minimum of 12 hours to equilibrate prior to sampling. To avoid biased chamber base placement within each exclosure/control pair, a random number was used to indicate the corner of a 1 m² area in the center of the plot where chambers were placed.

4.3.2 Field Sampling

Sampling was conducted two years after the previous lemming population high in 2007-2008 (Villarreal et al. 2012) and was restricted to dates between July 25th-August 10th (i.e. “peak” growing season) and close to solar noon (11am-3pm) to maintain similar ambient temperature (i.e. 9.6 °C, unpublished data) and climatic conditions. Within each exclosure and control plot, we measured depth of thaw (TD) using Circumpolar Active Layer Monitoring program (Brown 2000) protocols. Saturated soil layer (SSL) was measured close to but outside of the sampling area bordered by the chamber bases by drilling a hole into the soil to permafrost and inserting a 4 cm diameter porous PVC tube. We allowed the water table to equilibrate for a minimum of 12 hours, and used a ruler to determine the height of the water table relative to the soil surface and depth to permafrost (i.e. depth of inundated soil). Hyperspectral reflectance was measured with a portable PP Systems Dual detector narrowband spectrometer (Unispec DC, 350-1150 nm). Hyperspectral data were used to calculate a normalized difference vegetation index ($NDVI = (R_{IR} - R_{VIS}) / (R_{NIR} + R_{VIS})$; (Penuelas et al. 1993, Gamon et al. 2006). Surface albedo (short-wave surface reflectance) was measured using a net radiometer (CNR 2 Kipp and Zonen, Inc.) by isolating incoming and outgoing short-wave radiation (310-2800 nm) and calculating the percentage of reflected radiation. Land-atmosphere CO₂ fluxes were estimated using a LI-COR 6200 Photosynthesis System (LI-COR Inc., Lincoln, NB, USA) and four different thicknesses of shade cloth that were used to generate ecosystem light response curves (Shaver et al. 2007, Lasslop et al. 2010). Calculation of net ecosystem CO₂ exchange (NEE), ecosystem respiration (R_E), and gross ecosystem exchange (GEE) were made following (Oberbauer et al. 2007). Methane (CH₄) flux was measured using a photo-acoustic multi-gas analyzer (INNOVA 1312 AirTech Instruments A/S, Denmark; *sensu* (Lund et al. 2009, Sachs et al. 2010) and processed following methods described by Lund et al. (2009). To evaluate the combined GWP of daily ecosystem CO₂ and CH₄ flux, we converted CH₄ fluxes to CO₂ equivalents using a 100 year atmospheric residence time ($GWP_{100} = 23$ for CH₄, IPCC, 2001). Climate data were collected continuously for the duration of the study using a portable automatic weather station (Hobo AWS, Onset Computer, Bourne, Massachusetts, USA) setup near the field site. The AWS measured air temperature (2 m), relative humidity (2 m), barometric pressure (1 m), photosynthetically active radiation (3 m), and solar radiation (3 m) at one minute intervals.

4.3.3 Statistical Analysis

To determine if lemming exclusion altered ecosystem function, we used two-factor ANOVAs to test for differences between treatment (exclosure or controls: EX/CT) and LCT (dry, moist and wet) as main effects for each functional attribute measured. Differences between groups were analyzed using post-hoc, Tukey's honestly significant difference (HSD) tests. All data were checked for quality and transformed (GEE-natural log) prior to analysis where necessary to meet the assumptions of normality. All statistics were performed using JMP (version 10, Cary, NC).

Mean LCT-specific estimates for Albedo, NEE, CH₄, and GWP were used in combination with a high spatial resolution land cover map (Tweedie et al. submitted) to spatially extrapolate mean plot level measurements to the scale of the Barrow Peninsula (421 km²) and explore hypothetically how lemming presence and absence might affect ecosystem function at landscape to regional scales. Wet, moist and dry tundra constitute 22, 41, and 14% of the total land cover on the Barrow Peninsula, respectively. Aquatic tundra and open water cover 3 and 20% of the area and was not considered in this analysis.

4.4 RESULTS

The long-term exclusion of lemmings significantly reduced TD (Table 1) but the magnitude of this main effect varied among LCTs (Table 1, Figure 1). In both wet and dry LCTs, TD was greater in control plots than exclosures, but there was no difference between exclosure and control plots in the moist LCT. Differences in TD contributed to differences in SSL between exclosure and control plots, and the magnitude of this treatment effect also varied considerably among LCTs (Table 10; Figure 14). Not surprisingly, SSL increased with increasing soil moisture among LCTs (Figure 14). Lemming exclusion resulted in a reduced SSL in both wet and moist LCTs (Table 10; Figure 14); while no difference in SSL was found in dry LCTs. Soil temperature at 1 cm varied between LCTs (Table 10) but there was no difference between exclosure and control plots within a LCT.

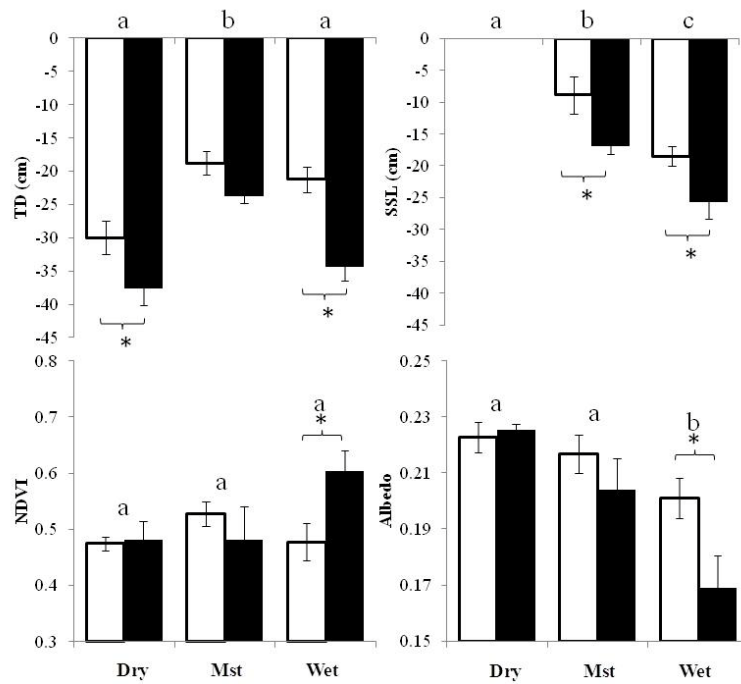


Figure 14: Mean (± 1 S.E.) of peak season thaw depth (TD), saturated soil layer (SSL), Normalized Difference Vegetation Index (NDVI), and Albedo for lemming exclosure (white) and control plots (black) in three land cover types (dry, moist, and wet tundra) near Barrow Alaska. Asterisks signify significant difference (tukey's HSD) at $P \leq 0.05$ between exclosures and control plots. Letters indicate differences among LCTs.

Table 10: F-statistics from a two-factor ANOVA of ten functional attributes using land-cover types (LCT; $df=2$), control/exclosure plots (EX/CT; $df=1$), and an interaction (EX/CT*LCT; $df=2$) as main effects. Significant differences are bolded ($\alpha < 0.1^\dagger$, $\alpha < 0.05^*$, and $\alpha < 0.01^{**}$).

VARIABLE	EX/CT	LCT	EX/CT*LCT
TD	28.22**	18.60**	2.70[†]
SSL	30.72**	109.58**	10.69**
NDVI	2.37	2.98[†]	4.93**
Albedo	4.55*	12.32**	2.36
Soil Temp. (1cm)	0.14	18.22**	0.82
GEE	2.89[†]	1.97	3.14[†]
R _E	0.02	4.85*	0.76
NEE	7.32**	2.21	3.42*
CH ₄ flux	3.71[†]	5.43**	2.97[†]
GWP ₁₀₀	3.24[†]	6.01**	1.10

Main effects for ANOVAs (Table 10) determined NDVI did not vary with lemming exclusion but did among LCT. However, post hoc tests found NDVI to be greater in wet tundra control plots than exclosure plots (Figure 14), suggesting there was more live plant biomass in wet control plots relative to

exclosures. No differences in NDVI were found in both dry and moist LCTs between exclosure and control plots. Albedo varied for both control-exclosure plot differences and LCT (Table 10, Figure 14). Exclosures in wet tundra had a significantly higher albedo than control plots and was the only LCT where a significant difference was recorded. We found GEE to vary in response to lemming exclusion, but did not find GEE to vary among LCTs (Table 10, Figure 15). Exclosures in wet tundra were found to have a lower GEE ($-1.93 \text{ g Cm}^{-2}\text{day}^{-1}$) than control plots ($-4.62 \text{ g Cm}^{-2}\text{day}^{-1}$; Figure 15), while no significant differences were found in moist and dry LCTs (Table 10, Figure 15). Although, marginally significant ($p = 0.06$), an interaction between lemming exclusion and LCT for GEE suggests herbivory may have varying degrees of impact among LCTs. Ecosystem respiration (R_E) varied with LCT (Table 10) and generally increased with soil moisture (Figure 15), but no differences between exclusion/control plots were uncovered for any LCT. Additionally, NEE varied significantly with lemming exclusion but not among LCTs (Table 10, Figure 15). Interestingly, the NEE of wet tundra was $+1.75 \text{ g Cm}^{-2} \text{ day}^{-1}$ greater in exclosures than control plots, suggesting sustained herbivore exclusion changes the ecological function of this land cover type from being a peak growing season carbon sink to a net source to the atmosphere. There was no difference found for moist and dry NEE in response to lemming exclusion (Figure 15). Methane (CH_4) flux varied for both exclosures and among LCTs (Table 10; Figure 15). As expected, wet tundra plots had the highest rates of emission, but control plots had higher CH_4 effluxes than exclosures (Figure 15). Global warming potential (GWP) varied for both exclosures and among LCTs (Table 10, Figure 16). Similar to trends documented for CO_2 and CH_4 fluxes, we found wet tundra exclusion plots to have a higher GWP than controls, suggesting sustained herbivore exclusion could shift wet tundra from being relatively GWP-neutral to enhancing GWP (Figure 16). Moist and dry LCTs did not vary significantly with respect to differences in GWP between exclosure and control plots (Figure 16).

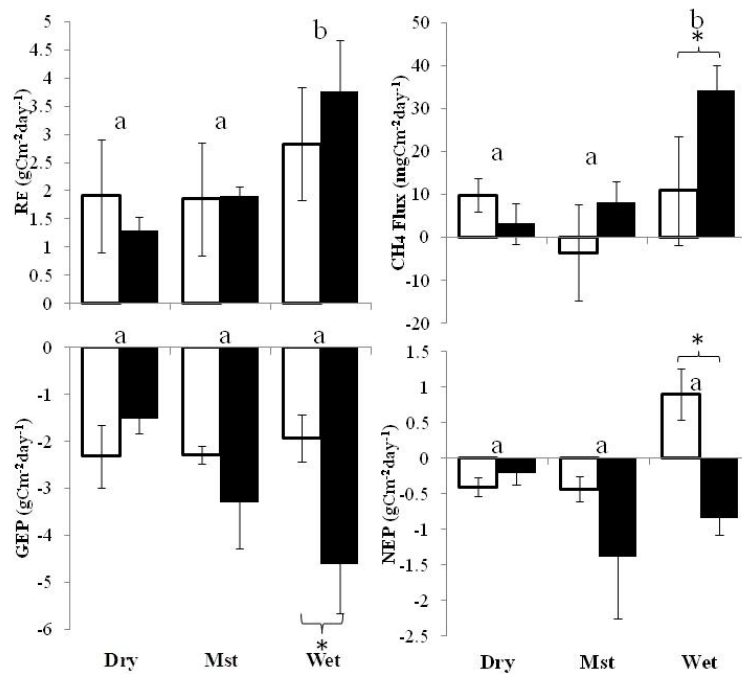


Figure 15: Means (± 1 S.E.) of peak season Gross Ecosystem Photosynthesis (GEE), Ecosystem Respiration (R_E), Net Ecosystem Exchange (NEE), and Methane flux (CH_4) for lemming exclosures (white) and control plots (black) among three land cover types in the coastal tundra near Barrow Alaska. Asterisk signifies significant difference (Tukey's HSD) at $p \leq 0.05$ between exclosures and control plots. Letters indicate differences among LCTs.

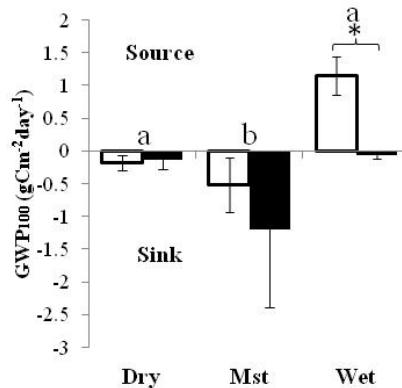


Figure 16: Mean (± 1 S.E.) of peak season tundra land cover type for exclosure (white bar) and control plots (black bar) for Global Warming Potential (GWP_{100}) integrated over a 100 year time horizon. Positive values indicate a positive warming potential while negative values a negative warming potential. Asterisk signifies significant difference (tukey's HSD) at $p \leq 0.05$ between exclosures and control plots. Letters indicate differences among LCTs.

Extrapolation of Albedo, NEE, CH_4 , and GWP to the Barrow Peninsula (Table 11), highlights the hypothetical and sustained impact of lemmings on ecosystem function at peak growing season. Spatial extrapolation of surface albedo (short-wave reflectance; Figure 18) reveals that if lemmings were

absent from the Barrow landscape, albedo would be higher, potentially increasing the solar energy reflected back to space by approximately $8.96 \text{ KWkm}^{-2} \text{ day}^{-1}$, an increase of 10 and 3%, for wet and all LCTs combined respectively. Additionally, the absence of lemmings on the tundra landscape would increase NEE by approximately $+0.748 \text{ tonnesC km}^{-2} \text{ day}^{-1}$ (96 %), lowering the sink strength to $-0.04 \text{ tonnesC km}^{-2} \text{ day}^{-1}$ or $-14.97 \text{ tonnesC } 420.6\text{km}^{-2} \text{ day}^{-1}$. Further, CH_4 fluxes would likely be lower if lemmings were absent ($+0.009 \text{ tonnesC km}^{-2} \text{ day}^{-1}$ or $+3.82 \text{ tonnesC } 420.6\text{km}^{-2} \text{ day}^{-1}$) (Table 11). Lastly, spatial extrapolation of GWP to the Barrow Peninsula (Table 11, Figure 18) shows: (1) that during peak growing season in 2010 with lemmings present, the landscape likely had a negative GWP ($-0.52 \text{ tonnesC km}^{-2} \text{ day}^{-1}$ or $-219 \text{ tonnesC } 420.6\text{km}^{-2} \text{ day}^{-1}$), but (2) the long-term absence of lemmings could shift GWP to being more positive ($+0.019 \text{ tonnesC km}^{-2} \text{ day}^{-1}$ or $+7.95 \text{ tonnesC } 420.6\text{km}^{-2} \text{ day}^{-1}$).

4.5 DISCUSSION

Sustained lemming exclusion over 50+ years differentially impacted peak growing season ecosystem function of different LCTs commonly found in northern Alaskan Coastal Plain. Ecosystem responses to lemming exclusion were most dramatic for wet LCTs (Figure 5), where graminoid cover and biomass was reduced as litter and moss cover and biomass increased (Johnson et al. 2011). In wet LCTs, peak growing season surface albedo increased and NDVI decreased, suggesting that sustained lemming herbivory can alter landscape surface reflectivity and landscape greenness of wet LCTs in northern Alaskan tundra, which is analogous to recent NDVI patterns found for population outbreaks of voles and lemmings in northern Sweden using satellite platforms (Olofsson et al. 2012). Further, GEE, and CH_4 flux decreased, while NEE increased in response to lemming exclusion, leading to an increase in GWP. These findings are comparable to other long-term grazing exclusion experiments in shrub dominated moorlands in northern England (Ward et al. 2007), suggesting long-term herbivore grazing enhances carbon sink strength in wet LCTs. Additionally, although, lemming exclusion altered the plant community composition of dry (increase lichen cover, decrease graminoid) and moist (increased lichen and litter cover, decrease graminoid) LCTs examined in this study (Johnson et al. 2011), no significant differences in land-atmosphere carbon exchange, albedo, or NDVI were found, highlighting that a change in plant community composition does not always correlate with a change in ecosystem function.

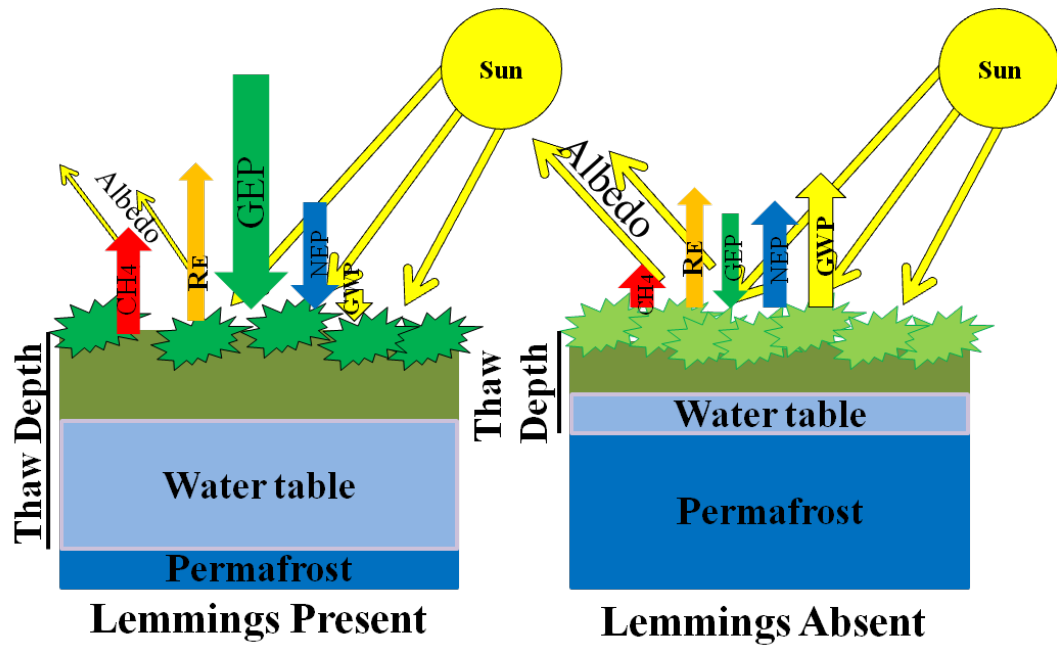


Figure 17: Schematic representation of functional changes observed in response to herbivore exclusion within wet land cover types (LCTs).

In contrast to results documented in this long-term exclusion study, several short-term studies focused on understanding ecosystem responses to herbivory in tundra landscapes (e.g. Welker et al. 2004; van Der Wal et al. 2007; Sjogersten et al. 2008, 2011; Elliott and Henry 2011) report herbivore presence to be related to decreases in carbon uptake through defoliation events, suggesting that the response of tundra to herbivory may be dependent on the duration of experimental observation and/or the timing of observation relative to lemming population outbreaks. Similarly, Villarreal et al. (2012), who documented plant community change from 1972-2010 in the Barrow area, found sampling periods with high lemming populations to have vastly different vegetation cover and abundance, than years with low lemming abundance. This difference was greater than any decadal time scale change attributable to climate or successional related changes. However, although, sustained long-term lemming exclusion altered community composition in all LCTs differently (Johnson et al. 2011), the most dramatic functional differences in response to lemming exclusion were found in wet LCTs, likely as exclusion appeared to transition a graminoid dominated community into one dominated by mosses, similar to that reported by Van der Wal and Brooker (2004) and Zimov (2005). Because the Alaskan Arctic coastal plain tundra is dominated by wet LCTs (CAVM 2003, Tweedie et al. submitted), we hypothesize lemmings to have a vital role in maintaining the structure and function, which is similar to other studies

in the Arctic (Van der Wal et al. 2004, Zimov 2005). With the sustained absence of lemmings hypothesized for wet landscapes near Barrow, land-atmosphere CO₂ exchange was dramatically altered as (1) graminoid dominated communities shifted to that dominated by mosses, decreasing the carbon uptake capacity; and (2) graminoid litter accumulated on the soil surface (e.g. increasing albedo) shading and insulating soils, while reducing GEE with the increased competition for resources (i.e. light, nutrients, and space). Furthermore, the absence of lemmings reduced CH₄ flux in wet LCTs. Similar to CO₂ responses, CH₄ fluxes were likely reduced due to cooler soils in response to lower albedo and potential heat transfer (Conrad, 1989; Kotsyurbenko, 2005), higher insulative moss and litter layers (Joabsson et al. 1999; Dorodnikov et al. 2011), which also enhances surface CH₄ oxidation potential (King et al 1998; Liebner et al. 2011). Additionally, CH₄ efflux could have been lowered due to a reduced volume of anaerobic waterlogged soil (Morrissey and Livingston, 1992; von Fischer et al. 2010), and lower cover graminoid vegetation that are known to be conduits of CH₄ from the soil to the air (Joabsson et al. 1999; Erikson et al. 2010) and allow CH₄ to bypass oxidative processes near the surface of some soils. Cumulatively, when considering the impact of the presence/absence of lemmings on GWP across the Barrow Peninsula, we estimate lemming presence to enhance peak season carbon sink capacity by approximately -219 tonnes of carbon equivalents per day, respectively, while the absence of lemmings promote a small loss to the atmosphere by approximately +8 tonnes of carbon equivalents per day, respectively (Table 11).

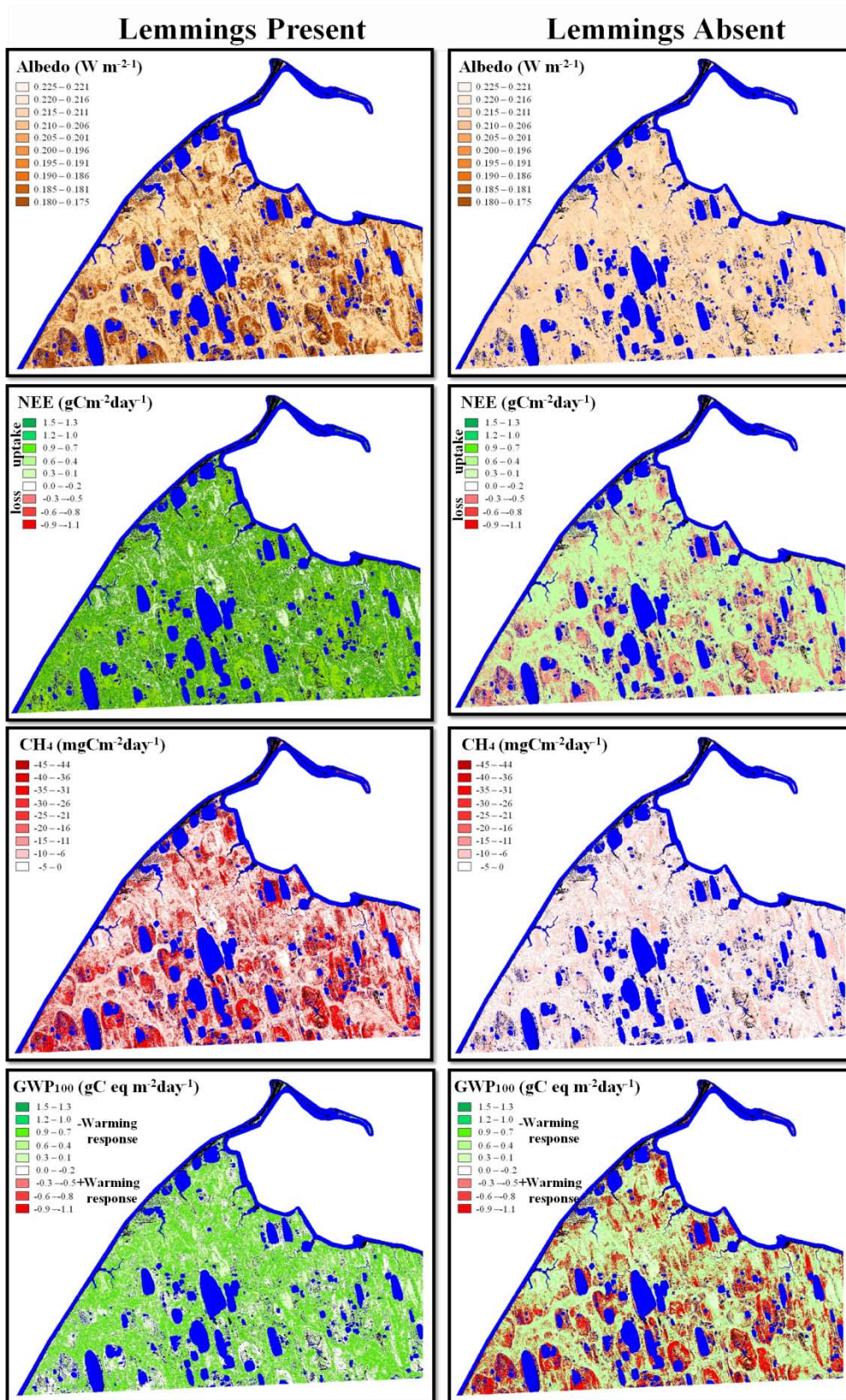


Figure 18: Up-scaled albedo and carbon (NEE, CH₄, and GWP) across the 421km² Barrow Peninsula. Values for albedo are represented by a light to dark orange gradient, where the lighter values portray the most reflective land surfaces. Maps for NEE, CH₄, and GWP are visualized with a green to red gradient, where green and red values indicate sink and source activity, respectively. See Table 11 for estimates.

This study rescued and revisited some of the oldest herbivore exclosures known in the Arctic. However, various logistical and infrastructural challenges limited intra/inter-season sampling, sample size and the inclusion of more LCTs. Accordingly, the findings of this study present a “snapshot” of ecosystem function during a two week period spanning the height of the growing season during 2010. Because of this, several caveats must be considered. Episodic cycles in lemming population densities near Barrow can dramatically affect vegetation composition (Johnson et al. 2011; Villarreal et al. 2012) and function (Lara et al. 2012), the differences in land-atmosphere CO₂ and CH₄ exchange between community transition states (e.g. graminoid and moss-dominated tundra) are greater than variation among low and high lemming population years (Lara et al. 2012). Furthermore, exclosure infrastructure (fences and stakes) have been shown to reduce light levels (i.e. shade) that cool soils (Ritchie et al. 1998), potential altering decomposition and N mineralization rates (Hobbie 1996, Keuper et al. 2012). Therefore, we sampled the inner most 1 x 1 m plot of each 2 x 2 m exclosure (Johnson et al. 2011) to minimize shading effects. In addition, we are uncertain of the potential fertilization affects birds may have had on enclosure plots as owls and jaegers have occasionally been observed resting on fences, and how these affects may impact our scaled results (Table 11) to the Barrow region.

Table 11: Spatial extrapolation of Albedo (kiloWatts day⁻¹) and Carbon (NEE, CH₄, GWP, tonnes C day⁻¹) fluxes across the Barrow Peninsula (420.6 km², respectively) using Land Cover Types (LCTs) dry, moist, and wet for lemming presence (Present) and lemming absence (Absent). We estimated functional metrics to 1 km² area, by determining the relative proportion of all LCTs across the region and used plot level m² values for extrapolation. Positive carbon flux values indicate loss from the ecosystem and negative values indicate uptake to the ecosystem.

Scale	Treatment	Metric	Dry	Moist	Wet	All
Barrow Peninsula (~420.6 km ²)	Present	Albedo	13561.2	34995.8	16979.9	65536.8
	Absent	Albedo	13393.9	37164.8	18744.0	69302.6
	Abs(%) change	Albedo	167.3(1)	2169.2(6)	1764.1(10)	3765.9(6)
	Present	NEE	-12.93	-237.48	-79.24	-329.64
	Absent	NEE	-24.34	-74.49	+83.87	-14.97
	Abs(%) change	NEE	11.4(88)	163.0(67)	163.1(206)	314.7(96)
	Present	CH₄ flux	+0.20	+1.41	+3.20	+4.82
	Absent	CH₄ flux	+0.59	+0.61	+1.02	+0.99
	Abs(%) change	CH₄ flux	0.39(195)	2.02(143)	2.19(68)	3.82(79)
	Present	GWP	-8.40	-204.94	-5.53	-218.87
	Absent	GWP	-10.79	-88.52	+107.26	+7.95
	Abs(%) change	GWP	2.4(28)	116.4(57)	112.8(2040)	226.8(104)
Barrow Peninsula (1 km ²)	Present	Albedo	32.25	83.23	40.38	155.87
	Absent	Albedo	31.86	88.39	44.58	164.83
	Abs(%) change	Albedo	0.40(1)	5.16(6)	4.20(10)	8.96(6)
	Present	NEE	-0.031	-0.565	-0.188	-0.784
	Absent	NEE	-0.058	-0.177	+0.199	-0.036
	Abs(%) change	NEE	0.027(88)	0.388(67)	0.388(206)	0.748(96)
	Present	CH₄ flux	+0.000	+0.003	+0.008	+0.011
	Absent	CH₄ flux	+0.001	+0.001	+0.002	+0.002
	Abs(%) change	CH₄ flux	0.001(196)	0.005(143)	0.005(68)	0.009(79)
	Present	GWP	-0.020	-0.487	-0.013	-0.521
	Absent	GWP	-0.026	-0.211	+0.255	+0.019
	Abs,% change	GWP	0.006(28)	0.277(57)	0.268(2040)	0.539(104)

In the absence of lemmings, the Barrow landscape is likely to look and function quite differently, particularly wet LCTs. Though, Bubier and Moore (1994) identified general limitations involved with scaling plot level results across landscapes, we undertook this spatial analysis largely as an intellectual and hypothesis generating exercise to demonstrate the potential importance of sustained lemming presence/absence on functional processes in Alaskan Arctic tundra ecosystems. Interestingly, when comparing the relative effects of lemming exclusion to other treatments (e.g. warming, hydrology, long term community change) on CO₂ flux in wet tundra during peak growing season within the Barrow area, we found exclusion to increase NEE by 200% respectively, and shifted species composition from a

graminoid to a moss dominated ecosystem. While, Oberbauer et al. 2007 finds passive warming treatments to decrease NEE by 30% respectively, Olivas et al. (2011) reports no difference in NEE in fine-scale polygon topography, however, interannual variation decreased NEE by 50% respectively. Lara et al. (2012) estimated wet communities to decrease NEE by 20% respectively, over a 38 year time span GEE increased through time. These results suggest, (1) lemming herbivory may among the most important factors to consider when describing long-term structural (Johnson et al. 2011, Villarreal et al. 2012) and functional change near Barrow, and (2) the presence of lemmings in this Arctic region, appears to assist in maintaining the historically strong carbon sink capacity during peak growing season of the tundra ecosystem.

This study highlights the important role lemmings have controlling ecosystem function in northern Alaskan Arctic Coastal Plain tundra, especially in wet LCTs where peak growing season NDVI and carbon uptake potential was reduced, and global warming potential and albedo increased in exclosures that have sustained lemming exclusion for more than 50 years. Our findings contrast with findings derived from short term herbivory studies, suggesting that it takes decades for tundra ecosystem structural and functional properties and processes to adjust to altered herbivory thereby reinforcing the need for long-term and sustained experimental manipulations and observations of these experiments to further understand how tundra ecosystems may respond to a range of interacting global change drivers.

Chapter 5: Response of ecosystem CO₂ and CH₄ flux to nutrient increase in *Arctophila fulva* aquatic tundra

5.1 ABSTRACT

High latitude tundra ecosystems are undergoing dramatic climate change and the impacts of change on biogeochemical cycling remain a key research focus. Near Barrow, Alaska, thaw depth, nutrient availability, and plant productivity have increased in tundra ponds, where the extent of aquatic tundra dominated by *Arctophila fulva*, a common arctic aquatic macrophyte, has also expanded over the past 40-50 years. This study examines the response of land-atmosphere ecosystem carbon dioxide (CO₂) and methane (CH₄) flux from *A. fulva* dominated tundra under elevated nitrogen and phosphorus levels. We extracted monoliths of aquatic tundra dominated by *A. fulva* from pond margins near Barrow. Monoliths were placed in a growth cabinet that controlled ambient conditions (light, air temperature, water table height) at 3 nutrient treatment levels (control: 0.0 mgN L⁻¹, 0.0 mgP L⁻¹, low: 1.5 mgN L⁻¹, 0.6 mgP L⁻¹, and high: 7.5 mgN L⁻¹, 3.0 mgP L⁻¹) and measured CO₂ and CH₄ flux continuously. The experiment lasted approximately nine weeks. In response to the high nutrient treatment, *A. fulva* biomass and steady state CH₄ emission (SE) increased but light use efficiency and gross ecosystem exchange (GEE) declined. There were no differences in CO₂ and CH₄ flux between control and low nutrient treatments. No differences in gas ebullition (GE) among nutrient treatments were found but a negative relationship between GE and biomass was documented ($R^2 = 0.34$, $p < 0.001$). Further, using CH₄ fluxes strictly during the pre-treatment period, we estimated that GE represented approximately 30-40% of the total CH₄ flux. Collectively, short-term experimental results suggest *A. fulva* biomass, CO₂ and CH₄ fluxes in aquatic habitats have likely been altered by increased nutrient availability, which supports long-term field based observations.

5.2 INTRODUCTION

Northern ecosystems have accumulated vast amounts of soil carbon over the last millennia, which cumulatively amount to half (e.g. 1672 Pg) of the world's total soil organic carbon and the majority of this carbon is stored in permafrost soils (Tarnocai et al 2009). Arctic warming has begun to thaw these carbon rich soils and increase decomposition over large geographic regions, and threatens to

release large carbon stores to the atmosphere thereby initiating a strong positive feedback to greenhouse warming (Tarnocai et al. 2009; Kuhry et al. 2010). Aquatic-wet ecosystems can dominate tundra landscapes and have directly/indirectly responded to warming in the Arctic over the past few decades through changes in drainage patterns (Yoshikawa and Hinzman 2003), nutrient availability (Lougheed et al. 2011), plant species composition (Elmendorf et al. 2012), and resulting in altered ecosystem CO₂ (Oberbauer et al. 2007), and CH₄ exchange rates (Dijkstra et al. 2012). Therefore, determining the dynamics of biogeochemical feedbacks to climate warming in response to a multitude of co-dependent interactions is a key research priority.

Generally, tundra plant productivity is considered to be limited by nutrient availability, with low temperature and poor substrate quality often restricting decomposition and the mineralization of nitrogen (N) and phosphorus (P) (Aerts et al. 1992). Changes in nutrient availability that may occur with increased soil temperature and thaw (Natali et al. 2011), therefore, are a major concern for tundra ecosystems and climate. Recent experimental evidence indicates that N, P, and other nutrients are released when permafrost thaws (Reyes and Lougheed, *in prep.*). This release may be biologically relevant (Mack et al. 2010) and partially controlled by an active microbial community in thawing permafrost (Mackelprang et al. 2011, Keuper et al. 2012). Further, anthropogenic pollutants and atmospheric nitrate deposition have steadily increased in Arctic regions (Goto-Azuma and Koerner 2001, Schlesinger 2009) due to human industrial activities (Bennett et al. 2001, Galloway and Cowling 2002). This relaxation of nutrient limitation may facilitate a negative feedback to warming by increasing plant productivity and biomass (Schuur et al. 2007; Hernandez 2012). However, the respiratory losses resulting from the decomposition of old soil carbon could be stronger than carbon uptake (Mack et al. 2004). Thus, there is a need to further understand the response of land-atmosphere trace gas exchange to increased N and P availability in tundra ecosystems.

Previous fertilization studies report varied responses for land-atmosphere CO₂ and CH₄ fluxes in peatland soils. Lund et al. (2009) report an increase in gross ecosystem exchange (GEE) and ecosystem respiration (R_E) in response to N and P fertilization in northern and southern Sweden. Bragazza et al. (2006) found N deposition enhanced decomposition rates and R_E in laboratory incubations.

Alternatively, Keller et al. (2005) reported no major effects on carbon exchange after six years of N and P fertilization at a temperate fen in northeastern Minnesota. Similarly, Bubier et al. (2007) found that high nutrients lowered GEE and hypothesized that this was a result of greater litter accumulation. There is a similar degree of uncertainty associated with how land-atmosphere CH₄ flux responds to increased soil nutrient availability. Saarnio et al. (2000) found that N fertilization marginally enhanced annual CH₄ flux in an oligotrophic mire. However, Nykanen et al. (2002) found no difference in CH₄ production or consumption in response to N fertilization in a *Sphagnum* dominated peatland. They did, however, report increased CH₄ flux with increased sedge cover, which is similar to observations made by Eriksson et al. (2010) in a fertilized boreal peatland. Lamb et al. (2011) found that warming coupled with fertilization increased plant cover and plant height over a 16 year period in a high Arctic heath, but treatments had limited effects on CO₂ and CH₄ fluxes. Similarly, Lund et al. 2009 found no change to CH₄ flux with N and P addition, while Pancotto et al. (2010) found fertilization decreased CH₄ emission in peatland microcosm experiments. Relative to other peatland systems, however, the responses of gas exchange to fertilization has been poorly studied in plant communities associated with aquatic-wet tundra pond margins. This is despite the sensitivity of these plant communities to warming (Silapaswan et al. 2001, Smith et al. 2005, Smol and Douglas 2007, Lin et al. 2012, Villarreal et al. 2012), which appears to be coupled with altered nutrient availability (Lougheed et al. 2011).

Early tundra limnology research conducted near Barrow, Alaska (Hobbie et al. 1980) reported that the primary production of tundra ponds is dominated by two emergent macrophyte species, *Carex aquatilis* and *Arctophila fulva* (Alexander et al. 1980). Recent land cover change (Lin et al. 2012), ground based repeat plant community sampling (Villarreal et al. 2012), and repeat photography (Lougheed et al. 2011; Andresen and Lougheed *in prep.*), indicate pond macrophyte cover has increased since the early 1970s. Also near Barrow and elsewhere in northern Alaska, air and pond temperatures have increased over recent decades (Hobbie et al. 1999, Lougheed et al. 2011) along with anthropogenic deposition of pollutants from both local and distant sources (Jaffe et al. 1991, Schindler et al. 2006), and N and P levels in pond habitats (Lougheed et al. 2011). Although several warming studies have examined responses of CO₂ exchange between the land and atmosphere for aquatic macrophyte

communities (Oberbauer et al. 2007; Lara et al. 2012), the coupled response of CO₂ and CH₄ exchange in response to fertilization has not been studied for these plant communities.

This study uses a customized continuous carbon flux monitoring system to examine the response of trace gas fluxes from monoliths dominated by *A. fulva* aquatic tundra, exposed to a range of elevated nitrogen and phosphorus levels. Specifically, we focus on understanding the effects of fertilization on *A. fulva* biomass, CH₄ emission (steady emission: SE, gas ebullition: GE, and total emission: TE), and CO₂ exchange (net ecosystem exchange: NEE, gross ecosystem exchange: GEE, and ecosystem respiration: R_E), to infer likely functional implications of long-term nutrient additions to aquatic macrophyte communities near Barrow, AK. Monoliths were extracted from a pond margin near Barrow, Alaska. A range of nutrient concentrations (control: 0.0 mgN L⁻¹, 0.0 mgP L⁻¹, low: 1.5 mgN L⁻¹, 0.6 mgP L⁻¹, and high: 7.5 mgN L⁻¹, 3.0 mgP L⁻¹) were used in the experiment that resembled nutrient concentrations measured in both, tundra ponds between 2008-2010 (low treatment; Lougheed et al. 2011) and experimentally measured releases of nutrients from permafrost (high treatment; Reyes and Lougheed, *in prep.*).

5.3 METHODS

5.3.1 Field Sampling and Monolith Collection

Our collection site was located on the northern most point of Alaska, within the Barrow Environmental Observatory (BEO, 71°17'N, 156°37'W) near the town of Barrow. Mean annual temperature and precipitation is -11.2 °C and 115 mm (1981-2010), with mean July and January temperatures 4.9 °C and -25.2 °C, respectively (<http://www.ncdc.noaa.gov/oa/climate/normal/newnormals.html>). The coastal tundra of the region has a low topographic relief (0-10 m a.s.l.) and is underlain by continuous permafrost (Brown et al. 1997). Maximum thaw depth ranges between 25-73 cm (Hinkel and Nelson 2003). Terrestrial landscapes are dominated by freshwater ponds and shallow lakes that comprise approximately 22% of the land area and more than 65% of the landscape is comprised of vegetated thaw lake basins (Hinkel et al. 2003). In aquatic ecosystems, the distribution of emergent vascular plant species *Carex aquatilis* and *Arctophila*

fulva are influenced by water table height (Alexander et al. 1980). *Carex aquatilis* is predominantly found in shallow pond margins (< 15cm) and *A. fulva* in both shallow and deeper water (15-25cm; Alexander et al. 1980).

To develop comparisons between field and laboratory CH₄ fluxes, we sampled nine low center polygon ponds and nine thermokarst/thaw lake bed ponds scattered across <1 km² area in the BEO during peak growing season (July 25th-August 10th) in 2010. We selected 22 plots with similar water table height (3-6 cm above the soil), nutrient concentrations, soil organic material, and coverage homogeneity of *A. fulva*. Plots (50 x 50 cm) were setup using a similar approach to other studies conducting short term land-atmosphere trace gas flux sampling (Lund et al. 2009, Lara et al. 2012), where aluminum chamber bases were inserted 5 cm into the soil and left for a minimum of 12h to equilibrate prior to sampling. CH₄ flux was measured using a photo-acoustic (IR) multi-gas analyzer (INNOVA 1312 AirTech Instruments A/S, Denmark; *sensu* Lund et al. 2009). Graminoid tiller counts and heights were recorded by counting all individuals present in each plot and using a ruler to measure the height (cm) from the soil to the tip of each tiller. After fluxes were measured, all aboveground plant biomass within the plots was harvested and separated to live and dead tissue then immediately dried at 60 °C and weighed (grams of dry weight: gdw).

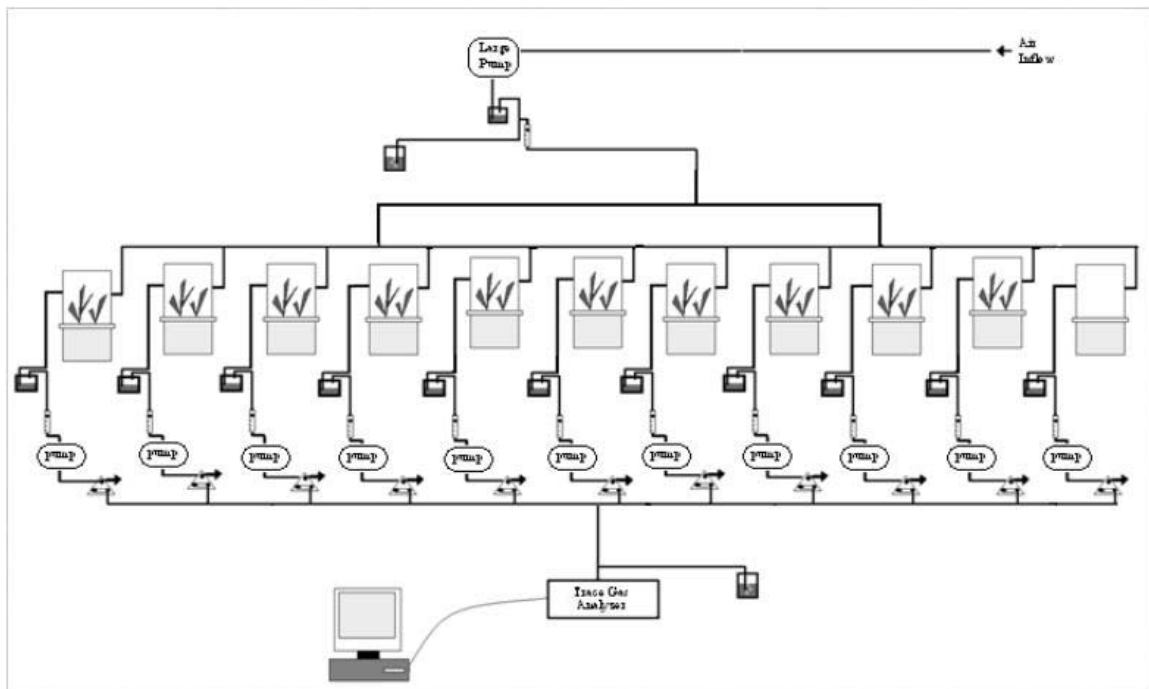


Figure 19: Schematic of the continuous flux monitoring setup. Outside air is pumped into the system at a rate of 13.2 L min^{-1} , humidified, and passed through plexiglass chambers containing monoliths at a rate of 1.2 L min^{-1} . Solenoid valves controlled by a computer allow sequential chamber sampling with an INNOVA 1312 photoacoustic trace gas analyzer. An empty chamber was used as a control for gas flux calibrations with the outside air.

Following pond draining on August 19th 2010, nine monoliths were extracted (20L x 20W x 23H cm) from a single shallow low center polygon pond within the BEO, in which 3 of the 22 field CH_4 fluxes were measured. All monoliths contained between 85-95% cover of *A. fulva*, <5% *Ranunculus trichophyllus*, and <15% bare ground cover. Following extraction, the monoliths were immediately shipped in insulated coolers to the University of Texas at El Paso. Upon arrival, all monoliths were placed in a custom controlled continuous flux monitoring system (Figure 19) built in inside a modified cold room. The design of this system is similar to that developed by Christensen et al. (2003) and is suitable for monitoring continuous land-atmosphere CO_2 and CH_4 exchange. Following protocols established by Christensen et al. (2003) monoliths were kept in the dark and temperature was maintained at 0.5°C until the experiment was initiated 8 months later in summer 2011.

5.3.2 Experimental Design

The continuous flux monitoring system (Figure 19) controlled ambient temperature, diurnal lighting cycles, water table height, and continuously monitored CO₂ and CH₄ concentrations at a rate of one chamber per minute (i.e. each chamber was sampled every 11 minutes). Monoliths were enclosed within Plexiglas chambers that were hermetically sealed with aluminum chamber bases using water channels. We used an “empty” chamber as a reference for outside gas flux. Chamber head space was continuously flushed with ambient air at an average flow rate of 1.2 L min⁻¹. Air flow was controlled using a series of solenoid valves (Parker: V² Valves) and rotameters (McMaster-Carr: 5079J66, 5079K63), powered by diaphragm pumps (HYBLOW:GP-40-0110, CD-8-1101) similar to that described by Christensen et al.(2003) and Strom et al. (2005). To simulate summer mean light levels recorded near Barrow during peak growing season (350-400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 2008-2010 Tweedie, unpublished data) we used a 1000w light source (BetterGrowHydro: 1000 MH Max-89), placed 40 cm above monoliths, which provided approximately 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation (PAR) at the top of the canopy inside the Plexiglass chambers. Lighting was programmed for a 12 hour diurnal cycle to allow for differences in day and night fluxes to be examined. Ambient room temperature and relative humidity was logged every minute (HOBO: Temp/RH/2x, H08-007-02). A PC was used for data logging and controlling solenoid valves using an external relay board (LabJack RB12).

At the initiation of the experiment on the 9th of April 2011, ambient room temperature was increased to approximately 10°C. Within the flux monitoring system, air temperature (day: 16 °C, night: 4 °C) and PAR (day: 300 $\mu\text{molm}^2\text{s}$, night: 0 $\mu\text{molm}^2\text{s}$) varied diurnally, while water table (+4 cm) was held constant for all monoliths. Monoliths were watered with filtered deionized water weekly to maintain water table height at the same level in all replicates. The experiment spanned approximately nine weeks, and began by establishing baseline levels of carbon fluxes (Pre-treatment: 4wks), that was followed by nutrient addition (Fertilization: 4wks). Above ground biomass was removed one week prior to the completion of the experiment to characterize the relative importance of above ground biomass to carbon fluxes.

In line with reported for pond nutrient concentrations (Lougheed et al. 2011), three nutrient solutions were synthesized (i.e. control (CT), low (L), and high (H)) containing two treatment levels of

nitrogen added as NH_4NO_3 (N) and phosphorus added as KH_2PO_4 (P). The “control” solution included only filtered deionized water with no added nutrients. The “low” nutrient solution contained 1.5 mgN L^{-1} , 0.6 mgP L^{-1} , similar to maximum concentrations observed at enriched sites (e.g. urban sites, thermokarst ponds) during the growing seasons between 2008-2011 (Lougheed unpublished data). The “high” solution contained 7.5 mgN L^{-1} , 3.0 mgP L^{-1} , which was five times higher than the “low” solution and a conservative estimate of N and P concentrations found to leach from permafrost soil under temperature manipulations (Reyes and Lougheed *in prep.*). Water column nutrient concentrations were quantified at the start and end of the manipulation, using standard methods (APHA, 1998). Monoliths were randomly selected for treatment exposure (control, $n=3$; low, $n=3$; high, $n=3$), whereby water was completely pumped from each monolith and replaced with nutrient concentrations matching those for the corresponding treatment described above.

Tiller counts and heights were recorded every other week prior to fertilization using the same method used for field measurements. To minimize physical disturbance to carbon fluxes during the fertilization treatment period, tiller counts and heights were not recorded during this period but measured at completion of the treatment period. Biomass was carefully removed from 1 cm below the soil surface in each monolith, then immediately dried and weighed. A linear relationship was found for cumulated tiller heights and biomass gdw m^{-2} (biomass = $0.2467 [\text{height}] - 4.7013$, $R^2 = 0.97$, $p < 0.001$) which was used to allometrically determine standing live plant biomass for monoliths throughout the experiment.

5.3.3 Data Analysis

Episodic and/or ebullition fluxes (gas bubbles) are filtered from data sets in a similar manner to that described by Christensen et al. (2003). An accepted range for absolute fluxes (i.e. vascular plant mediated and soil diffusion) was identified as steady emission (SE i.e. $<5 \text{ mg m}^{-2} \text{ hr}^{-1}$). Fluxes above SE were considered to contain (gas) ebullition events (GE i.e. $>5 \text{ mg m}^{-2} \text{ hr}^{-1}$ above SE). Total emission (TE) was calculated as the sum of SE and GE. To determine if changes in SE was a function of increased biomass (active transport via aerenchyma) or in response to altered methanogenic microbial activity with fertilization, we normalized SE (nSE) fluxes for live tiller biomass. If nSE fluxes did not

vary among fertilization treatments, this would suggest (1) SE fluxes were proportional to biomass, and (2) methanogenesis did not vary with increased nutrient availability.

The daytime CO₂ flux was considered net ecosystem exchange (NEE), night-time flux was considered ecosystem respiration (R_E), and gross ecosystem exchange (GEE) was estimated from the difference between R_E and NEE. To determine if plant growth impacted canopy light use efficiency (LUE), we normalized GEE (nGEE) by dividing the daily flux by biomass that was modeled for the duration of the experiment by linearly interpolating biomass between the allometric measurements described above (Figure 20). To evaluate the combined greenhouse warming potential (GWP) of ecosystem CO₂ and CH₄ flux, we converted CH₄ fluxes to CO₂ equivalents assuming a 100 year atmospheric residence time (GWP₁₀₀=23 for CH₄, Ramaswamy et al. 2001). We evaluated the effects of additional nutrient availability on biomass (gdw m⁻²), CH₄ flux (TE, SE, GE), and CO₂ flux (NEE, GEE, R_E) using a two-way analysis of variance (ANOVA), with nutrient levels (CT, L, H) and experimental period (Pre-treatment, Fertilization, Biomass Removal) as fixed factors. If ANOVAs detected significance at, $\alpha < 0.05$, Tukey's HSD post hoc tests were used to determine differences between treatment, period, and interactions. All data were logarithmically or arcsine transformed prior to statistical analysis to satisfy statistical assumptions of normality. All statistical analyses were performed in JMP version 10.0.

5.4 RESULTS

5.4.1 Effects on Above Ground Biomass

Monolith vegetation was acclimatized for four weeks during the pre-treatment period. Immediately prior to fertilization, there was no difference in estimated tiller biomass among CT, L and H treatments (ANOVA, $p > 0.05$). The biomass of the H nutrient level increased over time and was significantly higher than the other treatments (+57 gdw m⁻²), whereas CT and L treatments did not differ from each other throughout the experiment (+16, +10 gdw m⁻²; respectively). A week before the end of the experiment, all above ground live graminoids and standing/soil litter were removed. We estimated live and dead biomass (with standard deviation) during the biomass removal period for all nutrient levels

as follows: H (live: 125 ± 33 , dead: 401 ± 62 gdw m^{-2}), L (live: 65 ± 9 , dead: 285 ± 131 gdw m^{-2}), CT (live: 74 ± 6 , dead: 252 ± 142 gdw m^{-2}).

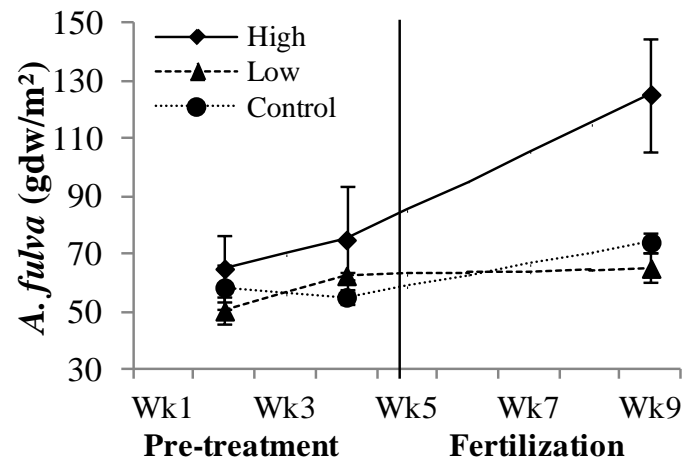


Figure 20: Biomass estimates of *A. fulva* from Pre-treatment (Week 1-4) and Fertilization periods (Week 5-9). Error bars indicate ± 1 S.D. The vertical line indicates the start of fertilization during week 5.

5.4.2 Effects on CO₂ Flux

We found NEE to vary among experimental periods, nutrient levels and with the interaction between these (Table 12). During the pre-treatment period all nutrient levels had a negative NEE, where a negative NEE indicates carbon uptake. In response to fertilization, the H nutrient level switched to a positive NEE (HSD: $p < 0.05$; Figure 23) while both L and CT treatments remained negative (Figure 23). For all nutrient levels, biomass removal significantly altered NEE to a state of positive carbon release (HSD: $p < 0.05$; Figure 23) similar to R_E rates.

Table 12: Main effects for two-way ANOVAs on experimental period means of the CO₂ flux components (net ecosystem exchange: NEE, gross ecosystem exchange: GEE, ecosystem respiration: RE, and biomass normalized gross ecosystem exchange: nGEE).

CO₂ flux: Two-way ANOVA				
	Univariate Responses	DF	F value	P value
NEE	Experimental Period	2	261.06	< 0.001
	Nutrient Level	2	3.37	0.038
	Exp. Period x Nt. Level	4	45.7	< 0.001
	Error	117		
GEE	Experimental Period	2	97.04	< 0.001
	Nutrient Level	2	7.87	< 0.001
	Exp. Period x Nt. Level	4	15.47	< 0.001
	Error	117		
nGEE	Experimental Period	1	94.15	< 0.001
	Nutrient Level	2	4.66	0.012
	Exp. Period x Nt. Level	2	49.69	< 0.001
	Error	86		
RE	Experimental Period	2	34.72	< 0.001
	Nutrient Level	2	34.03	< 0.001
	Exp. Period x Nt. Level	4	1.61	0.176
	Error	117		

Because GEE is directly related to live biomass, and biomass varied among experimental periods (Table 12, Figure 23), it was not surprising that GEE responded strongly to experimental period, nutrient level, and the interaction between them both (Table 12). Although H treatment biomass was greater during the fertilization period relative to pre-treatment, GEE was found to be significantly lower (Figure 23). This finding appeared contradictory, but is explained when we normalized GEE by biomass (nGEE). This analysis revealed that H nutrient levels had lower nGEE relative (HSD: $p < 0.05$) to L and CTs (HSD: $p > 0.05$), suggesting that canopy LUE was reduced in H treatments by dense tiller growth, but not for L or CTs.

Similar to all other variables, R_E varied among experimental periods and nutrient levels, but no interaction between these main effects was found (Table 12). There were no differences among nutrient levels in response to fertilization, (Figure 23), however, R_E was slightly reduced in all nutrient levels in response to biomass removal (neutralization of autotrophic respiration), but only significantly so in

control (HSD: $p < 0.05$; Figure 23). This suggests (1) R_E was primarily heterotrophic and (2) fertilization may have stimulated decomposition leading to slightly higher losses of soil carbon in L and H nutrient levels.

5.4.3 Effects on CH_4 Flux

Both rates of SE measured within the laboratory and those recorded in the field, increased linearly with *A. fulva* biomass (Figure 21), suggesting (1) fluxes in the laboratory were similar to those recorded in the field, and (2) the greater the *A. fulva* biomass or cover, the higher expected flux of CH_4 to the atmosphere

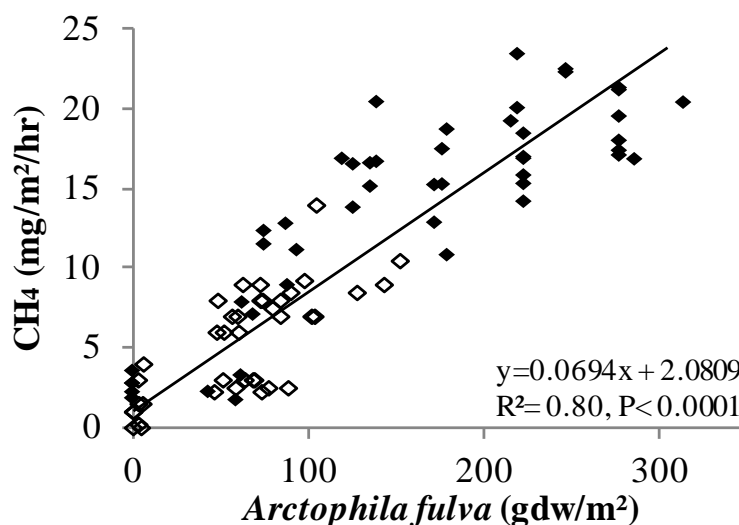


Figure 21: Methane flux was found to increase linearly with *Arctophila fulva* above ground biomass under both field and experimental conditions. Closed diamonds represent CH_4 steady emission (SE) fluxes from field based measurements near Barrow, Alaska, while open diamonds represent SE collected from laboratory experimentations.

We found TE to vary significantly among experimental periods and among nutrient levels, but no interaction between experimental period and nutrient levels was found (Table 13). Interestingly, post hoc tests revealed that within all nutrient levels, TE did not differ significantly with fertilization or upon total biomass removal (Figure 23).

Although we did not find TE to respond to fertilization, SE responded to experimental period, nutrient levels, and the interaction between experimental period and nutrient levels (Table 13). Consistent with expected dominant control of tiller biomass on SE, we found biomass to be proportional

to SE fluxes. Similar to TE, SE for both CT and L nutrient levels did not differ from one another during pre-treatment and fertilization periods (Figure 23), and both had a lower SE relative to the H nutrient level (HSD: $p < 0.05$). However, in the H nutrient level, fertilization resulted in significantly higher SE rates (HSD: $p < 0.05$; Figure 23) relative to the pre-treatment period by approximately $1.5 \text{ mg m}^{-2} \text{ hr}^{-1}$. Not surprisingly, during the biomass removal period, SE rates for all nutrient levels halted dramatically to rates $\leq 0.5 \text{ mg m}^{-2} \text{ hr}^{-1}$ (Table 14; Figure 23), confirming the strong control biomass has on SE.). Although biomass and SE increased in response to fertilization in H treatments, fertilization significantly reduced nSE in both H and L treatments (HSD: $p < 0.05$), but not in CTs, suggesting fertilization may have inhibited methanogenesis.

Table 13: Main effects for two-way ANOVAs on experimental period means of the CH_4 flux components (total emission: TE, steady emission: SE, gas ebullition: GE, and biomass normalized steady emission: nSE).

CH_4 flux: Two-way ANOVA				
	Univariate Responses	DF	F value	P value
TE	Experimental Period	2	8.71	< 0.001
	Nutrient Level	2	64.9	< 0.001
	Exp. Period x Nt. Level	4	1.31	0.265
	Error	153		
SE	Experimental Period	2	569.4	< 0.001
	Nutrient Level	2	176.2	< 0.001
	Exp. Period x Nt. Level	4	47.6	< 0.001
	Error	153		
nSE	Experimental Period	1	50.47	< 0.001
	Nutrient Level	2	307.12	< 0.001
	Exp. Period x Nt. Level	2	12.65	< 0.001
	Error	119		
GE	Experimental Period	2	25.26	< 0.001
	Nutrient Level	2	5.52	0.005
	Exp. Period x Nt. Level	4	0.58	0.676
	Error	153		

Next, we examined experimental period and nutrient level effects on GE. Differences were noted both between nutrient levels and over experimental periods, but there was no significant interaction

(Table 13). GE increased significantly in both H and CT nutrient levels during the biomass removal period (HSD: $p < 0.05$; Figure 23); however, post-hoc tests revealed no difference in GE among nutrient levels. In addition, we uncovered a negative relationship between GE and *A. fulva* biomass (Figure 22; $R^2 = 0.34$; $p < 0.001$), suggesting GE rates decrease with increasing biomass; a relationship that to our knowledge has not yet been recorded in the literature.

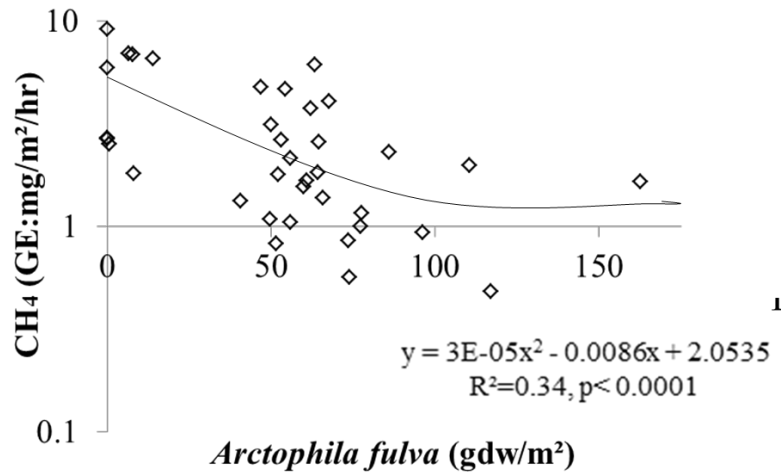


Figure 22:CH₄ gas ebullition (GE) decreased with increasing *A. fulva* above ground tiller biomass. Note: logarithmic scale for y-axis.

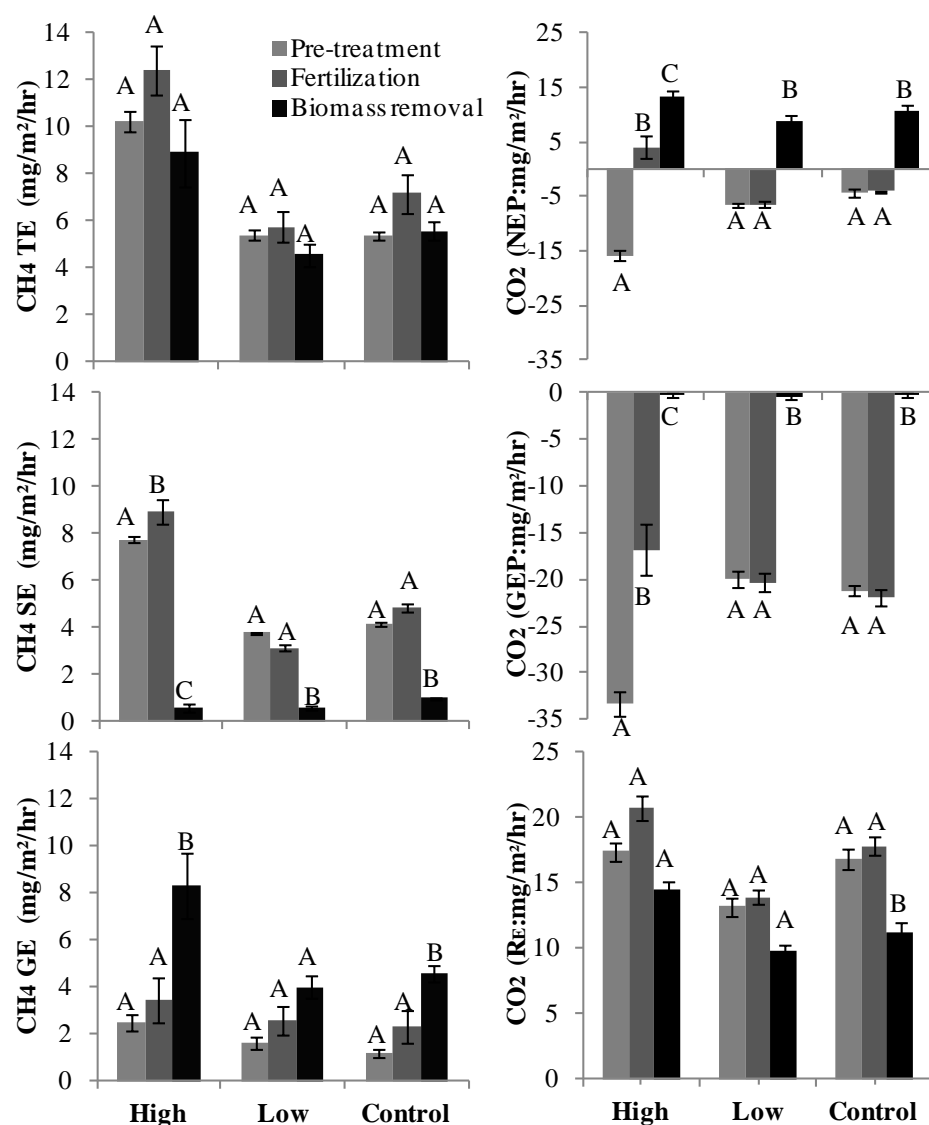


Figure 23: Experimental period (Pre-treatment, Fertilization, Biomass removal) effects on CH₄ (left panels: TE, SE, GE) and CO₂ fluxes (right panels: NEE, GEE, RE). Error bars indicate ± 1 S.E. Letter differences indicate significant differences among experimental periods

5.5 DISCUSSION

We found the H monolith fertilization treatments to respond greater than L treatments with respect to biomass, CH₄, and CO₂ fluxes. In the H nutrient treatment, *A. fulva* biomass was approximately 3.5 times higher than that of the CT treatments, similar to responses reported by van Wijk et al. (2003), and Mack et al. (2004), while L treatments did not differ in biomass, CH₄, and CO₂ fluxes from CTs. Rates of SE increased with plant tiller biomass in post fertilization measurements, which is likely related to the plants acting as conduits of CH₄ from the soil to the air (Joabsson et al. 1999; Erikson et al. 2010, Figure 21), allowing CH₄ to bypass oxidative processes near the surface of the soil.

Although biomass varied between experimental periods and nutrient levels, we determined CH₄ production may have been inhibited in fertilized monoliths. This is similar to findings made by (Conrad and Klose 1999), which attributed such inhibitory affects to either methanogen competition for hydrogen or toxicity of denitrification products to methanogens. Interestingly, we found TE not to differ with experimental period or nutrient level. This is likely a result of the following (1) methanogenesis was constant in waterlogged monolith soils and ultimately CH₄ was transported to the atmosphere regardless of specific transfer mechanism (i.e. diffusion, ebullition, active transport); (2) despite the removal of above ground biomass after the fertilization period, TE did not significantly vary, potentially as clipping increased below ground (i.e. root) detritus available for decomposition while the loss of biomass insulative properties increased soil warming potential, leading to higher rates of GE fluxes, or (3) monolith sample size may have been too low and the trend versus the variability displayed in the results meant that a true signal was not detected.

The removal of all above ground biomass restricted all plant mediated gas exchange for CH₄ fluxes to solely soil diffusion (measured as a component of SE) and GE as the primary flux mechanisms. As a result, SE fluxes decreased to approximately 0.7 mg m⁻² hr⁻¹ (Table 14). Additionally we estimated GE to represent approximately 30-40% of CH₄ TE for monoliths (pre-treatment estimations). Large GE events are generally not well accounted for in the field using current chamber methods due to relatively short sampling periods and characteristically stochastic episodic events, additionally, major GE events which can be many orders of magnitude greater than SE, are often treated as outliers or erroneous measurements, and cannot be accurately extrapolated over space and time. In response to monolith CO₂ fluxes for H treatments, we attribute the reduction in photosynthesis and carbon sink strength to increased canopy cover via biomass growth which reduced LUE, and potentially monolith nutrient toxicity, similar to that reported by Bubier et al. (2007) and Juutinen et al. (2010). Although no changes in R_E were found in response to fertilization, rates of R_E did not decrease significantly following biomass removal, suggesting heterotrophic respiration dominated R_E. Though the experimental apparatus used for this study was able to efficiently capture high temporal resolution, trace gas fluxes under controlled conditions, the system was unable to fully replicate natural environmental conditions.

As the average water table height for *A. fulva* in ponds near Barrow varies between 15-25cm (Alexander et al. 1980), architectural limitations of the monitoring system were only capable of maintaining a constant water table height of +6 cm. However, mechanistically, the dominate determinate of CH₄ production is soil anaerobicity (Lai 2009) and as the water-logged environment remained uncompromised, gaseous carbon exchange is likely to be minimally altered. Additionally, the artificial light source used in this study, yielded approximately 50-100 $\mu\text{mol m}^{-2}\text{s}^{-1}$ lower than the mean summer PAR for Barrow, thus the maximum photosynthesis rates reported are likely to be reduced compared to those recorded in the field, which typically range from 4.25 to 5.75 $\text{gC m}^{-2} \text{day}^{-1}$ for this plant community (Lara et al. 2012). Also unlike aquatic tundra environments which experience a steady nutrient input, our monitoring system was unable to replicate this as we fertilized monolith plots in pulses, similar to Sullivan et al. (2007). Generally, other environmental conditions within the monitoring system were similar to natural conditions and we achieved comparable CH₄ and CO₂ fluxes, but to holistically replicate Arctic tundra environments is extremely difficult within a laboratory environment.

Table 14: Mean (\pm 1S.D.) of calculations for CH₄, CO₂, and GWP. Using CO₂ equivalence (100yr time horizon; CH₄=23 x CO₂; IPCC 2004; 2007) GWP is calculated using SE +NEE and TE + NEE to determine the warming potential using different metrics of CH₄ fluxes. Negative values represent carbon uptake, while positive represent carbon loss to the atmosphere (i.e. positive warming feedback).

	EXPERIMENTAL PERIOD	CH ₄			CO ₂			SE +NEE	TE +NEE
		TE	SE	GE	NEE	GEE	R _E	GWP	
High	Pre-treatment	10.24 \pm 1.9	7.70 \pm 0.5	2.49 \pm 1.5	-15.81 \pm 3.7	-33.24 \pm 5.9	17.43 \pm 3.2	161.29	219.61
	Fertilization	12.41 \pm 5.0	8.95 \pm 2.4	3.45 \pm 4.6	4.01 \pm 7.3	-16.78 \pm 9.7	20.79 \pm 3.5	209.97	289.35
	Biomass removal	8.91 \pm 4.9	0.58 \pm 0.5	8.32 \pm 4.7	13.36 \pm 3.2	-0.10 \pm 0.9	14.56 \pm 2.0	26.79	218.22
Low	Pre-treatment	5.41 \pm 1.1	3.78 \pm 0.2	1.63 \pm 1.0	-6.74 \pm 1.7	-19.93 \pm 3.7	13.19 \pm 3.3	80.19	117.71
	Fertilization	5.74 \pm 3.1	3.15 \pm 0.5	2.58 \pm 3.0	-6.42 \pm 1.8	-20.31 \pm 3.4	13.89 \pm 2.0	66.05	125.50
	Biomass removal	4.56 \pm 1.6	0.56 \pm 0.3	3.99 \pm 1.6	8.93 \pm 2.8	-0.40 \pm 1.0	9.84 \pm 1.5	21.90	113.71
Control	Pre-treatment	5.36 \pm 0.9	4.14 \pm 0.3	1.22 \pm 0.7	-4.30 \pm 3.7	-21.20 \pm 2.5	16.90 \pm 3.5	91.00	119.06
	Fertilization	7.16 \pm 3.7	4.83 \pm 0.9	2.32 \pm 3.4	-4.09 \pm 1.0	-21.94 \pm 2.9	17.85 \pm 2.4	107.08	160.53
	Biomass removal	5.57 \pm 1.4	0.98 \pm 0.3	4.59 \pm 1.2	10.69 \pm 3.4	-0.15 \pm 1.2	11.22 \pm 2.2	33.30	138.75

Several implications can be drawn from the results of this experiment in combination with observed changes in elevated air/water temperatures, N and P availability (Lougheed et al. 2011), and

the change in cover and extent of aquatic tundra *A. fulva* communities in the Barrow area over the last 40 to 50 years (Villarreal et al. 2012). Although we found biomass and ecosystem function to respond significantly only in the H nutrient treatment, the magnitude of ecosystem functional change is likely to be community (Lara et al. 2012) and species specific (Strom et al. 2005, Strom et al. 2012). Similar to patterns found in a retrogressive functional modeling study (Lara et al. 2012), the increase in *A. fulva* coverage in pond habitats near Barrow, is likely to have increased the emission of CH₄ over time. However, as *A. fulva* predominantly grows within a depth range of (15-25cm), and retrospective studies of the Barrow area suggest the expansion of ponds (Lin et al. 2012), it is plausible that increased pond margin areas will allow increased rooting zone and further expansion of *A. fulva* as found by Villarreal et al. (2012) and Andresen and Lougheed (*in prep.*).

Key findings from this study are as follows: (1) the laboratory flux monitoring system did a good job at replicating carbon fluxes recorded in the field; (2) above ground *A. fulva* biomass increased with H fertilization approximately to a mass approximately 3.5 times greater than the CT, while L fertilization did not differ from CTs; (3) biomass was positively and linearly correlated with SE, while GE was negatively and non-linearly correlated; (4) GE represented 30-40% of the total CH₄ flux in *A. fulva* monoliths; (5) by not accounting for GE when estimating the combined global warming potential (GWP) of both CH₄ and CO₂ exchange in the field, TE and total potential GWP can be greatly underestimated (Table 14); and (6) H fertilization treatments increased SE and decreased carbon uptake potential by decreasing canopy LUE. We cannot yet predict how warming will effect landscape level carbon dynamics in Arctic aquatic macrophyte dominated tundra ecosystems, as (1) quantifiable rates of nutrient release from permafrost in response to warming has not yet been established, but are in progress (Lougheed et al. *in prep.*), (2) under natural conditions, increased nutrient availability may not immediately decrease canopy LUE and carbon uptake potential in tundra ponds; instead it is likely that increased nutrient availability may initiate an increased lateral spread of rhizomes and macrophyte growth across ponds, which may increase macrophyte cover/density and gradually decrease LUE; and (3) further field and remote sensing studies are needed to investigate the short to long-term dynamics of

macrophyte expansion in light of environmental change and in relation to anomalous warm years over the half-century time scale in the Barrow tundra ponds.

5.6 CONCLUSION

This is one of the first studies to examine the functional responses of aquatic macrophyte communities under controlled conditions indicative of ongoing and potential environmental change documented in high northern latitudes. Findings support other studies that have examined the effect of fertilization on biomass (Bret-Harte et al. 2008), CH₄ flux (Christensen et al. 2003; Eriksson et al. 2010, Strom et al. 2012), CO₂ flux (Mack et al. 2004, Lund et al. 2009), but add to these studies by detailing the coupled responses of TE, SE, GE, NEE, GEE, and R_E to two fertilization treatment levels similar to concentrations measured in tundra ponds during 2008-10 near Barrow (L treatment) and in experiments where permafrost has been warmed (H treatment). We conclude that (1) increased nutrient availability can alter biomass and ecosystem CH₄ and CO₂ exchange in aquatic macrophyte dominated communities; (2) there was a discernible difference in responses between H and L nutrient levels, which suggests a potential threshold between L and H nutrient concentrations or specifically between N and P; (3) GE was not stochastic and was predictable using a non-linear negative relationship with tiller biomass; (4) GE sustained a relatively continuous flux of approximately 2 mg m⁻² hr⁻¹ with vegetation present and 5.5 mg m⁻² hr⁻¹ following removal of tillers; and (5) the expansion of aquatic plant communities and extent of *A. fulva* near Barrow, AK, might be a response to increased nutrient availability as a result of climatic warming and thawing permafrost, but further work is needed to understand if the responses to fertilization in this study can be replicated in the field.

Chapter 6: General Discussion

Northern ecosystems play an important role in global biogeochemical cycling, particularly carbon. Of particular concern is how the large soil organic carbon store in the Arctic (Tarnocai et al. 2009) will respond to rapidly increasing temperatures (Kaufman et al. 2009). If soil carbon is lost to the atmosphere, greenhouse warming will be enhanced (McGuire et al. 2010, Schuur et al. 2011, McGuire et al. 2012). Improved understanding of the complex biophysical interactions, controls, and stores of carbon fate and transport in the Arctic is key to addressing this research challenge.

This dissertation addresses several research challenges that to date have been difficult to address due to the lack of decade-time scale observations and novel statistical linkages between ecosystem structural and functional measurements. Moreover, this dissertation fully/partly addresses many of the current research challenges outlined by Luo et al. (2011) including:

1. Carbon dynamics

- a. Partition relative contribution of carbon sources from biomass, exudates of plants, microorganisms, and their decomposition products (Chapter 5).
- b. Understand mechanisms underlying retention of organic carbon in soils as regulated by physical protection within the soil matrix, association with minerals, anaerobiosis, and water limitation (Chapter 5).

2. Nutrient regulation

- a. Estimate the relative effects of various global change factors on N mineralization, immobilization, plant uptake, fixation, and loss under various soil moisture regimes (Chapter 2, 3, 4, 5)
- b. Quantify long-term accrual and depletion of ecosystem N and P under multifactor global change (Chapter 5)
- c. Understand microbial regulation of C and N processes via mineralization, priming, and the decomposition of old and new soil organic matter (SOM) (Chapter 5)

3. Species composition

- a. Identify temporal and spatial scales of species compositional shifts under global change (Chapter 2, 3, 4, 5)
- b. Develop generalizable patterns across various studies that can be used to improve model prediction of species responses to global change (Chapter 2,3)
- c. Understand mechanisms underlying species expansion or contraction of their geographic ranges (Chapter 2, 3, 4, 5)
- d. Estimate disproportionate rates and magnitudes of climatic changes within species ranges and across biomes (Chapter 5)
- e. Delineate nonlinear shifts in species composition and consequent asymmetrical changes in ecosystem processes (Chapter 2, 3)

The ultimate goal of global change research is to enhance how future ecosystem and climate states can be projected at decadal, century, or longer time scales. However, current ecosystem and global climate models that project ecosystem responses and feedbacks to global change over century time scales (e.g. IPCC models: 300 years) and are typically parameterized by short-term data despite ecosystem responses to global change being recognized for being regulated by long-term and slow processes (Rastetter 1996). This dissertation contributes to a knowledge base that is considerably limited by the number long-term studies. In particular this dissertation assesses the likelihood of ecosystem functional change near Barrow, Alaska between 1972-2010 (e.g. 38 yrs) and on Baffin Island, Canada between 1964-2009 (e.g. 46 yrs) using a novel retrogressive analysis technique (see Chapter 2 and 3). In addition, several studies were executed to further understand ecosystem properties and processes associated with long-term change in ecosystem structure and function. Near Barrow, the impact of long-term herbivore exclusion (1959-2010: 51 yrs) on ecosystem function was investigated, and a high resolution CO₂ and CH₄ flux system was built to determine the functional implications for elevated nutrient concentrations (N and P) recently documented in tundra ponds between 1972-2010 (see Chapter 5). Thus, this dissertation provides a new knowledge base founded on decade-time scale change

observations that can be used to test and constrain ecosystem models, which may help to improve projections of ecosystem dynamics at decadal or perhaps century time scales.

6.1 RECAPITULATION OF OBJECTIVES

Here, key findings from the dissertation are summarized and discussed as they pertain to the specific objectives outlined for this dissertation in Section 1.3.1.

Objective 1: Determine how landscape and plant community change has altered productivity, soil moisture, and albedo between 1964-2009 in a recently deglaciated site in the high arctic.

In 2009, sites established in 1964 near the northern limit of the Barnes Ice Cap, Baffin Island, Canada were resampled and assessed for change in ecosystem function by using a multivariate-geospatial modeling technique developed and published by Lara et al. (2012). In collaboration with John Jacobs at Memorial University of Newfoundland, Canada, regional climate over the past 50 years was reconstructed. Time series analysis of this climate dataset showed that summer periods have become warmer and wetter over time. Generally, the greatest change in ecosystem function was noted for plant communities with high soil moisture regimes. For example, two pond margin communities: *Campylium-Aulacomnium*-moss meadows and *Eriophorum-Pleuropogon* wetlands increased in biomass by 178% and 46%, while NDVI increased 35% and 16%, respectively. Soil moisture was found to decrease in *Carex stans* wet meadows and *Campylium-Aulacomnium*-moss meadows by 30% and 24%, respectively. Other changes were largely plant community specific. *Saxifraga oppositifolia*-Cryptogamic crust communities typical of rock barrens were found to increase in NDVI, and this change was determined to be partly attributed to increases in the cover of the rock lichen *Alectoria minuscula*. Additionally, the driest communities *Poa-Papaver* barren and *Cassiope-Sphenolobus* snowbed were the most resistant to change, as no change in productivity, albedo, or VWC was detected.

Using an NEE ecosystem model developed for the Beringia region (Lin 2012), a sensitivity analysis was run in order to assess how changes in summer temperature have likely altered ecosystem carbon uptake potential during peak growing season. Results suggest that an increase in air temperature

by 2 °C decreased VWC over the past-half century has increased NEE to a greater degree than that offset by increased NDVI (Section 2.4). This change is likely the result of an increase in ecosystem respiration outweighing increases in photosynthesis. This modeling effort suggests that dry plant communities experienced the greatest magnitude change (+114%) between 1964-2009, and wet plant communities experienced the greatest absolute change (+0.479 gC m⁻² day⁻¹). These findings are particularly striking because dry moisture regimes comprise a relatively large component of the study area and wet were the most functionally dynamic. Changes appear to be attributable to warmer summer temperatures and plant successional patterns following deglaciation.

Objective 2: Determine the extent of ecosystem functional change from 1972-2010 near Barrow Alaska, with the development of a novel multivariate-geospatial community level model, which links ecosystem structure and function

Marked plots established near Barrow in 1972 were revisited and resampled in 1999, 2008, and 2010 to assess plant community change. Ecosystem function studies were made close to peak growing season in 2010 adjacent to structurally similar marked plots. Measurements included land-atmosphere CH₄ and CO₂ exchange, hyperspectral reflectance, albedo, water table height, soil moisture, and plant species cover and abundance. Species cover and abundance data from marked and destructive plots were analyzed together using non-metric multidimensional scaling (NMS) ordination. NMS axis scores from destructive plots were kriged to create surface plots of ecosystem functional variables in ordination space, from which time series of functional attributes for the resampled plots were derived. Generally, the greatest change in ecosystem function was found for aquatic and wet plant communities, where productivity varied and soil moisture increased along with methane flux over time. Interestingly, our functional models appeared to be responsive to the lemming high of 2008, which was found to decrease albedo and NDVI, while increasing methane fluxes for both aquatic *Carex* graminoid and wet graminoid tundra. These effects were likely a response to increased grazing, which removed above ground litter and green graminoid cover resulting in darker and more exposed soils that likely warmed causing increased methane flux. Further, the least change in ecosystem function between 1972-2010 was found

in moist and dry communities which decreased in soil moisture, and appeared more stable through time. Findings suggest that the Barrow landscape could have become less productive with the exception of aquatic communities, and less responsive to change and disturbance over the past few decades, which agrees with a recent landscape level study in the Barrow area (Lin et al. 2012).

Objective 3: Assess the functional implications of a half century of herbivore exclusion on tundra near Barrow, Alaska.

During the summer of 2010, a range of ecosystem functional properties were measured in replicate 2 x 2 m herbivore exclosure plots, and adjacent control plots established in dry, moist and wet land cover types near Barrow, Alaska in 1959. Data were collected at peak growing season in conjunction with a companion study that tested for shifts in vegetation composition in the same control and exclosure plots (Johnson et al. 2011). Herbivore effects varied between land cover types and the strongest differences between exclosures and control plots were found in wet graminoid tundra. Herbivore exclusion in wet tundra increased albedo (+10%), but decreased thaw depth (-37%), saturated soil layer (-28%), normalized difference vegetation index (-20%), methane flux ($-23\text{mgC m}^{-2} \text{ day}^{-1}$), and increased loss of CO_2 to the atmosphere through increased net ecosystem exchange ($+1.75\text{gC m}^{-2} \text{ day}^{-1}$). Sustained lemming exclusion altered peak growing season global warming potential (GWP_{100} : integrated over a 100 year time horizon), of wet graminoid tundra from a neutral/slight sink (control) to a net source of carbon to the atmosphere ($+1.15\text{gCeq m}^{-2} \text{ day}^{-1}$). Further, lemming exclusion decreased saturated soil layer (-47%) for moist land cover types, and decreased thaw depth (-20%) for dry land cover types, while no other significant exclusion effects were detected for these land cover types. Measurements of ecosystem function for grazed (control) and ungrazed (exclosure) states were extrapolated over the Barrow Peninsula (421 km^2) using a high spatial resolution land cover map (Tweedie et al. submitted). Substantial differences in landscape processes are hypothesized to occur in the absence of grazing at the landscape scale, particularly for wet tundra landscapes that are typically associated with drained but vegetated thaw lake basins. Across the Barrow Peninsula, we found strong differences between modeled ungrazed and grazed tundra, specifically for albedo ($+3766 \text{ kilowatts day}^{-1}$

¹), NEE (+315 tonnesC day⁻¹), CH₄ (-3.8 tonnesC day⁻¹), and GWP₁₀₀ (+227 tonnesCeq day⁻¹). Scaled across the Barrow Peninsula grazed tundra was estimated to maintain a historically accurate peak growing season carbon sink at -219 tonnesCeq day⁻¹, respectively, while ungrazed tundra was estimated to function as a small source +8tonnesCeq day⁻¹. Thus, a shift in lemming herbivory has the capacity to dramatically alter ecosystem function at plot to landscape scales and should be regarded as a more important component of the changing Arctic System than what has been the case in the past.

Objective 4: Determine species specific functional responses to elevated levels of N and P in pond macrophyte communities dominated by *Arctophila fulva*.

This objective was motivated by recent studies suggesting the extent of aquatic tundra near Barrow, Alaska dominated by *Arctophila fulva*, has increased over the past half-century (Villarreal et al. 2012, Lin et al. 2012), which appear to have occurred concurrently with increases in nitrogen and phosphorus in aquatic ecosystems in the same area (Lougheed et al. 2011). This study examined the response of ecosystem carbon dioxide (CO₂) and methane (CH₄) flux from *A. fulva* dominated tundra under elevated nitrogen and phosphorus levels. Monoliths were extracted from a pond margin near Barrow, dominated by *A. fulva* and placed in a custom continuous flux monitoring system, that controlled environmental conditions (light, air temperature, water table height) at 3 nutrient treatment levels (control: 0.0 mgN L⁻¹, 0.0 mgP L⁻¹, low: 1.5 mgN L⁻¹, 0.6 mgP L⁻¹, and high: 7.5 mgN L⁻¹, 3.0 mgP L⁻¹). The continuous flux monitoring system built for this study appears to be one of only a few in North America and required extensive planning, engineering, and software development.

The nutrient addition experiment was run for approximately nine weeks and collected more than 50,000 CO₂ and CH₄ flux data points. In response to the high nutrient treatment, *A. fulva* biomass and steady state CH₄ emission (SE) increased with increased biomass, which appear to act as gas conduits from the soil to the air (Joabsson et al. 1999, Koelbener et al. 2010), but contrary to expectations, GEE decreased as vascular plant biomass increased. The increase in canopy cover likely lead to a reduction in light use efficiency similar to that reported by Bubier et al. (2007) and Juutinen et al. (2010). There were no differences in CO₂ and CH₄ flux between control and low nutrient treatments. No differences in gas

ebullition (GE) among nutrient treatments were found, however, a negative relationship between GE and biomass was documented ($R^2 = 0.34$, $p < 0.001$), which to our knowledge is the first time a correlation between vegetation leaf biomass and GE has been recorded. Further, using CH_4 fluxes during the pre-treatment period, we estimated that GE represented approximately 30-40% of the total CH_4 flux in the monoliths sampled. Collectively, short-term experimental results suggest *A. fulva* biomass, CO_2 and CH_4 fluxes in aquatic habitats have likely been altered by increased nutrient availability, which supports long-term field based observations and suggests there will be substantial functional implications for future aquatic vegetation change in the Barrow area, and potentially tundra landscapes elsewhere in the Arctic.

6.2 SYNTHESIS

This dissertation contributed to the International Polar Year - Back to the Future (IPY-BTF) project (see Callaghan et al. 2011). This project was focused on revisiting and resampling historic (>25 yrs) research sites situated in tundra ecosystems to assess patterns and implications of decade-time scale environmental change. Work presented in this dissertation specifically addressed how biophysical changes in the environment were related to change in ecosystem function at the species, community, and landscape level. We developed a novel analytical model that linked ecosystem structure and function (Section 2.3.4 and 3.3.3) and used these to estimate functional change. Although, Barrow and Baffin Island landscapes have considerably different climates (Section 1.2), models found similar functional patterns of change. For example, the greatest functional change was documented in wet communities, while dry communities remained relatively stable. This suggests that for tundra ecosystems and within local areas, decade-time scale patterns of change in ecosystem function may be similar at different locations. Discussed in Section 3.4, functional change models suggested wet-moist communities near Barrow AK appeared to be sensitive to herbivory, while we found 50+ years of herbivore exclusion to similarly, but more intensely alter wet community and landscape function (Section 4.4). Within these dynamic aquatic-wet communities, where structural and functional change is documented, studies report increased abundance of *A. fulva* (Villarreal et al. 2012) and nutrients in tundra ponds since the early 1970s (Lougheed et al. 2011), therefore we explored the potential for functional change over time,

finding the ecosystem functional dynamics associated with these aquatic ecosystems to hold tremendous implications for the observed changes (Section 5.4). Further, our site based assessments, validate trends detected through large scale remote sensing and modeling projections (Sitch et al. 2007, Bhatt et al. 2010, McGuire et al. 2010, McGuire et al. 2012).

Generally, observed changes documented over decadal-time scales in northern ecosystems (Callaghan et al. 2011, Myers-Smith et al. 2011, Elmendorf et al. 2012) as well as those projected for the future (McGuire et al. 2006, Schuur et al. 2011, McGuire et al. 2012), suggest these temperature sensitive ecosystems have/will continue to be within a constant state of structural and functional change. Determining the specific “pressure points” or mechanisms driving circumpolar Arctic change, remains a key research challenge. Work presented in this dissertation, highlights the following future research priorities: (1) plant communities higher in soil moisture have changed over decade-time scales at higher rates relative to drier communities, suggesting these functionally dynamic communities may be more vulnerable to ongoing climate and environmental change, (2) lemming exclusion highly impacted ecosystem function in wet northern Alaskan tundra, increased observations and experimental studies are needed on multiple tundra land cover types and among varying points in the lemming cycle to better understand the spatial and temporal functional effects of exclusion on the Arctic Coastal Plain tundra, and (3) the expansion of aquatic plant communities and extent of *A. fulva* near Barrow, AK, might be a response to increased nutrient availability as a result of climatic warming and thawing permafrost, but further work is needed to understand if the fertilization responses (see Chapter 5) can be replicated in the field.

6.3 CONSIDERATIONS FOR FUTURE RESEARCH

Findings from this research have begun to address several key questions that global change researchers to date have not been able to address due to the lack of long-term observations and novel statistical approaches useful for linking changes in ecosystem structure with ecosystem function. Several important and new research challenges have emerged as a result of this dissertation and are presented below relative to the two locations where research for this study was conducted and to demonstrate the importance of species specific responses to change.

6.3.1 High Polar Desert Arctic: Baffin Island, Canada

Warming in the High Arctic has intensified over recent years and is increasing rates of deglaciation. Vegetation assembly of High Arctic tundra is known to begin on proglacial chronosequences (Hodkinson et al. 2003), similar to that found at our study site in the Lewis Valley. Glacial forelands are nutrient poor, and early successional cyanobacteria-cryptogamic crusts greatly enhance nitrogen fixation (Matthews 1992; Dickson 2000), which can facilitate the colonization and establishment of vascular flora. In High Arctic Svalbard, Hodkinson et al. (2003) report the cover of cryptogamic crusts over 60 years of post deglaciation to increase in cover approximately 34%. Additionally, sensitivity analysis (Chapter 2.4) determined that the most abundant, dry land cover type in the Baffin Island study area underwent the greatest magnitude of change in NEE from 1964-2009. After enough nitrogen is fixed, vascular plants begin to colonize and cryptogamic crust decline (Matthews 1992; Dickson 2000). At our site on Baffin Island, Villarreal et al. (*in prep.*), found cryptogamic crust to increase across all plant communities, though many communities have been deglaciated for >750 yrs. Future work is needed to understand how rapid warming is affecting rates of nitrogen fixation by cyanobacteria-cryptogamic crusts and how this is impacting plant colonization, community establishment, and implications on ecosystem function across young-old deglaciation chronosequences in High Arctic sites. Retreat of ice caps and glaciers are forecast to continue, and it may be that these High Arctic landscapes could provide a large potential sink for atmospheric carbon and nitrogen in the future.

6.3.2 Species Response to Change: Barrow, Alaska

There is now a broad consensus among the scientific community on many aspects on the relationship between biodiversity and ecosystem functioning (Hooper et al. 2005). Certain species combinations are complementary in their patterns of resource use and can increase productivity and nutrient retention. In wet tundra, certain plant species have found to be disproportionately more or less important to biogeochemical cycling (Hansell et al. 1998). Although, the nutrient experiment on *A. fulva* detailed in section 5 was focused on the functional implications of elevated nutrients, field based studies

along the North Slope (i.e. Barrow and Atkasuk, AK), suggest that this plant species may play an important role regulating regional biogenic methane emissions (Section 5.4). Methane flux rates were significantly higher for this species than for *Carex aquatilis*, another common aquatic macrophyte in northern Alaska (unpublished data). As such, *A. fulva*, and possibly other species (following further study) may prove to be useful indicator species worthy of enhanced monitoring.

References

- Abdalati, W., W. Krabill, E. Frederick, S. Manizade, C. Martin, J. Sonntag, R. Swift, R. Thomas, J. Yungel, and R. Koerner. 2004. Elevation changes of ice caps in the Canadian Arctic Archipelago. *Journal of Geophysical Research-Earth Surface* **109**.
- ACIA. 2005. Arctic climate impact assessment scientific report. Cambridge University Press, Cambridge, UK.
- Aerts, R., J. H. C. Cornelissen, and E. Dorrepaal. 2006. Plant performance in a warmer world: General responses of plants from cold, northern biomes and the importance of winter and spring events. *Plant Ecology* **182**:65-77.
- Andrews, J. T., Webber, P.J. 1964. A lichenometrical study of the northwestern margin of the Barnes Ice Cap: a geomorphological technique. *Geographical Bulletin* **22**:80-104.
- Armenakis, C. 2008. Determination of geospatial changes of the Barnes Ice Cap using EO data. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences* **37**:1437-1442.
- Avis, C. A., A. J. Weaver, and K. J. Meissner. 2011. Reduction in areal extent of high-latitude wetlands in response to permafrost thaw. *Nature Geoscience* **4**:444-448.
- Bartlett, K. B., P. M. Crill, R. L. Sass, R. C. Harriss, and N. B. Dise. 1992. Methane Emissions from Tundra Environments in the Yukon-Kuskokwim Delta, Alaska. *Journal of Geophysical Research-Atmospheres* **97**:16645-16660.
- Batzli, G. O. 1980. Patterns of Vegetation and Herbivory in Arctic Tundra - Results from the Research on Arctic Tundra Environments (Rate) Program - Preface. *Arctic and Alpine Research* **12**:401-402.
- Batzli, G. O. and F. A. Pitelka. 1975. Vole Cycles - Test of Another Hypothesis. *American Naturalist* **109**:482-487.
- Batzli, G. O., F. A. Pitelka, and G. N. Cameron. 1983. Habitat Use by Lemmings near Barrow, Alaska. *Holarctic Ecology* **6**:255-262.
- Bennett, E. M., S. R. Carpenter, and N. F. Caraco. 2001. Human impact on erodable phosphorus and eutrophication: A global perspective. *Bioscience* **51**:227-234.
- Bhatt, U. S., D. A. Walker, M. K. Raynolds, J. C. Comiso, H. E. Epstein, G. S. Jia, R. Gens, J. E. Pinzon, C. J. Tucker, C. E. Tweedie, and P. J. Webber. 2010. Circumpolar Arctic Tundra Vegetation Change Is Linked to Sea Ice Decline. *Earth Interactions* **14**.
- Bragazza, L., C. Freeman, T. Jones, H. Rydin, J. Limpens, N. Fenner, T. Ellis, R. Gerdol, M. Hajek, T. Hajek, P. Lacumin, L. Kutnar, T. Tahvanainen, and H. Toberman. 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proceedings of the National Academy of Sciences of the United States of America* **103**:19386-19389.
- Brathen, K. A., R. A. Ims, N. G. Yoccoz, P. Fauchald, T. Tveraa, and V. H. Hausner. 2007. Induced shift in ecosystem productivity ? Extensive scale effects of abundant large herbivores. *Ecosystems* **10**:773-789.
- Bret-Harte, M. S., M. C. Mack, G. R. Goldsmith, D. B. Sloan, J. DeMarco, G. R. Shaver, P. M. Ray, Z. Biesinger, and F. S. Chapin. 2008. Plant functional types do not predict biomass responses to removal and fertilization in Alaskan tussock tundra. *Journal of Ecology* **96**:713-726.
- Briner, J. P., P. T. Davis, and G. H. Miller. 2009. Latest Pleistocene and Holocene glaciation of Baffin Island, Arctic Canada: key patterns and chronologies. *Quaternary Science Reviews* **28**:2075-2087.

- Brown, J., Hinkel, K. M., Nelson, F. E. 2000. The circumpolar active layer monitoring (CALM) program: Research designs and initial results. *Polar Geography* **24**:166-258.
- Brown, J., Miller, P.C., Tieszen, L.L., Bunnell, F.L. 1980. An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Inc. (Stroudsburg, PA).
- Bubier, J. L. and T. R. Moore. 1994. An Ecological Perspective on Methane Emissions from Northern Wetlands. *Trends in Ecology & Evolution* **9**:460-464.
- Bubier, J. L., T. R. Moore, and L. A. Bledzki. 2007. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biology* **13**:1168-1186.
- Callaghan, T. V., L. O. Bjorn, F. S. Chapin, III, Y. Chernov, T. R. Christensen, B. Huntley, R. Ims, M. Johansson, D. J. Riedlinger, S. Jonasson, N. Matveyeva, W. Oechel, N. Panikov, G. Shaver, C. Simon, L. Arris, and B. Heal. 2005. Arctic tundra and Polar Desert ecosystems. *Arctic Climate Impact Assessment*:243-352.
- Callaghan, T. V., L. O. Bjorn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, S. Schaphoff, S. Sitch, and C. Zockler. 2004. Key findings and extended summaries. *Ambio* **33**:386-392.
- Callaghan, T. V., C. E. Tweedie, J. Akerman, C. Andrews, J. Bergstedt, M. G. Butler, T. R. Christensen, D. Cooley, U. Dahlberg, R. K. Danby, F. J. A. Daniels, J. G. de Molenaar, J. Dick, C. E. Mortensen, D. Ebert-May, U. Emanuelsson, H. Eriksson, H. Hedenas, G. H. R. Henry, D. S. Hik, J. E. Hobbie, E. J. Jantze, C. Jaspers, C. Johansson, M. Johansson, D. R. Johnson, J. F. Johnstone, C. Jonasson, C. Kennedy, A. J. Kenney, F. Keuper, S. Koh, C. J. Krebs, H. Lantuit, M. J. Lara, D. Lin, V. L. Loughheed, J. Madsen, N. Matveyeva, D. C. McEwen, I. H. Myers-Smith, Y. K. Narozhniy, H. Olsson, V. A. Pohjola, L. W. Price, F. Riget, S. Rundqvist, A. Sandstrom, M. Tamstorf, R. Van Bogaert, S. Villarreal, P. J. Webber, and V. A. Zemtsov. 2011. Multi-Decadal Changes in Tundra Environments and Ecosystems: Synthesis of the International Polar Year-Back to the Future Project (IPY-BTF). *Ambio* **40**:705-716.
- Carroll, M. L., J. R. G. Townshend, C. M. DiMiceli, T. Loboda, and R. A. Sohlberg. 2011. Shrinking lakes of the Arctic: Spatial relationships and trajectory of change. *Geophysical Research Letters* **38**.
- Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology* **76**:694-711.
- Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, T. S. Rupp, A. H. Lynch, J. P. Schimel, J. Beringer, W. L. Chapman, H. E. Epstein, E. S. Euskirchen, L. D. Hinzman, G. Jia, C. L. Ping, K. D. Tape, C. D. C. Thompson, D. A. Walker, and J. M. Welker. 2005. Role of land-surface changes in Arctic summer warming. *Science* **310**:657-660.
- Christensen, T. R., N. Panikov, M. Mastepanov, A. Joabsson, A. Stewart, M. Oquist, M. Sommerkorn, S. Reynaud, and B. Svensson. 2003. Biotic controls on CO₂ and CH₄ exchange in wetlands - a closed environment study. *Biogeochemistry* **64**:337-354.
- Clymo, R. S. 1984. The Limits to Peat Bog Growth. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **303**:605-654.
- Conrad, R. 1989. Control of Methane Production in Terrestrial Ecosystems. Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere **47**:39-58.
- Conrad, R. and M. Klose. 1999. Anaerobic conversion of carbon dioxide to methane, acetate and propionate on washed rice roots. *FEMS Microbiology Ecology* **30**:147-155.
- Dickson, L. G. 2000. Constraints to nitrogen fixation by cryptogamic crusts in a polar desert ecosystem, Devon Island, NWT, Canada. *Arctic Antarctic and Alpine Research* **32**:40-45.
- Duchesne, D., G. Gauthier, and D. Berteaux. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia* **167**:967-980.

- Dyke, A. S., Prest, V.K. 1987. Late Wisconsinan and Holocene history of the Laurentide Ice Sheet. *Geographie Physique Et Quaternaire* **41**:237-263.
- Edwards, K. A. and R. L. Jefferies. 2010. Nitrogen uptake by *Carex aquatilis* during the winter-spring transition in a low Arctic wet meadow. *Journal of Ecology* **98**:737-744.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Bjork, N. Boulanger-Lapointe, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, E. Dorrepaal, T. G. Elumeeva, M. Gill, W. A. Gould, J. Harte, D. S. Hik, A. Hofgaard, D. R. Johnson, J. F. Johnstone, I. S. Jonsdottir, J. C. Jorgenson, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, M. Lara, E. Levesque, B. Magnusson, J. L. May, J. A. Mercado-Diaz, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, V. G. Onipchenko, C. Rixen, N. M. Schmidt, G. R. Shaver, M. J. Spasojevic, P. E. Porhallsdottir, A. Tolvanen, T. Troxler, C. E. Tweedie, S. Villareal, C. H. Wahren, X. Walker, P. J. Webber, J. M. Welker, and S. Wipf. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* **2**:453-457.
- Epstein, H. E., M. P. Calef, M. D. Walker, F. S. Chapin, and A. M. Starfield. 2004. Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology* **10**:1325-1334.
- Epstein, H. E., M. K. Raynolds, D. A. Walker, U. S. Bhatt, C. J. Tucker, and J. E. Pinzon. 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters* **7**.
- Eriksson, T., M. G. Oquist, and M. B. Nilsson. 2010. Production and oxidation of methane in a boreal mire after a decade of increased temperature and nitrogen and sulfur deposition. *Global Change Biology* **16**:2130-2144.
- Euskirchen, E. S., A. D. McGuire, and F. S. Chapin. 2007. Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming. *Global Change Biology* **13**:2425-2438.
- Euskirchen, E. S., A. D. McGuire, D. W. Kicklighter, Q. Zhuang, J. S. Clein, R. J. Dargaville, D. G. Dye, J. S. Kimball, K. C. McDonald, J. M. Melillo, V. E. Romanovsky, and N. V. Smith. 2006. Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology* **12**:731-750.
- Galloway, J. N. and E. B. Cowling. 2002. Reactive nitrogen and the world: 200 years of change. *Ambio* **31**:64-71.
- Gamon, J. A., Y. F. Cheng, H. Claudio, L. MacKinney, and D. A. Sims. 2006. A mobile tram system for systematic sampling of ecosystem optical properties. *Remote Sensing of Environment* **103**:246-254.
- Gorham, E. 1991. Northern Peatlands - Role in the Carbon-Cycle and Probable Responses to Climatic Warming. *Ecological Applications* **1**:182-195.
- Gornall, J. L., I. S. Jonsdottir, S. J. Woodin, and R. Van der Wal. 2007. Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia* **153**:931-941.
- Goto-Azuma, K. and R. M. Koerner. 2001. Ice core studies of anthropogenic sulfate and nitrate trends in the Arctic. *Journal of Geophysical Research-Atmospheres* **106**:4959-4969.
- Hansell, R. I. C., J. R. Malcolm, H. Welch, R. L. Jefferies, and P. A. Scott. 1998. Atmospheric change and biodiversity in the Arctic. *Environmental Monitoring and Assessment* **49**:303-325.
- Hill, G. B. and G. H. R. Henry. 2011. Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology* **17**:276-287.
- Hinkel, K. M., W. R. Eisner, J. G. Bockheim, F. E. Nelson, K. M. Peterson, and X. Y. Dai. 2003. Spatial extent, age, and carbon stocks in drained thaw lake basins on the Barrow Peninsula, Alaska. *Arctic Antarctic and Alpine Research* **35**:291-300.

- Hinkel, K. M. and F. E. Nelson. 2003. Spatial and temporal patterns of active layer thickness at Circumpolar Active Layer Monitoring (CALM) sites in northern Alaska, 1995-2000. *Journal of Geophysical Research-Atmospheres* **108**:.
- Hobbie, J. E., B. J. Peterson, N. Bettez, L. Deegan, W. J. O'Brien, G. W. Kling, G. W. Kipphut, W. B. Bowden, and A. E. Hershey. 1999. Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. *Polar Research* **18**:207-214.
- Hobbie, S. E. 1992. Effects of Plant-Species on Nutrient Cycling. *Trends in Ecology & Evolution* **7**:336-339.
- Hobbie, S. E. and F. S. Chapin. 1996. Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry* **35**:327-338.
- Hobbie, S. E., K. J. Nadelhoffer, and P. Hogberg. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil* **242**:163-170.
- Hodkinson, I. D., S. J. Coulson, and N. R. Webb. 2003. Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. *Journal of Ecology* **91**:651-663.
- Hollesen, J., B. Elberling, and P. E. Jansson. 2011. Future active layer dynamics and carbon dioxide production from thawing permafrost layers in Northeast Greenland. *Global Change Biology* **17**:911-926.
- Hollister, R. D. and K. J. Flaherty. 2010. Above- and below-ground plant biomass response to experimental warming in northern Alaska. *Applied Vegetation Science* **13**:378-387.
- Hollister, R. D., P. J. Webber, and C. Bay. 2005. Plant response to temperature in Northern Alaska: Implications for predicting vegetation change. *Ecology* **86**:1562-1570.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* **75**:3-35.
- Hudson, J. M. G. and G. H. R. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology* **90**:2657-2663.
- Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Global Change Biology* **17**:1013-1021.
- Hurrell, J. W. and C. Deser. 2009. North Atlantic climate variability: The role of the North Atlantic Oscillation. *Journal of Marine Systems* **78**:28-41.
- Ims, R. A., N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. *Proceedings of the National Academy of Sciences of the United States of America* **108**:1970-1974.
- IPCC. 2007. Intergovernmental Panel on Climate Change (IPCC):the scientific basis. Geneva:881.
- Ives, J. D., Andrews, J.T. 1963. Studies in the physical geography of north central Baffin Island, N.W.T. *Geographical Bulletin* **19**:5-48.
- Jacobs, J. D., R. Heron, and J. E. Luther. 1993. Recent Changes at the Northwest Margin of the Barnes Ice Cap, Baffin-Island, Nwt, Canada. *Arctic and Alpine Research* **25**:341-352.
- Jaffe, D. A., R. E. Honrath, J. A. Herring, S. M. Li, and J. D. Kahl. 1991. Measurements of Nitrogen-Oxides at Barrow, Alaska during Spring - Evidence for Regional and Northern Hemispheric Sources of Pollution. *Journal of Geophysical Research-Atmospheres* **96**:7395-7405.
- Joabsson, A. and T. R. Christensen. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology* **7**:919-932.
- Joabsson, A., T. R. Christensen, and B. Wallen. 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends in Ecology & Evolution* **14**:385-388.

- Johansson, T., N. Malmer, P. M. Crill, T. Friborg, J. H. Akerman, M. Mastepanov, and T. R. Christensen. 2006. Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biology* **12**:2352-2369.
- Juutinen, S., J. Alm, T. Larmola, J. T. Huttunen, M. Morero, S. Saarnio, P. J. Martikainen, and J. Silvola. 2003. Methane (CH₄) release from littoral wetlands of Boreal lakes during an extended flooding period. *Global Change Biology* **9**:413-424.
- Juutinen, S., J. L. Bubier, and T. R. Moore. 2010. Responses of Vegetation and Ecosystem CO₂ Exchange to 9 Years of Nutrient Addition at Mer Bleue Bog. *Ecosystems* **13**:874-887.
- Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K. C. Mo, C. Ropelewski, J. Wang, A. Leetmaa, R. Reynolds, R. Jenne, and D. Joseph. 1996. The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society* **77**:437-471.
- Kapfer, J., R. Virtanen, and J. A. Grytnes. 2012. Changes in arctic vegetation on Jan Mayen Island over 19 and 80 years. *Journal of Vegetation Science* **23**:771-781.
- Kaufman, D. S., D. P. Schneider, N. P. McKay, C. M. Ammann, R. S. Bradley, K. R. Briffa, G. H. Miller, B. L. Otto-Bliesner, J. T. Overpeck, B. M. Vinther, and M. Arctic Lakes 2k Project. 2009. Recent Warming Reverses Long-Term Arctic Cooling. *Science* **325**:1236-1239.
- Keller, J. K., S. D. Bridgman, C. T. Chapin, and C. M. Iversen. 2005. Limited effects of six years of fertilization on carbon mineralization dynamics in a Minnesota fen. *Soil Biology & Biochemistry* **37**:1197-1204.
- Keuper, F., P. M. van Bodegom, E. Dorrepaal, J. T. Weedon, J. van Hal, R. S. P. van Logtestijn, and R. Aerts. 2012. A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology* **18**:1998-2007.
- King, J. Y., W. S. Reeburgh, and S. K. Regli. 1998. Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment. *Journal of Geophysical Research-Atmospheres* **103**:29083-29092.
- Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Global Change Biology* **17**:1611-1624.
- Koelbener, A., L. Strom, P. J. Edwards, and H. O. Venterink. 2010. Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil. *Plant and Soil* **326**:147-158.
- Koppen, W. 1931. Climates of the Earth. *Petermanns Mitteilungen* **77**:44-44.
- Kotsyurbenko, O. R. 2005. Trophic interactions in the methanogenic microbial community of low-temperature terrestrial ecosystems. *Fems Microbiology Ecology* **53**:3-13.
- La Puma, I. P., T. E. Philippi, and S. F. Oberbauer. 2007. Relating NDVI to ecosystem CO₂ exchange patterns in response to season length and soil warming manipulations in arctic Alaska. *Remote Sensing of Environment* **109**:225-236.
- Lai, D. Y. F. 2009. Methane Dynamics in Northern Peatlands: A Review. *Pedosphere* **19**:409-421.
- Lamb, E. G., S. Han, B. D. Lanoil, G. H. R. Henry, M. E. Brummell, S. Banerjee, and S. D. Siciliano. 2011. A High Arctic soil ecosystem resists long-term environmental manipulations. *Global Change Biology* **17**:3187-3194.
- Lara, M. J., S. Villarreal, D. R. Johnson, R. D. Hollister, P. J. Webber, and C. E. Tweedie. 2012. Estimated change in tundra ecosystem function near Barrow, Alaska between 1972 and 2010. *Environmental Research Letters* **7**.
- Lasslop, G., M. Reichstein, D. Papale, A. D. Richardson, A. Arneth, A. Barr, P. Stoy, and G. Wohlfahrt. 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biology* **16**:187-208.

- Liljedahl, A. K., L. D. Hinzman, Y. Harazono, D. Zona, C. E. Tweedie, R. D. Hollister, R. Engstrom, and W. C. Oechel. 2011. Nonlinear controls on evapotranspiration in arctic coastal wetlands. *Biogeosciences* **8**:3375-3389.
- Lin, D. H., D. R. Johnson, C. Andresen, and C. E. Tweedie. 2012. High spatial resolution decade-time scale land cover change at multiple locations in the Beringian Arctic (1948-2000s). *Environmental Research Letters* **7**.
- Lougheed, V. L., M. G. Butler, D. C. McEwen, and J. E. Hobbie. 2011. Changes in Tundra Pond Limnology: Re-sampling Alaskan Ponds After 40 Years. *Ambio* **40**:589-599.
- Lund, M., T. R. Christensen, M. Mastepanov, A. Lindroth, and L. Strom. 2009. Effects of N and P fertilization on the greenhouse gas exchange in two northern peatlands with contrasting N deposition rates. *Biogeosciences* **6**:2135-2144.
- Luo, Y. Q., J. Melillo, S. L. Niu, C. Beier, J. S. Clark, A. T. Classen, E. Davidson, J. S. Dukes, R. D. Evans, C. B. Field, C. I. Czimczik, M. Keller, B. A. Kimball, L. M. Kueppers, R. J. Norby, S. L. Pelini, E. Pendall, E. Rastetter, J. Six, M. Smith, M. G. Tjoelker, and M. S. Torn. 2011. Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology* **17**:843-854.
- Mack, M. C., M. S. Bret-Harte, T. N. Hollingsworth, R. R. Jandt, E. A. G. Schuur, G. R. Shaver, and D. L. Verbyla. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. *Nature* **475**:489-492.
- Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**:440-443.
- Mackelprang, R., M. P. Waldrop, K. M. DeAngelis, M. M. David, K. L. Chavarria, S. J. Blazewicz, E. M. Rubin, and J. K. Jansson. 2011. Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. *Nature* **480**:368-U120.
- Madsen, J., C. Jaspers, M. Tamstorf, C. E. Mortensen, and F. Riget. 2011. Long-Term Effects of Grazing and Global Warming on the Composition and Carrying Capacity of Graminoid Marshes for Moulting Geese in East Greenland. *Ambio* **40**:638-649.
- Malmer, N., T. Johansson, M. Olsrud, and T. R. Christensen. 2005. Vegetation, climatic changes and net carbon sequestration in a North-Scandinavian subarctic mire over 30 years. *Global Change Biology* **11**:1895-1909.
- Mastepanov, M., C. Sigsgaard, E. J. Dlugokencky, S. Houweling, L. Strom, M. P. Tamstorf, and T. R. Christensen. 2008. Large tundra methane burst during onset of freezing. *Nature* **456**:628-U658.
- McCune, B., and Grace, J. B. 2002. Analysis of Ecological Communities. Chapter 16: Nonmetric Multidimensional Scaling:125-142.
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. D. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* **79**:523-555.
- McGuire, A. D., F. S. Chapin, J. E. Walsh, and C. Wirth. 2006. Integrated regional changes in arctic climate feedbacks: Implications for the global climate system. *Annual Review of Environment and Resources* **31**:61-91.
- McGuire, A. D., T. R. Christensen, D. Hayes, A. Heroult, E. Euskirchen, J. S. Kimball, C. Koven, P. Lafleur, P. A. Miller, W. Oechel, P. Peylin, M. Williams, and Y. Yi. 2012. An assessment of the carbon balance of Arctic tundra: comparisons among observations, process models, and atmospheric inversions. *Biogeosciences* **9**:3185-3204.
- McGuire, A. D., D. J. Hayes, D. W. Kicklighter, M. Manizza, Q. Zhuang, M. Chen, M. J. Follows, K. R. Gurney, J. W. McClelland, J. M. Melillo, B. J. Peterson, and R. G. Prinn. 2010. An analysis of the carbon balance of the Arctic Basin from 1997 to 2006. *Tellus Series B-Chemical and Physical Meteorology* **62**:455-474.

- McIntire, E. J. B. and D. S. Hik. 2005. Influences of chronic and current season grazing by collared pikas on above-ground biomass and species richness in subarctic alpine meadows. *Oecologia* **145**:288-297.
- Moen, J. and O. Danell. 2003. Reindeer in the Swedish mountains: An assessment of grazing impacts. *Ambio* **32**:397-402.
- Muller, S. V., A. E. Racoviteanu, and D. A. Walker. 1999. Landsat MSS-derived land-cover map of northern Alaska: extrapolation methods and a comparison with photo-interpreted and AVHRR-derived maps. *International Journal of Remote Sensing* **20**:2921-2946.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Levesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Menard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* **6**.
- Nakatsubo, T., M. Fujiyoshi, S. Yoshitake, H. Koizumi, and M. Uchida. 2010. Colonization of the polar willow *Salix polaris* on the early stage of succession after glacier retreat in the High Arctic, Ny-Alesund, Svalbard. *Polar Research* **29**:385-390.
- Natali, S. M., E. A. G. Schuur, C. Trucco, C. E. H. Pries, K. G. Crummer, and A. F. B. Lopez. 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Global Change Biology* **17**:1394-1407.
- Nelson, F. E., K. M. Hinkel, N. I. Shiklomanov, G. R. Mueller, L. L. Miller, and D. A. Walker. 1998. Active-layer thickness in north central Alaska: Systematic sampling, scale, and spatial autocorrelation. *Journal of Geophysical Research-Atmospheres* **103**:28963-28973.
- Ng, E. and P. C. Miller. 1977. Validation of a Model of Effect of Tundra Vegetation on Soil Temperatures. *Arctic and Alpine Research* **9**:89-104.
- Nykanen, H., H. Vasander, J. T. Huttunen, and P. J. Martikainen. 2002. Effect of experimental nitrogen load on methane and nitrous oxide fluxes on ombrotrophic boreal peatland. *Plant and Soil* **242**:147-155.
- Oberbauer, S. F., C. E. Tweedie, J. M. Welker, J. T. Fahnestock, G. H. R. Henry, P. J. Webber, R. D. Hollister, M. D. Walker, A. Kuchy, E. Elmore, and G. Starr. 2007. Tundra CO₂ fluxes in response to experimental warming across latitudinal and moisture gradients. *Ecological Monographs* **77**:221-238.
- Oechel, W. C., S. J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers, and N. Grulke. 1993. RECENT CHANGE OF ARCTIC TUNDRA ECOSYSTEMS FROM A NET CARBON-DIOXIDE SINK TO A SOURCE. *Nature* **361**:520-523.
- Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane. 2000. Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* **406**:978-981.
- Olivas, P. C., S. F. Oberbauer, C. Tweedie, W. C. Oechel, D. Lin, and A. Kuchy. 2011. Effects of Fine-Scale Topography on CO₂ Flux Components of Alaskan Coastal Plain Tundra: Response to Contrasting Growing Seasons. *Arctic Antarctic and Alpine Research* **43**:256-266.
- Olivas, P. C., S. F. Oberbauer, C. E. Tweedie, W. C. Oechel, and A. Kuchy. 2010. Responses of CO₂ flux components of Alaskan Coastal Plain tundra to shifts in water table. *Journal of Geophysical Research-Biogeosciences* **115**:.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* **15**:2681-2693.
- Olofsson, J., S. Stark, and L. Oksanen. 2004. Reindeer influence on ecosystem processes in the tundra. *Oikos* **105**:386-396.

- Pancotto, V. A., P. M. van Bodegom, J. van Hal, R. S. P. van Logtestijn, P. Blokker, S. Toet, and R. Aerts. 2010. N deposition and elevated CO₂ on methane emissions: Differential responses of indirect effects compared to direct effects through litter chemistry feedbacks. *Journal of Geophysical Research-Biogeosciences* **115**.
- Penuelas, J., J. A. Gamon, K. L. Griffin, and C. B. Field. 1993. Assessing Community Type, Plant Biomass, Pigment Composition, and Photosynthetic Efficiency of Aquatic Vegetation from Spectral Reflectance. *Remote Sensing of Environment* **46**:110-118.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoyer, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological Dynamics Across the Arctic Associated with Recent Climate Change. *Science* **325**:1355-1358.
- Post, E. and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America* **105**:12353-12358.
- Qian, H. F., R. Joseph, and N. Zeng. 2010. Enhanced terrestrial carbon uptake in the Northern High Latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections. *Global Change Biology* **16**:641-656.
- Ramaswamy, V., M. L. Chanin, J. Angell, J. Barnett, D. Gaffen, M. Gelman, P. Keckhut, Y. Koshelkov, K. Labitzke, J. J. R. Lin, A. O'Neill, J. Nash, W. Randel, R. Rood, K. Shine, M. Shiotani, and R. Swinbank. 2001. Stratospheric temperature trends: Observations and model simulations. *Reviews of Geophysics* **39**:71-122.
- Rastetter, E. B. 1996. Validating models of ecosystem response to global change. *Bioscience* **46**:190-198.
- Raynolds, M. K., D. A. Walker, H. E. Epstein, J. E. Pinzon, and C. J. Tucker. 2012. A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. *Remote Sensing Letters* **3**:403-411.
- Riordan, B., D. Verbyla, and A. D. McGuire. 2006. Shrinking ponds in subarctic Alaska based on 1950-2002 remotely sensed images. *Journal of Geophysical Research-Biogeosciences* **111**:.
- Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, J. Gurevitch, and Gcte-News. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**:543-562.
- Saarnio, S., T. Saarinen, H. Vasander, and J. Silvola. 2000. A moderate increase in the annual CH₄ efflux by raised CO₂ or NH₄NO₃ supply in a boreal oligotrophic mire. *Global Change Biology* **6**:137-144.
- Sachs, T., M. Giebel, J. Boike, and L. Kutzbach. 2010. Environmental controls on CH₄ emission from polygonal tundra on the microsite scale in the Lena river delta, Siberia. *Global Change Biology* **16**:3096-3110.
- Schindler, D. W., P. J. Dillon, and H. Schreier. 2006. A review of anthropogenic sources of nitrogen and their effects on Canadian aquatic ecosystems. *Biogeochemistry* **79**:25-44.
- Schlesinger, W. H. 2009. On the fate of anthropogenic nitrogen. *Proceedings of the National Academy of Sciences of the United States of America* **106**:203-208.
- Schultz, A. M. 1964. The nutrient-recovery hypothesis for arctic microtine cycles II. Ecosystem variables in relation to the arctic microtine cycles:57-68.
- Schuur, E. A. G., B. Abbott, and P. C. Network. 2011. High risk of permafrost thaw. *Nature* **480**:32-33.
- Schuur, E. A. G., J. Bockheim, J. G. Canadell, E. Euskirchen, C. B. Field, S. V. Goryachkin, S. Hagemann, P. Kuhry, P. M. Lafleur, H. Lee, G. Mazhitova, F. E. Nelson, A. Rinke, V. E.

- Romanovsky, N. Shiklomanov, C. Tarnocai, S. Venevsky, J. G. Vogel, and S. A. Zimov. 2008. Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *Bioscience* **58**:701-714.
- Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp. 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* **459**:556-559.
- Shaver, G. R., J. Canadell, F. S. Chapin, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melillo, L. Pitelka, and L. Rustad. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* **50**:871-882.
- Shaver, G. R., L. E. Street, E. B. Rastetter, M. T. 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.
- Shiklomanov, N. I., D. A. Streletskiy, F. E. Nelson, R. D. Hollister, V. E. Romanovsky, C. E. Tweedie, J. G. Bockheim, and J. Brown. 2010. Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow, Alaska. *Journal of Geophysical Research-Biogeosciences* **115**:.
- Silapaswan, C. S., D. L. Verbyla, and A. D. McGuire. 2001. Land cover change on the Seward Peninsula: The use of remote sensing to evaluate the potential influences of climate warming on historical vegetation dynamics. *Canadian Journal of Remote Sensing* **27**:542-554.
- Sitch, S., A. D. McGuire, J. Kimball, N. Gedney, J. Gamon, R. Engstrom, A. Wolf, Q. Zhuang, J. Clein, and K. C. McDonald. 2007. Assessing the carbon balance of circumpolar Arctic tundra using remote sensing and process modeling. *Ecological Applications* **17**:213-234.
- Sjogersten, S., R. van der Wal, M. J. J. E. Loonen, and S. J. Woodin. 2011. Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry* **106**:357-370.
- Sjogersten, S., R. van der Wal, and S. J. Woodin. 2008. Habitat type determines herbivory controls over CO₂ fluxes in a warmer arctic. *Ecology* **89**:2103-2116.
- Sjogersten, S., R. van der Wal, and S. J. Woodin. 2012. Impacts of Grazing and Climate Warming on C Pools and Decomposition Rates in Arctic Environments. *Ecosystems* **15**:349-362.
- Smith, L. C., Y. Sheng, G. M. MacDonald, and L. D. Hinzman. 2005. Disappearing Arctic lakes. *Science* **308**:1429-1429.
- Smol, J. P. and M. S. V. Douglas. 2007. Crossing the final ecological threshold in high Arctic ponds. *Proceedings of the National Academy of Sciences of the United States of America* **104**:12395-12397.
- Speed, J. D. M., E. J. Cooper, I. S. Jonsdottir, R. van der Wal, and S. J. Woodin. 2010. Plant community properties predict vegetation resilience to herbivore disturbance in the Arctic. *Journal of Ecology* **98**:1002-1013.
- Stow, D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, C. Racine, M. Sturm, K. Tape, L. Hinzman, K. Yoshikawa, C. Tweedie, B. Noyle, C. Silapaswan, D. Douglas, B. Griffith, G. Jia, H. Epstein, D. Walker, S. Daeschner, A. Petersen, L. M. Zhou, and R. Myneni. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment* **89**:281-308.
- Stoy, P. C., M. Williams, M. Disney, A. Prieto-Blanco, B. Huntley, R. Baxter, and P. Lewis. 2009. Upscaling as ecological information transfer: a simple framework with application to Arctic ecosystem carbon exchange. *Landscape Ecology* **24**:971-986.
- Strom, L. and T. R. Christensen. 2007. Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. *Soil Biology & Biochemistry* **39**:1689-1698.
- Strom, L., M. Mastepanov, and T. R. Christensen. 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry* **75**:65-82.

- Strom, L., T. Tagesson, M. Mastepanov, and T. R. Christensen. 2012. Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. *Soil Biology & Biochemistry* **45**:61-70.
- Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky. 2005. Winter biological processes could help convert arctic tundra to shrubland. *Bioscience* **55**:17-26.
- Sullivan, P. F., M. Sommerkorn, H. M. Rueth, K. J. Nadelhoffer, G. R. Shaver, and J. M. Welker. 2007. Climate and species affect fine root production with long-term fertilization in acidic tussock tundra near Toolik Lake, Alaska. *Oecologia* **153**:643-652.
- Symstad, A. J., F. S. Chapin, D. H. Wall, K. L. Gross, L. F. Huenneke, G. G. Mittelbach, D. P. C. Peters, and D. Tilman. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *Bioscience* **53**:89-98.
- Tape, K. D., R. Lord, H. P. Marshall, and R. W. Ruess. 2010. Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. *Ecoscience* **17**:186-193.
- Tarnocai, C. 2009. The Impact of Climate Change on Canadian Peatlands. *Canadian Water Resources Journal* **34**:453-466.
- Tarnocai, C., J. G. Canadell, E. A. G. Schuur, P. Kuhry, G. Mazhitova, and S. Zimov. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles* **23**:-.
- Torn, M. S. and F. S. Chapin. 1993. Environmental and Biotic Controls over Methane Flux from Arctic Tundra. *Chemosphere* **26**:357-368.
- Turunen, J., E. Tomppo, K. Tolonen, and A. Reinikainen. 2002. Estimating carbon accumulation rates of undrained mires in Finland - application to boreal and subarctic regions. *Holocene* **12**:69-80.
- Van der Wal, R. and R. W. Brooker. 2004. Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology* **18**:77-86.
- van Wijk, M. T., K. E. Clemmensen, G. R. Shaver, M. Williams, T. V. Callaghan, F. S. Chapin, J. H. C. Cornelissen, L. Gough, S. E. Hobbie, S. Jonasson, J. A. Lee, A. Michelsen, M. C. Press, S. J. Richardson, and H. Rueth. 2004. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology* **10**:105-123.
- van Wijk, M. T., M. Williams, L. Gough, S. E. Hobbie, and G. R. Shaver. 2003. Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? *Journal of Ecology* **91**:664-676.
- Villarreal, S., R. D. Hollister, D. R. Johnson, M. J. Lara, P. J. Webber, and C. E. Tweedie. 2012. Tundra vegetation change near Barrow, Alaska (1972-2010). *Environmental Research Letters* **7**.
- Villarreal, S., Hollister, R. D., Johnson, D. R., Lara, M. J., Webber, P. J., Tweedie, C. E. submitted. Plant community change near Barrow, Alaska (1972-2010). *Ambio*.
- von Fischer, J. C., R. C. Rhew, G. M. Ames, B. K. Fossdick, and P. E. von Fischer. 2010. Vegetation height and other controls of spatial variability in methane emissions from the Arctic coastal tundra at Barrow, Alaska. *Journal of Geophysical Research-Biogeosciences* **115**.
- Walker, D. A., M. K. Raynolds, F. J. A. Daniels, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. Yurtsev, and C. Team. 2005. The Circumpolar Arctic vegetation map. *Journal of Vegetation Science* **16**:267-282.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jonsdottir, J. A. Klein, B. Magnusson, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, O. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber,

- and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* **103**:1342-1346.
- Walter, K. M., S. A. Zimov, J. P. Chanton, D. Verbyla, and F. S. Chapin. 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. *Nature* **443**:71-75.
- Ward, S. E., R. D. Bardgett, N. P. McNamara, J. K. Adamson, and N. J. Ostle. 2007. Long-term consequences of grazing and burning on northern peatland carbon dynamics. *Ecosystems* **10**:1069-1083.
- Webber, P. J. 1971. Gradient analysis of the vegetation around the Lewis Valley, North Central Baffin Island, Northwest Territories, Canada. Ph.D. dissertation, Queen's University, Kingston, Ontario:366.
- Webber, P. J. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. In: Tieszen, L. L. (ed.), *The Ecology of Primary Producer Organisms in the Alaskan Arctic Tundra*:Springer-Verlag, Inc., New York, 37-112.
- Welker, J. M., J. T. Fahnestock, K. L. Povirk, C. J. Bilbrough, and R. E. Piper. 2004. Alpine grassland CO₂ exchange and nitrogen cycling: Grazing history effects, medicine bow range, Wyoming, USA. *Arctic Antarctic and Alpine Research* **36**:11-20.
- Whalen, S. C. 2005. Biogeochemistry of methane exchange between natural wetlands and the atmosphere. *Environmental Engineering Science* **22**:73-94.
- Whalen, S. C. and W. S. Reeburgh. 1990. Consumption of Atmospheric Methane by Tundra Soils. *Nature* **346**:160-162.
- Wookey, P. A., R. Aerts, R. D. Bardgett, F. Baptist, K. A. Brathen, J. H. C. Cornelissen, L. Gough, I. P. Hartley, D. W. Hopkins, S. Lavorel, and G. R. Shaver. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology* **15**:1153-1172.
- Wrona, F. J., T. D. Prowse, J. D. Reist, J. E. Hobbie, L. M. J. Levesque, and W. F. Vincent. 2006. Climate impacts on Arctic freshwater ecosystems and fisheries: Background, rationale and approach of the Arctic Climate Impact Assessment (ACIA). *Ambio* **35**:326-329.
- Yoshikawa, K. and L. D. Hinzman. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska. *Permafrost and Periglacial Processes* **14**:151-160.
- Yoshitake, S., M. Uchida, H. Koizumi, H. Kanda, and T. Nakatsubo. 2010. Production of biological soil crusts in the early stage of primary succession on a High Arctic glacier foreland. *New Phytologist* **186**:451-460.
- Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, M. C. Chapin, and J. F. Reynolds. 1995a. Effects of Mammals on Ecosystem Change at the Pleistocene-Holocene Boundary. *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences* **113**:127-135.
- Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, J. F. Reynolds, and M. C. Chapin. 1995b. Steppe-Tundra Transition - a Herbivore-Driven Biome Shift at the End of the Pleistocene. *American Naturalist* **146**:765-794.
- Zimov, S. A., E. A. G. Schuur, and F. S. Chapin. 2006. Permafrost and the global carbon budget. *Science* **312**:1612-1613.
- Zona, D., W. C. Oechel, J. Kochendorfer, K. T. P. U, A. N. Salyuk, P. C. Olivas, S. F. Oberbauer, and D. A. Lipson. 2009. Methane fluxes during the initiation of a large-scale water table manipulation experiment in the Alaskan Arctic tundra. *Global Biogeochemical Cycles* **23**.

Biographical Sketch

Mark Lara earned his Bachelor of Science degree in Ecology and Evolution from the University of Texas at El Paso in 2008. Later in May of 2008 he joined the doctoral program at UTEP. Dr. Lara has been the recipient of various honors and awards, including: a fellowship to participate in the National Science Foundation (NSF) funded GK-12 program, and numerous scholarships for conference participation from the: International Arctic Research Center (IARC), National Oceanic and Atmospheric Administration (NOAA), the Arctic Ocean Sciences Board (AOSB), International Arctic Science Committee (IASC), and Arctic Research Consortium of the U.S. (ARCUS), and the Research Council of Norway. He also served as a committee member for the ARCUS Polar TREC program in 2010.

He has presented his research at international conference meetings including: 2012 American Geophysical Union (AGU) 45th Annual Fall Meeting, 2012 International Polar Year (IPY) 2012 Montréal conference “From knowledge to action”, 2011: Ecological Society of America (ESA) Conference, 2010. State of the Arctic Conference (SOA), 2010 International Polar Year (IPY) Oslo Science Conference, 2009 Back to the Future (BTF) International meeting, 2007-09. Society for the Advancement of Chicanos and Native Americans in Science (SACNAS), and 2008 and Ecological Society of America (ESA) Conference. He has also attended workshops including: “From Knowledge to Careers” Montréal, Canada 22-23 of April 2012, “20th Anniversary of the International Tundra Experiments (ITEX)” El Paso, Texas 17-21 of January 2012, “IPY Oslo Science workshop” Oslo, Norway 5-7 of June 2010., “ITEX community change synthesis” Vancouver, Canada 2-6 of May 2010, and “Learn to Return: Wilderness first aid, helicopter, and bear safety training” Boulder, Colorado 24-27 of March 2009.

This dissertation was supervised by Dr. Craig E. Tweedie and publications generated during this dissertation are followed: (1) **Lara MJ**, Villarreal S, Johnson DR, Hollister RD, Webber PJ, Tweedie CE. 2012. Estimated change in tundra ecosystem function near Barrow, Alaska between 1972 and 2010.

Environmental Research Letters 7:015507, doi:[10.1088/1748-9326/7/1/015507](https://doi.org/10.1088/1748-9326/7/1/015507); (2) Villarreal S, Johnson DR, **Lara MJ**, Hollister RD, Webber PJ, Tweedie CE. 2012. Tundra Vegetation change near Barrow, Alaska (1972-2010). *Environmental Research Letters*. 7:015508, doi:[10.1088/1748-9326/7/1/015508](https://doi.org/10.1088/1748-9326/7/1/015508) (3) Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA⁷, Dorrepaal E, Elumeeva TG, Gill M, Gould WA, Harte J, Hik DA, Hofgaard A, Johnson DR, Johnstone JF, Jónsdóttir IS, Jorgenson JC, Klanderud K, Klein JA, Koh S, Kudo G, **Lara MJ**, Lévesque E, Magnússon B, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Onipchenko VG, Rixen C, Schmidt NM, Shaver GR, Spasojevic MJ, Þórhallsdóttir ÞE, Tolvanen A, Troxler T, Tweedie CE, Villareal S, Wahren CH, Walker X, Webber PJ, Welker JM, Wipf S. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2: doi: [10.1038/NCLIMATE1465](https://doi.org/10.1038/NCLIMATE1465) (4) Johnson DR, **Lara MJ**, Shaver GR, Batzli GO, Shaw JD, Tweedie CE. 2011. Exclusion of brown lemmings reduces vascular plant cover and biomass in arctic coastal tundra resampling of a 50+ year herbivore exclosure experiment near Barrow, Alaska. *Environmental Research Letters* 6:045507, doi:[10.1088/1748-9326/6/4/045507](https://doi.org/10.1088/1748-9326/6/4/045507); (5) Callaghan TV, Tweedie CE, Åkerman J, Andrews C, Bergstedt J, Butler MG, Christensen TR, Cooley D, Dahlberg U, Danby RK, Daniëls FJA, de Molenaar JG, Dick J, Mortensen CE, Ebert-May D, Emanuelsson U, Eriksson H, Hedenås H, Henry GHR, Hik DS, Hobbie JE, Jantze EJ, Jaspers C, Johansson C, Johansson M, Johnson DR, Johnstone JF, Jonasson C, Kennedy C, Kenney AJ, Keuper F, Koh S, Krebs CJ, Lantuit H, **Lara MJ**, Lin D, Loughheed VL, Madsen J, Matveyeva N, McEwen DC, Myers-Smith IH, Narozhniy YK, Olsson H, Pohjola VA, Price LW, Rigét F, Rundqvist S, Sandström A, Tamstorf M, Bogaert RV, Villarreal S, Webber PJ, Zemtsov VA. 2011 Multi-decadal changes in tundra environments and ecosystems: synthesis of the International Polar Year-Back to the Future Project (IPY-BTF) *Ambio* 40 705–16; (6) **Lara MJ**, Lin DH, Johnson DR, Loughheed VL, Tweedie CE. *in prep.* Response of ecosystem CO₂ and CH₄ flux to nutrient increase in *Arctophila fulva* dominated tundra.

Arctic Antarctic and Alpine Research; (7) **Lara MJ**, Johnson DR, Tweedie CE. *in prep.* 50+ years of Lemming Exclusion Alters Carbon and Energy Exchange of Alaskan Coastal Tundra. *Journal of Ecology*; (8) **Lara MJ**, Villarreal S, Johnson DR, Webber PJ, Tweedie CE. *in prep.* Decade-time scale change in plant productivity and soil moisture at a recently deglaciated site in the Canadian High Arctic. *Global Change Biology*

Lara has accepted a post-doctoral position at the University of Alaska at Fairbanks (UAF) in Dr. David McGuire's, Spatial Ecology Laboratory. He will be joining a network of permafrost/carbon researchers and will be integrating newly synthesized data sets in collaboration with the Next-Generation Ecosystem Experiments (NGEE) project, to improve climate model predictions through advanced understanding of coupled processes in Arctic terrestrial ecosystems.