

RESEARCH ARTICLE

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Key Points:

- Greenhouse gas exchange varies among vegetation communities defined by landscape position and presence of grazing
- The effects of grazing on greenhouse gas fluxes are most apparent when examining the drivers of greenhouse gas exchange
- CH₄ flux is most responsive to temperature change in grazed communities so changes in extent of grazed area could affect future emissions

Supporting Information:

- Figure S1

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Interactions among vegetation, climate, and herbivory control greenhouse gas fluxes in a subarctic coastal wetland

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Abstract High-latitude ecosystems are experiencing the most rapid climate changes globally, and in many areas these changes are concurrent with shifts in patterns of herbivory. Individually, climate and herbivory are known to influence biosphere-atmosphere greenhouse gas (GHG) exchange; however, the interactive effects of climate and herbivory in driving GHG fluxes have been poorly quantified, especially in coastal systems that support large populations of migratory waterfowl. We investigated the magnitude and the climatic and physical controls of GHG exchange within the Yukon-Kuskokwim Delta in western Alaska across four distinct vegetation communities formed by herbivory and local microtopography. Net CO₂ flux was greatest in the ungrazed *Carex* meadow community (3.97 ± 0.58 [SE] $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), but CH₄ flux was greatest in the grazed community (14.00 ± 6.56 $\text{nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$). The grazed community is also the only vegetation type where CH₄ was a larger contributor than CO₂ to overall GHG forcing. We found that vegetation community was an important predictor of CO₂ and CH₄ exchange, demonstrating that variation in regional gas exchange is best explained when the effect of grazing, determined by the difference between grazed and ungrazed communities, is included. Further, we identified an interaction between temperature and vegetation community, indicating that grazed regions could experience the greatest increases in CH₄ emissions with warming. These results suggest that future GHG fluxes could be influenced by both climate and by changes in herbivore population dynamics that expand or contract the vegetation community most responsive to future temperature change.

1. Introduction

High-latitude ecosystems are experiencing more rapid climate change than those in temperate regions [Post *et al.*, 2009; Elmendorf *et al.*, 2012]. In addition to climate change, high-latitude ecosystems are also affected by the grazing pressure of migratory herbivores. Herbivory is an important driver of change in high-latitude ecosystems because the effects of grazing on vegetation and soil properties are compounded with other constraints inherent in arctic and subarctic systems including cold temperatures, short growing seasons, and low nutrient availability. Both climate and herbivory affect ecosystem properties that control biosphere-atmosphere exchange of greenhouse gases (GHGs) [Welker *et al.*, 2004; Davidson and Janssens, 2006]; however, the extent to which climate and grazing interact to drive GHG fluxes, and the differential effects on CO₂, CH₄, and N₂O fluxes, remains uncertain. Quantifying the interactions between changing climate and herbivory on GHG exchange in high-latitude systems is critical for informing predictive models of future GHG forcing and will ultimately aid in determining whether many grazing-influenced, high-latitude ecosystems will function as a source or a sink of GHGs to the atmosphere under future climate conditions [Sjögersten *et al.*, 2011; Cahoon *et al.*, 2012].

Many coastal wetlands throughout the circumpolar north support large populations of migratory herbivorous geese [Sedinger, 1996; Stickney and Ritchie, 1996; Abraham *et al.*, 1999; van Der Wal *et al.*, 2007; Sjögersten *et al.*, 2011]. Geese modify ecosystems through trampling, defecation, and offtake of biomass, and these actions change ecosystem function by altering net primary production, nutrient cycling, and soil physical properties such as soil temperature and moisture [Zacheis *et al.*, 2002; Person *et al.*, 2003; Stark *et al.*, 2003; Van der Wal and Brooker, 2004; Welker *et al.*, 2004; Brathen *et al.*, 2007]. High-latitude wetlands also play a significant role in the emission and uptake of GHGs. These regions contain large stocks of temperature protected organic carbon that are vulnerable to warming and likely to play a role in future exchange of

carbon dioxide (CO₂) [Hobbie et al., 2000; Davidson and Janssens, 2006; Schuur et al., 2015]. High-latitude wetlands are also an important source of atmospheric methane (CH₄) [Bloom et al., 2010; Bousquet et al., 2011; Turetsky et al., 2014] and contribute to global emissions of nitrous oxide (N₂O) [Ma et al., 2008; Tian et al., 2012]. Despite the importance of herbivores in these coastal systems, and the role of coastal wetlands in global GHG emissions, the interaction between grazing activity and climate in driving GHG exchange remains largely unexamined.

The Yukon-Kuskokwim (YK) Delta in western Alaska is an ideal location to investigate the interaction of climate controls and herbivory on GHG emissions. As one of the largest river delta ecosystems in the world, the YK Delta is an important breeding, hatching, and rearing area for nearly a million migratory geese [Fischer and Stehn, 2014]. All of these species nest and raise young within 15 km of the coast where their preferred plant communities are most common [Sedinger and Raveling, 1984; Babcock and Ely, 1994; Schmutz, 2001], and through grazing the geese have a profound effect on local vegetation communities and ecosystem structure [Person et al., 2003].

The effects of goose grazing are also closely tied with the microtopography of this region. The low-relief topography of the coastal delta has created a gradient of vegetation communities which are distinguished by only centimeters of elevation [Jorgenson, 2000]. The lowest elevation landscape positions are occupied by tidal mud flats and interior brackish ponds, which are barren of vegetation. Upland from the tidal mud flats and pond margins are brackish wet sedge meadows dominated by *Carex* species [Jorgenson, 2000]. This is the most aerially expansive vegetation type, and geese graze heavily on regions within these wet sedge meadows. Slightly higher in elevation are the slough levees which are characterized by a moist meadow vegetation community including *Salix ovalifolia* and *Deschampsia caespitosa* [Jorgenson, 2000].

The interacting effects of goose grazing and microtopography have resulted in two discrete vegetation communities within the wet sedge meadows, distinguished by the growth form of *Carex ramenskii*, the dominant *Carex* species. *Carex ramenskii* has two growth forms that some consider distinct species, and these growth forms exist through a dynamic feedback with goose grazers [Person et al., 2003]. Under high grazing intensity the normally tall and erect growth form known as *C. ramenskii* will morph to a shorter stature plant with prostrate leaves historically referred to as *Carex subspathacea*. Goose grazing maintains the canopy height of *C. subspathacea* swards at 0.5 to 1.5 cm [Kincheloe and Stehn, 1991], but without grazing the swards will revert back to the taller growth form [Ruess et al., 1997; Person et al., 1998]. Because geese focus their grazing in low-elevation regions, they create discontinuous "grazing lawns" of *C. subspathacea* distributed along pond margins in bands ranging from 10 cm wide to swards of up to 0.25 km² (Figure 1). This interaction of microtopography and goose grazing activity has resulted in a landscape-scale mosaic of vegetation communities with variable ecosystem properties and the potential for variable GHG emissions.

Grazing affects many ecosystem properties that are important controls on GHG exchange including soil temperature, soil moisture, vegetation cover, and community composition [Zimov et al., 1995; Van der Wal and Brooker, 2004; Gornall et al., 2007], with implications for local biosphere-atmosphere CO₂ exchange. Grazing reduces vegetation shading of the ground surface and leads to higher soil temperatures and therefore higher rates of soil respiration [Welker et al., 2004]. Nutrient input from fecal matter in grazed regions can contribute to greater ecosystem respiration and gross primary productivity [Sjögersten et al., 2008], but grazing can also reduce ecosystem C sink strength due to the removal of biomass [van Der Wal et al., 2007; Sjögersten et al., 2011]. Furthermore, the absence of grazing can cause shifts in ecosystem composition that change ecosystem C storage and net C flux [Cahoon et al., 2012]. Overall, grazing effects on soil and vegetation conditions have substantial implications for local C balance.

Changes in soil and vegetation characteristics as a result of grazing also have the potential to alter other trace GHG emissions such as CH₄ and N₂O. Waterfowl grazing in wetland ecosystems can have highly variable effects on CH₄ emissions. By decreasing plant biomass, grazing reduces carbon and oxygen delivery to the soil, which can both lower the rate of CH₄ production and limit the rate of CH₄ consumption [Segers, 1998]. Grazing can decrease CH₄ emissions by altering the production activity of methanogenic organisms [Bodelier et al., 2006], but conversely, grazing can also increase CH₄ emissions by decreasing diffusive resistance to CH₄ transportation through forage species [Dingemans et al., 2011], and in some cases grazing has no effect on CH₄ emissions [Sjögersten et al., 2011]. The effects of grazing can also alter N₂O emissions. Grazing can also accelerate N cycling and N transformation rates [Gao et al., 2008] through the effects of

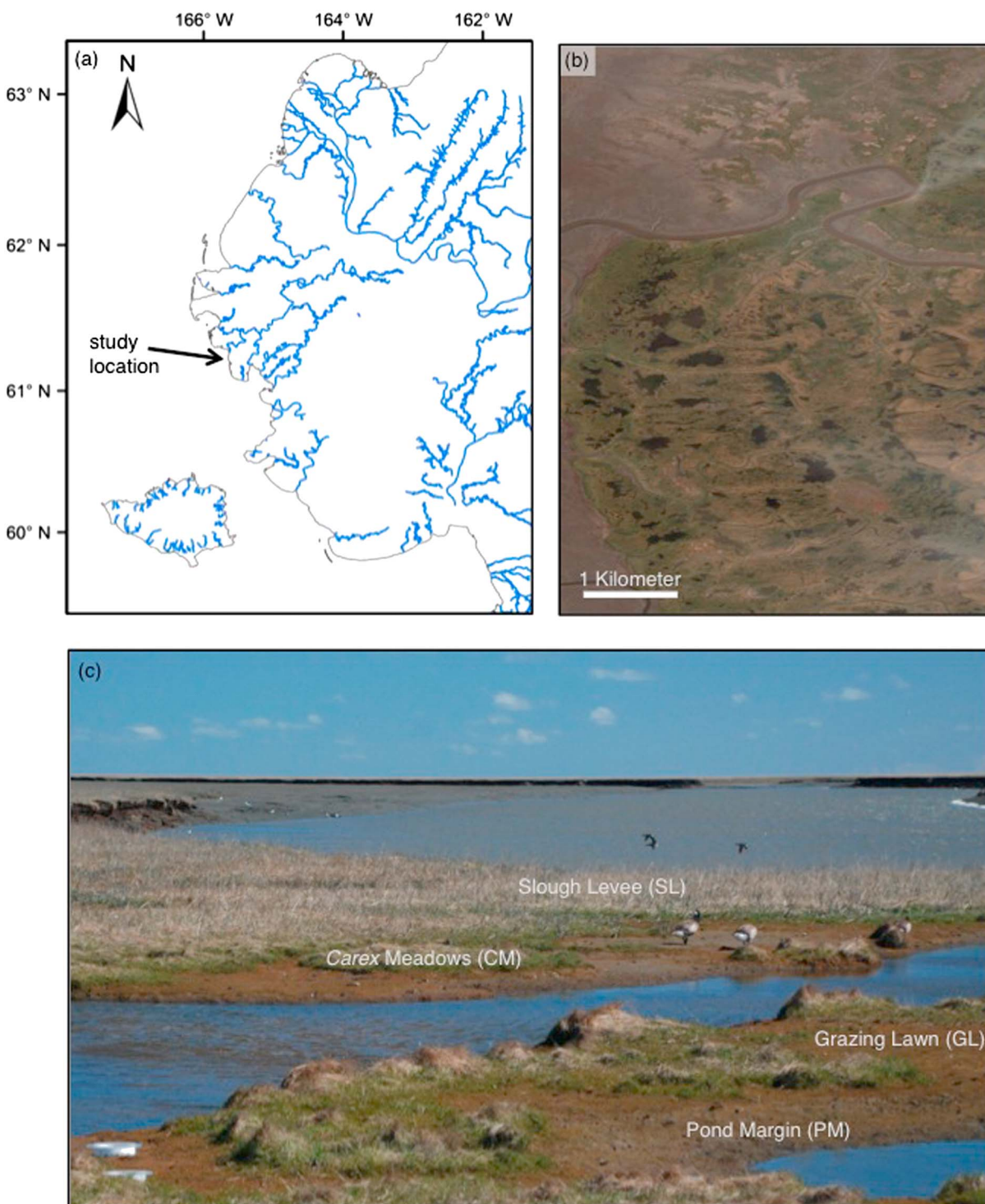


Figure 1. (a) Location of study site in western Alaska, USA. (b) True color Worldview-3 image of area surrounding Tutakoke study site. (c) Photograph of vegetation communities present at Tutakoke study site.

nutrient input and trampling, and these impacts have implications for regional fluxes of N_2O [Oenema *et al.*, 1997]. Despite the potential influence of grazing on gas exchange in subarctic regions, gas exchange measurements of any type are extremely rare on the expansive YK Delta due to the remoteness of this region [except see Bartlett *et al.*, 1992], especially in the coastal regions of the Delta where goose grazing is most prevalent. We expect that the distinct vegetation communities on the YK Delta that exist due to herbivory

and microtopography will have variable CO₂, CH₄, and N₂O fluxes, and the environmental controls on GHG fluxes in these communities will vary between vegetation types.

The purpose of this work was to quantify the magnitude and the drivers of GHG exchange across the variable vegetation communities imposed by grazing and microtopography to provide insights into how the interactions of grazing and future climate change will influence regional GHG emissions. The primary objectives of this work were (1) to investigate the variation in CO₂, CH₄, and N₂O fluxes across ecological gradients created by the influence of herbivory and microtopography and (2) to explore how physical controls on CO₂, CH₄, and N₂O fluxes, such as soil temperature, moisture, and vegetation characteristics, vary between these vegetation communities.

2. Materials and Methods

2.1. Study Site

This study was conducted near the mouth of the Tutakoke River in the central portion of the coastal YK Delta in western Alaska, (61°15'N, 165°30'W; Figure 1). The YK Delta is a region of more than 75,000 km² of wetlands extending between the Yukon and Kuskokwim Rivers along the coast of the Bering Sea. The local climate is moderated by the Bering Sea, and the mean monthly air temperatures range from −14°C in midwinter to 10°C in midsummer [Jorgenson and Ely, 2001]. The study site is located in the active floodplain portion of the delta where tidally influenced sloughs dissect wet sedge and graminoid meadows. The landscape is underlain by massive deposits of silts and sands and is characterized by low elevations (<2 m) and neutral soil pH [Jorgenson, 2000]. Active sedimentation prevents the accumulation of an organic horizon, and no permafrost is present in the active floodplain zone [Jorgenson, 2000].

2.2. Study Design

In the summer of 2015 we established five transects designed to characterize the variability in GHG exchange between terrestrial ecosystems and the atmosphere across an ecological gradient. Each transect consisted of four vegetation communities: unvegetated pond margin (PM), monospecific grazing lawns of *C. subspathecea* (GL), *C. ramenskii*-dominated meadows (CM), and the slough levee (SL) community that occurs along the elevated depositional levees bordering the sloughs and drainages that dissect the region (Figure 1). Each of the five transects contained one plot location in each vegetation type (PM, GL, CM, and SL), for a total of 20 study plots.

2.3. Greenhouse Gas Measurements

Polyvinyl chloride (PVC) flux chamber collars were inserted at each study plot along the five transects for a total of 20 collars at the site. The collars were 15 cm in diameter and 10 cm tall and were inserted 5.5 cm into the soil. The collars have a 3.2 cm wide flange at the top of the collar as a means of securing the chamber to the collar during measurements. No measurements were made within the first 48 h after collars were installed. All vegetation within the collars was left intact throughout the duration of the study.

We measured GHG exchange at each collar between 8 June and 19 July 2015. All measurements were made within 4 h of solar noon. Carbon dioxide exchange was measured at every collar four times (16 June, 25 June, 28 June, and 11 July). Gas measurements were made by using a translucent PVC chamber 21 cm tall and 13 cm in diameter with a 4.2 cm wide flange at the base that was lined with a rubber gasket. During each measurement, the flange of the chamber was attached to the flange of the collar by using three hand clamps to ensure a gas-tight seal. To measure CO₂ exchange, gas from the chamber was circulated to an infrared gas analyzer (model 820 Licor Inc., Lincoln Nebraska) through 150 cm of 4 mm internal diameter Bev-A-Line tubing at a rate of 1000 mL min^{−1}. An additional fan was used to enhance circulation in the chamber. Flux measurements were performed by using the translucent chamber first to obtain a measurement of net ecosystem exchange (NEE). Once the chamber was removed from the collar following the NEE measurement, and CO₂ concentration and relative humidity in the chamber returned to ambient conditions, a second measurement was performed with the chamber covered in opaque cloth to obtain a measurement of ecosystem respiration (ER). Gross primary productivity (GPP) was calculated as the difference between ER and NEE. Concentrations of CO₂, chamber temperature, and humidity were recorded at 1 Hz for 2 min during dark and light measurements (model CS215 Campbell Scientific, Logan, Utah).

Methane and N₂O fluxes were measured concurrently at each collar as frequently as weather conditions permitted (approximately 2 times per week for a total of 12 measurements per collar) from 8 June through 19 July 2015. Methane and N₂O flux measurements were made by using an opaque PVC chamber of the same dimensions as that for CO₂ exchange, and a Picarro Cavity Ring-Down Spectroscopy Analyzer (Model G2308, Picarro Inc., Santa Clara, California). As with the CO₂ exchange measurements, the flange of the chamber was attached to the flange of the collar by using three hand clamps to ensure a gas-tight seal. Gas was circulated from the chamber to the instrument at a rate of 230 mL min⁻¹ through ~1000 cm of 4 mm internal diameter Bev-A-Line tubing, and an additional fan was used to enhance circulation within the chamber. Concentrations of CH₄ and N₂O were measured every 5 s for 5 min. Chamber temperature (type T thermocouple) and pressure (Model 278, Setra, Boxborough, Massachusetts) were measured every 5 s by using a data logger (model CR800 Campbell Scientific, Logan, Utah).

Flux of CO₂ was calculated by correcting for the dry CO₂ concentration (ppm) and fitting an exponential model $d\text{CO}_2/dt$ for the period of consistent [CO₂] change in the chamber. The change in CO₂ concentration through time was determined between approximately 30 and 120 s after chamber deployment. Initial chamber values and the exponential fit were used to determine CO₂ flux at the time of chamber closure. Flux of CH₄ and N₂O were determined by using the same method as CO₂ except that the change in CH₄ and N₂O concentration through time was determined between approximately 60 and 300 s after chamber deployment, and the slope of the regression was determined according to a nonlinear model [Hutchinson and Mosier, 1981] used by Soil Flux Processor (SFP) software developed by Picarro Inc. Uncertainty in the regression fit of CH₄ and N₂O fluxes was characterized by using a bootstrap analysis that estimates the 1-sigma uncertainty in the flux, using the Picarro SFP program. Global warming potential calculated as CO₂ equivalents was determined by using the 100 year horizon global warming potential of 34 for CH₄ and 298 for N₂O [Myhre *et al.*, 2013]. The average of all flux measurements for each gas through the study season was converted to global warming potential of each vegetation community by multiplying the average flux by the global warming potential of each gas.

2.4. Environmental Conditions

Soil and environmental conditions at the study site were measured through a combination of continuous sensors with data loggers and in situ measurements made at the time of the gas flux measurements. We collected continuous measurements of air temperature, precipitation, and photosynthetically active radiation (PAR) every minute by using a meteorological station established at the study site for the duration of the summer season. Air temperature was measured at a height of 2 m by using a temperature probe (model HMP60 Vaisala, Helsinki, Finland). Precipitation at 1 m was measured by using a tipping bucket precipitation gauge (model TE525 Texas Electronics, Dallas, Texas), and PAR was measured at 2.5 m by using a quantum sensor (model LI190R Licor Inc., Lincoln Nebraska). All data collected from the meteorological station were recorded on a CR1000 data logger. Continuous soil temperature at each collar was measured by using iButtons (Maxim Integrated, San Jose, California) installed at a depth of 10 cm below the soil surface.

In situ measurements of soil temperature, soil water table position, and vegetation height were also recorded at the time of each CH₄ and N₂O gas exchange measurement. Soil temperature was recorded at 10 cm below the soil surface by using a portable thermocouple. One 2.54 cm internal diameter PVC well was installed at every collar, and water table position (the distance from the top of the water table to the soil surface within the well) was measured manually. Vegetation height was manually measured and recorded at five random locations in each collar at the time of each gas flux measurement and averaged to one height measurement.

Soil temperature at the time of each CO₂ exchange measurement was determined from the iButtons in place at each collar. When CO₂ flux measurements did not occur on the same day as CH₄ and N₂O flux measurements, water table position was determined by interpolating between the two closest measurement dates spanning the missing date. For a portion of the season (50%), the wells at the SL plots, which were shorter than the wells present at the other plots, went dry.

Vegetation percent cover was recorded for every collar at one time during the study season (22 June) by using a line-point transect grid. A 1 m × 1 m grid with wire intercepts every 10 cm was overlain on the collar and surrounding area. Percent vegetation cover was determined by identifying the presence or absence of vegetation at every wire intercept. The ratio of unvegetated to vegetated area was used to determine percent

vegetation cover. Biomass within each collar was determined at the termination of the study by harvesting all of the aboveground biomass present within a 5 cm × 5 cm square in the center of each collar.

2.5. Soil Incubations

Soil incubations were conducted to explore the isolated effects of temperature on fluxes of CO₂, CH₄, and N₂O from the four vegetation communities investigated in this study. Three replicate samples of each vegetation community were incubated for a period of 5 days at two different temperatures. Soils were incubated at 8°C and 22°C; these temperatures were designed to represent an early season soil temperature and a scenario of extreme warming.

Soil blocks (20 cm × 20 cm) were collected from the surface to a depth of 10 cm within each of the four vegetation communities. There is very little organic layer present in the soils so the samples were recovered entirely from mineral soil. Soils were carefully cut by hand by using a soil knife and a trowel, frozen in the field, and transported frozen to the laboratory. While frozen, soil samples were cut to 3 cm × 5 cm × 10 cm blocks, weighed, placed into glass jars (~473 mL), and stored in an incubator set to a constant temperature (8°C and 22°C). Soil gas fluxes were measured once every 24 h. Prior to measurement, and between measurements, all samples were left open to the air. At the start of the measurement, the jar containing the soil sample was capped, and the gas from the jar was circulated to the Picarro G2308 instrument and then returned to the jar through valves in the jar lid. The concentration of CO₂, CH₄, and N₂O was measured once every 5 s for a period of 3 min. Following measurement, each sample was watered to replace water lost to evaporation during incubation by weighing the sample, and then adding deionized water to bring the sample weight back to its original value. All samples remained at room temperature for the duration of the measurement, and then were returned to the incubator. Fluxes of CO₂ were calculated according to the following equation:

$$F_c = \frac{VP_0(1 - \frac{w_0}{1000})}{RM_sT_0 + 273.15} \frac{\partial[\text{CO}_2]}{\partial t}$$

where F_c is the CO₂ flux from the soil (μmol CO₂ g⁻¹ s⁻¹), V (cm³) is the volume of the head space in the jar plus the analyzer and tubing, P_0 is the initial pressure (kPa), w_0 is the initial water vapor (mmol mol⁻¹), R is the ideal gas constant (8.314 × 10³ kPa cm³ K⁻¹ mol⁻¹), M_s is the mass of soil (g), T_0 is the initial air temperature (°C), and $\frac{\partial[\text{CO}_2]}{\partial t}$ is the rate of change of CO₂ with time (μmol mol⁻¹ s⁻¹) [Liang *et al.*, 2015]. Fluxes of CH₄ and N₂O were calculated by using the same method, but the dry concentration of CH₄ and N₂O was used for calculating fluxes of those gases, so the water correction term was not needed. Five-day cumulative fluxes were calculated by interpolating between the measurements from each day, and then integrating across the incubation period.

2.6. Statistical Analyses

Analysis of variance (ANOVA) was used to determine differences in the magnitude of gas fluxes from the four vegetation communities. Gas fluxes were considered significantly different where $p < 0.05$. We used the Tukey's honestly significant differences post hoc test to investigate which vegetation community fluxes were significantly different from one another.

We used a linear mixed modeling framework to investigate the environmental controls on gas fluxes across vegetation communities. The predictor variables included in the mixed models were soil temperature, air temperature, water table position, vegetation percent cover, biomass, stem height, PAR, and the categorical predictor of vegetation community type (i.e., PM, GL, CM, and SL). The response variable was gas flux. For each component of greenhouse gas exchange (NEE, GPP, ER, CH₄, and N₂O), we established a suite of 85 models including a null model. Each model suite included all possible combinations of predictor variables and all two-way interactions. The models were restricted a priori to those including three terms or fewer (including interactions), according to the number of observations we were modeling [Bolker *et al.*, 2009]. Air temperature and soil temperature were never included in the same model because of their covariance. Similarly, each model only included one of the following: biomass, vegetation percent cover, or vegetation stem height. The response variable, gas flux, was square-root transformed to produce a normal distribution prior to analysis. All continuous predictor variables were centered and scaled such that the mean value equaled zero and the standard deviation equaled 1. The explanatory variables were checked for collinearity, and all residuals were checked for normality and homogeneity of variance. The transect identification of each

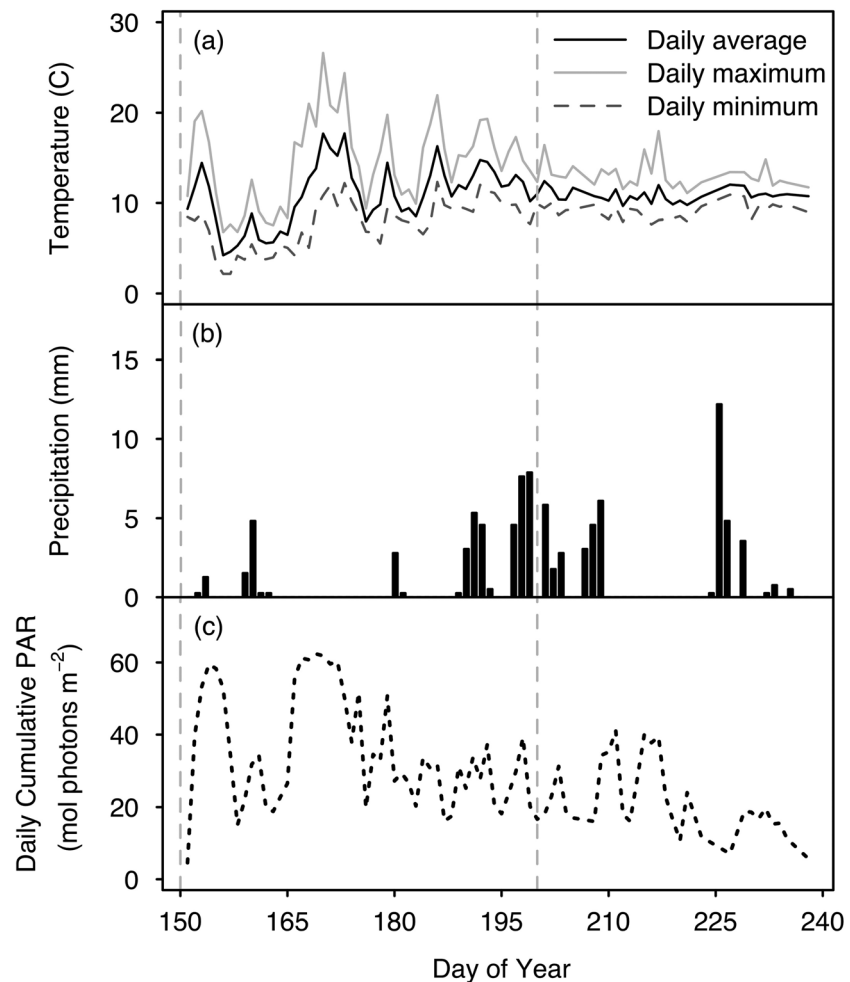


Figure 2. (a) Daily average, minimum, and maximum air temperature at 2 m; (b) daily total precipitation at 1 m; (c) daily cumulative incoming photosynthetically active radiation (PAR) at 2.5 m. The vertical gray dashed lines indicate the length of the study season.

collar was included as a random effect (lmer function in the R package lme4 [Bates *et al.*, 2015 R Core Development Team]) to account for variability between transects. Only the PM, GL, and CM communities were included in this modeling effort; the SL community was excluded because part of the water table position record for these plots was not captured. The PM community was coded as the reference level for the categorical variable of vegetation community. For each model we determined the Akaike information criteria (AIC) [MuMIn package, Bartón, K., 2014, R Core Development Team]; we chose to base our model selection on AIC rather than other information criteria because AIC is preferred for selecting among multiple incompletely specified models [Aho *et al.*, 2014]. We determined goodness-of-fit using a pseudo r^2 calculated according to the recommendation of Nakagawa and Schielzeth [2013].

3. Results

3.1. Seasonal Environmental Conditions

Air temperature in our study area peaked in early June, and then remained relatively steady through the end of August following the termination of the study (Figure 2). Mean air temperature was 11.2°C during the course of the study with the coolest daily minimum temperature of 3.8°C observed on 9 June and the warmest daily maximum temperature of 26.6°C observed on 20 June (Figure 2). Precipitation was greatest in July. The greatest insolation was in late June when maximum day length coincided with clear, warm, and dry weather.

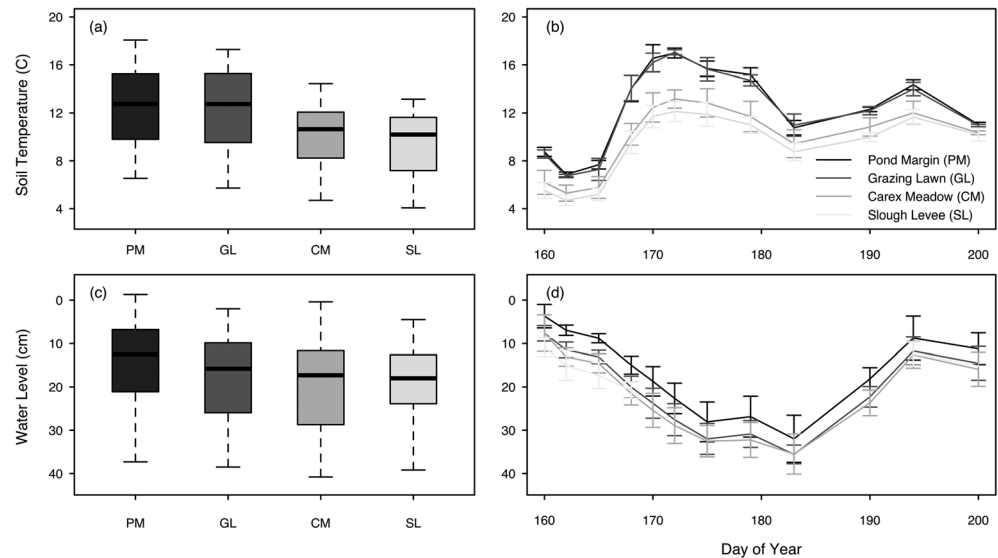


Figure 3. (a) Study average soil temperature by vegetation community; pond margin (PM), grazing lawn (GL), *Carex* meadow (CM), and slough levee (SL). (b) Average soil temperature by vegetation community for each day of gas measurement. (c) Study average water table depth by vegetation community. (d) Average water table depth by vegetation community for each day of measurement. For the box plots (Figures 3a and 3c) the lines represent the median, the boxes represent the interquartile range, and the whiskers represent the range. For the line plots (Figures 3b and 3d) the whiskers represent the standard deviation.

Soil temperature varied among the four vegetation communities. In general, soil temperature followed the same seasonal trend as air temperature with a peak in early June (Figure 3). Seasonal mean soil temperature was greatest in the PM and GL communities, lower in the CM community, and lowest in the SL community (Figure 3). This trend in the relative soil temperature of the four vegetation communities was consistent throughout the season. Water table position generally increased (became deeper) through the first half of the study period, and then decreased at the end of July (Figure 3). Water table position was shallowest in the PM community and greater in the GL, CM, and, SL vegetation communities (Figure 3). Again, the trend in relative water table position among the four vegetation communities was consistent throughout the season.

Live vegetation biomass, vegetation stem height, and vegetation percent cover also varied among the four vegetation communities (Table 1). The PM community had the lowest vegetation biomass, cover, and height. Vegetation biomass and height both increased across the transects with the greatest values present in the SL community; however, the greatest live vegetation cover was present in the CM community, and the SL community had the greatest standing dead vegetation cover (Table 1).

3.2. CO₂, CH₄, and N₂O Flux

ER increased along the transects with the lowest respiration in the PM plots (0.66 ± 0.06 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and the greatest respiration in the SL plots (7.63 ± 50.58 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; Figure 4). GPP also varied along the transects; GPP was largest in the CM community (-7.17 ± 0.33 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), lower in the SL and GL communities (-3.66 ± 0.57 [SE] and -3.39 ± 0.22 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, respectively), and lowest in the PM community (-0.66 ± 0.13 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; Figures 4 and S1 in the supporting information). The largest net source of CO₂ to the atmosphere during the study period was the SL community (3.97 ± 0.58 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; Figure 4). The PM and GL communities both had negligible net fluxes of CO₂ (0.001 ± 0.14 [SE] and 0.16 ± 0.29 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$, respectively), and the CM community was a net sink (-1.63 ± 0.33 [SE] $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; Figure 4).

The study period mean CH₄ flux was positive from all vegetation communities, indicating a source of methane to the atmosphere (Figure 4). The greatest growing season CH₄ flux occurred in the GL community (14.00 ± 6.56 [SE] $\text{nmol CH}_4 \text{m}^{-2} \text{s}^{-1}$), and smallest flux occurred in the SL community (0.41 ± 0.21 [SE] $\text{nmol CH}_4 \text{m}^{-2} \text{s}^{-1}$). The GL regions also had the greatest variability in methane flux, which was a result of

Table 1. Vegetation Characteristics by Community (Average ± Standard Deviation)^a

Ecotype	Biomass (mg cm ⁻²)	Vegetation Height (cm)	Vegetation % Cover Live	Vegetation % Cover Dead
Pond margin (PM)	0.00 ± 0.0	0.51 ± 0.70	7.80 ± 8.83	0.24 ± 0.45
Grazing lawn (GL)	6.65 ± 4.55	1.10 ± 0.20	66.76 ± 11.86	1.22 ± 2.17
Carex meadow (CM)	36.26 ± 7.24	15.55 ± 4.61	96.34 ± 4.39	3.68 ± 4.15
Slough levee (SL)	69.49 ± 26.39	20.73 ± 2.55	80.24 ± 12.46	19.46 ± 12.54

^aBiomass and vegetation height represent vegetation present at the end of the study period. Biomass from the pond margin (PM) is 0, while vegetation cover is greater than 0 because vegetation cover was collected from the area in and surrounding each collar, whereas vegetation biomass was only collected from a small sample area in the center of the collar.

both seasonal and spatial variability (Figure S1). N₂O fluxes were negligible from all communities through the entire season (Figures 4 and S1).

Total study period average GHG forcing expressed as CO₂ equivalents indicated that SL community was the greatest GHG source (3.98 μmol CO₂ eq m⁻² s⁻¹), the CM community was the greatest GHG sink (-1.63 μmol CO₂ eq m⁻² s⁻¹), and PM and GL communities were both small GHG sources (0.08 and 0.51 μmol CO₂ eq m⁻² s⁻¹, respectively; Figure 5). The GL community was the only vegetated community where CH₄ made up the largest component of total GHG forcing (Figure 5); in contrast, CO₂ was the dominant component of total GHG forcing in the ungrazed CM and SL vegetation types.

3.3. Generalized Linear Mixed Models of Gas Exchange

Greenhouse gas exchange at this study site was driven by combinations of both soil conditions and vegetation characteristics including vegetation community (PM, GL, CM, and SL), which was present in the best performing model of every component of greenhouse gas exchange except ER. The best performing models of CO₂ exchange (ER, GPP, and NEE) all included both a vegetation variable (biomass or percent cover) and a soil environment variable (temperature or water table position). Water table position and percent vegetation cover were the primary controls on ER across all vegetation communities, with vegetation percent cover as a more important predictor than water table position (pseudo r² = 0.77; Table 2). NEE and GPP both included vegetation community and soil temperature in the best performing model, with GPP also including vegetation biomass (pseudo r² = 0.85), whereas NEE included percent cover (pseudo r² = 0.41; Table 2).

Both environmental conditions and vegetation were important drivers of CH₄ emissions; CH₄ flux was governed by air temperature, vegetation community type, and the interaction of these two variables (pseudo

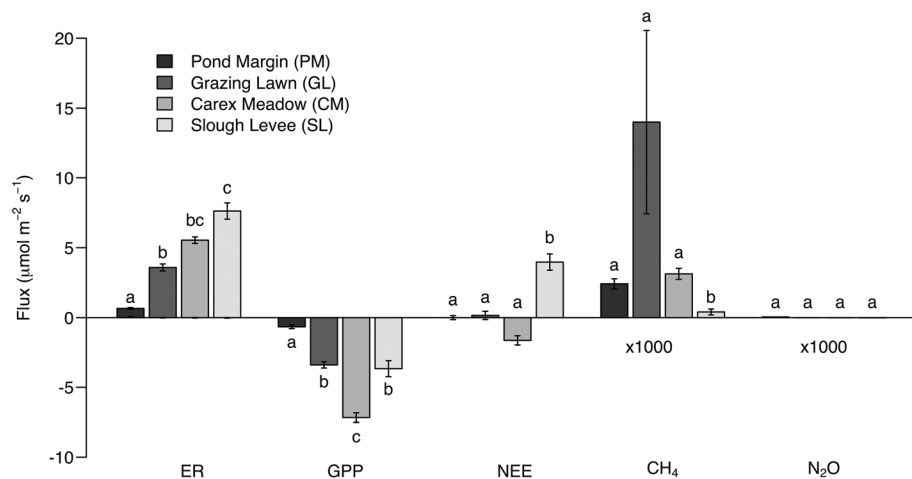


Figure 4. Study average ecosystem respiration (ER), gross primary productivity (GPP), net ecosystem exchange (NEE), CH₄, and N₂O flux by vegetation community. Letters indicate significantly separate groups. Error bars show standard error of the mean.

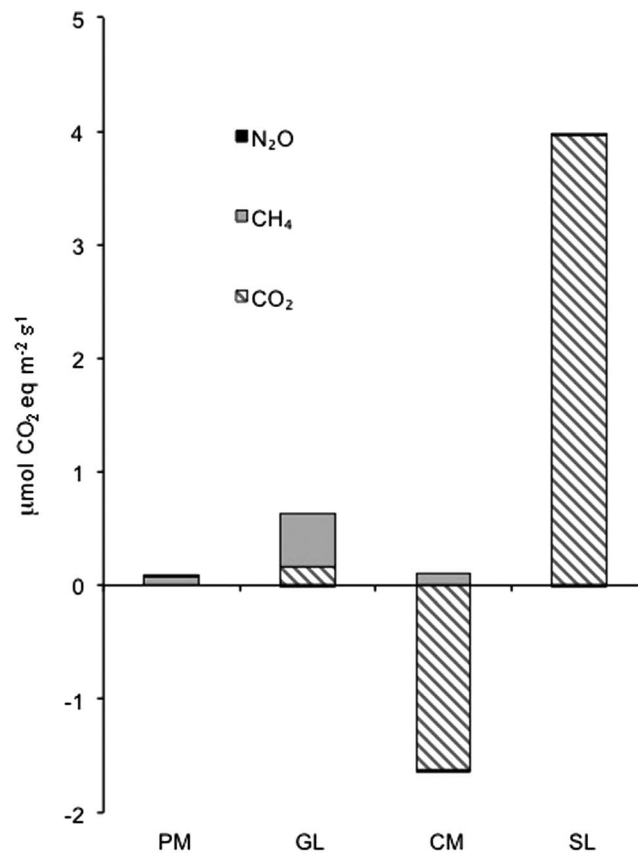


Figure 5. Study average exchange of all greenhouse gases expressed in CO₂ equivalents across the four vegetation communities: pond margin (PM), grazing lawn (GL), *Carex* meadow (CM), and slough levee (SL). In some bars N₂O fluxes are too small to be visible.

Figure 6). The CM community also had the greatest net increase in flux between the cool and warm temperature.

The incubation results also indicated an interaction between temperature and vegetation community in CH₄ emissions. Warmer soil conditions increased CH₄ emissions in the PM, GL, and CM communities, but the GL community showed both the largest percent increase in emissions at warmer temperature, and largest net increase in emissions from 0.38 ± 0.25 [SD] nmol CH₄ g⁻¹ d⁻¹ at the cooler temperature to 3.80 ± 0.63 [SD] nmol CH₄ g⁻¹ d⁻¹ at the warmer temperature. CH₄ emissions were near zero in the SL community under both cool and warm conditions. N₂O emissions remained negligible in all ecosystems, even under conditions of warming.

4. Discussion

We found that the magnitude and controls on GHG emissions varied among four vegetation communities defined by differences in vegetation, herbivory, and microtopography. The variation we observed in GHG gas fluxes among vegetation communities cannot be explained by soil and vegetation characteristics alone, but rather was more completely explained when grazing, as determined by the difference between grazed and ungrazed communities, is included. We also find in the grazed regions that the largest proportion of total GHG forcing is from CH₄ emissions, in contrast to the ungrazed regions (CM and SL), where total GHG forcing is dominated by emissions of CO₂. Both field and laboratory analyses identified an interaction of temperature and vegetation community as a driver of CH₄ flux, indicating that future warming may have the largest effect on GHG emissions in regions affected by grazing. Taken together our results suggest that future changes in gas exchange in this region could occur as a direct response to changing climate, particularly changing

$r^2 = 0.39$). The interaction between temperature and vegetation community indicates that the effect of temperature on CH₄ flux varies among vegetation communities. The best performing model of N₂O flux included soil temperature, vegetation biomass, and vegetation community (pseudo $r^2 = 0.11$).

3.4. Incubations

Our laboratory incubation experiments identified interactions between temperature and vegetation community type as a control on GHG fluxes. ER generally increased with increasing soil temperature (Figure 6) in all vegetation communities, but the greatest percent increase in ER between the cool and warm temperatures was observed in the PM and GL communities (220% and 250% increase, respectively), while greatest net CO₂ emissions were observed from the CM community at both the cooler and warmer temperature (9.60 ± 2.02 [SD] and 16.78 ± 1.14 μmol CO₂ g⁻¹ d⁻¹;

Table 2. Parameter Estimates for the Fixed Effects in the Linear Mixed Model of Gas Fluxes^a

<i>Ecosystem Respiration; r² = 0.77</i>			
Parameter	Estimate	SE	t
Intercept	-0.035	0.102	-0.340
Vegetation percent cover	0.853	0.064	13.277
Water table position	0.120	0.064	1.868
<i>Gross Primary Productivity; r² = 0.85</i>			
Parameter	Estimate	SE	t
Intercept	-1.161	0.215	-5.407
Soil temperature	0.419	0.065	6.402
Vegetation biomass	0.315	0.182	1.733
Vegetation community: Grazing lawn	1.217	0.141	8.578
Vegetation community: <i>Carex</i> meadow	2.054	0.427	4.808
<i>Net Ecosystem Exchange; r² = 0.41</i>			
Parameter	Estimate	SE	t
Intercept	2.583	0.724	3.568
Soil temperature	-0.704	0.141	-4.978
Vegetation percent cover	-2.311	0.815	-2.835
Vegetation community: Grazing Lawn	-2.311	0.815	-2.835
Vegetation community: <i>Carex</i> Meadow	-5.004	1.236	-4.047
<i>Methane; r² = 0.39</i>			
Parameter	Estimate	SE	t
Intercept	-0.358	0.217	-1.649
Air temperature	0.493	0.102	4.830
Vegetation community: Grazing lawn	0.814	0.146	5.588
Vegetation community: <i>Carex</i> meadow	0.237	0.146	1.620
Air T* vegetation community: Grazing lawn	-0.436	0.144	-3.027
Air T* vegetation community: <i>Carex</i> meadow	-0.346	0.148	-2.342
<i>Nitrous Oxide; r² = 0.11</i>			
Parameter	Estimate	SE	t
Intercept	-0.537	0.373	-1.438
Soil temperature	0.157	0.101	1.571
Vegetation biomass	-0.784	0.386	-2.030
Vegetation community: Grazing lawn	-0.161	0.276	-0.584
Vegetation community: <i>Carex</i> meadow	1.725	0.888	1.944

^aFor all species these were the best performing models as evaluated by AIC.

exchanges between grazed and ungrazed vegetation communities; however, the effect of grazing was elucidated when the drivers of CO₂ exchange were examined.

The modeling analyses identified the combined effects of soil environment, vegetation characteristics, and vegetation community type (PM, GL, CM, and SL) as the most important controls on CO₂ exchange. Vegetation community type was present in the best performing model of both GPP and NEE, along with soil temperature and vegetation characteristics (biomass for GPP and vegetation percent cover for NEE; Table 2). The presence of vegetation community type in the model indicates that there are important drivers of gas exchange, likely related to grazing status and microtopographic position, which are not represented by the soil and vegetation characteristics we observe here. The GL community in particular may experience some effects of grazing that are not explicitly addressed in our analyses such as additional nutrient inputs of labile organic material from goose defecation [Hik and Jefferies, 1990; Welker et al., 2004] and trampling by geese that can incorporate this material into the soil [Zacheis et al., 2002].

The best performing models of ER included vegetation percent cover and water table position (Table 2). ER was greater in the presence of more vegetation and was reduced by shallow water table depths (Table 2). In addition to these modeling results from the field data, the laboratory incubation experiments also identified an interaction between temperature and vegetation community such that the positive effect of temperature on ER was greatest in the GL community. This interaction was absent in the field analyses where moisture conditions were variable and potentially limiting to ER, but was present in the laboratory experiments where

temperature, or as an indirect response to changes in the relative area of different vegetation communities that alter the extent of the vegetation type most responsive to climate change.

4.1. Carbon Dioxide Exchange

All the vegetation communities investigated here have rates of carbon exchange comparable to other high-latitude wetland sites [Wickland et al., 2006; Chivers et al., 2009; Sturtevant and Oechel, 2013], but the net carbon exchange varies between communities with some functioning as sources of carbon, and some as sinks. The study average flux from the SL was positive (CO₂ source), the study average flux from the CM community was negative (CO₂ sink), and the PM and GL communities were neutral (Figure 4). GPP differed among vegetation communities with the ungrazed CM communities exhibiting higher GPP than GL communities, likely due to removal of standing biomass in the grazed GL communities [Welker et al., 2004; Sjögersten et al., 2008, 2011]. GPP was the only component of CO₂ exchange to show a statistical difference in the magnitude of CO₂

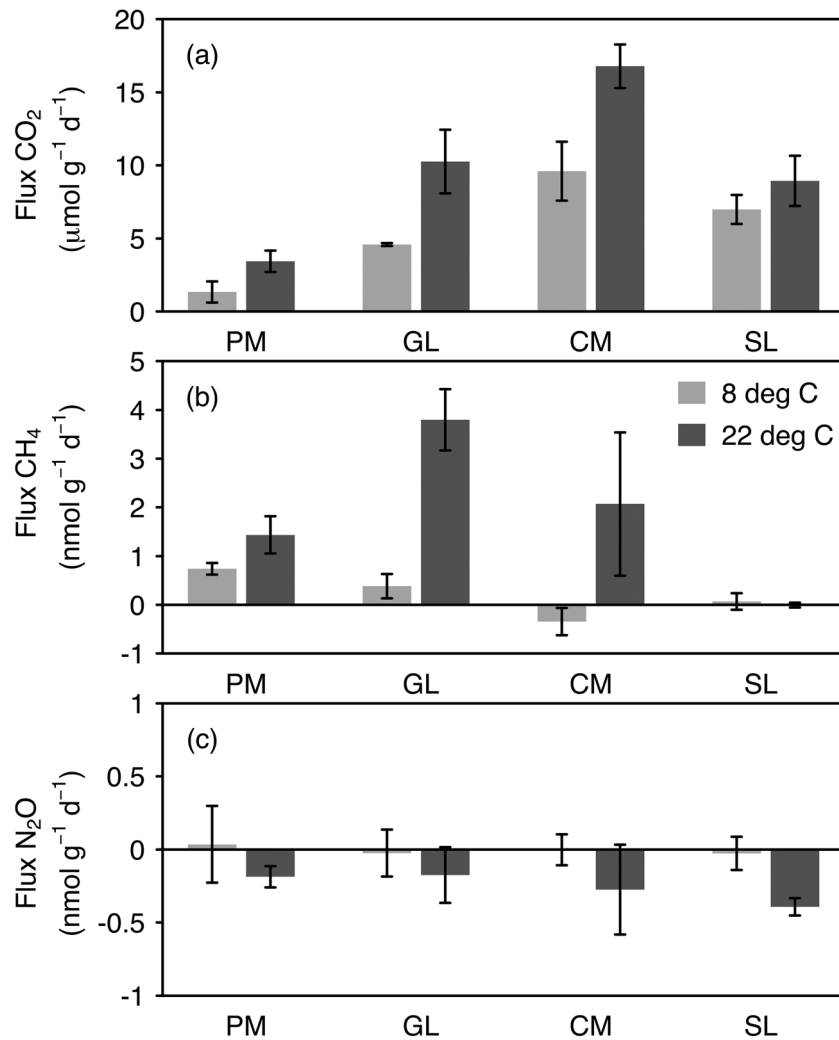


Figure 6. (a) Soil CO₂ flux response to two temperature treatments (8°C and 22°C) from all four vegetation communities: pond margin (PM), grazing lawn (GL), *Carex* meadow (CM), and slough levee (SL). (b) Soil CH₄ flux response to two temperature treatments (8°C and 22°C) for all vegetation communities. (c) Soil N₂O flux response to two temperature treatments (8°C and 22°C) for all four vegetation communities.

soil moisture conditions were held constant. Overall ER is controlled by vegetation biomass, which was driven by vegetation community, with water table position and soil temperature as secondary controls in different conditions.

4.2. Methane Emissions

Methane emissions at this subarctic site were comparable or slightly lower than methane emissions observed from other Arctic and subarctic wetlands [Bartlett *et al.*, 1992; Bartlett and Harriss, 1993; Schimel, 1995; Kutzbach *et al.*, 2004; Sabrekov *et al.*, 2014; Turetsky *et al.*, 2014]. Methane emissions across vegetation communities were not directly correlated with many individual soil environmental factors, but rather were governed by an interaction of temperature and vegetation community type. The best performing model of CH₄ emissions contained air temperature, vegetation community type, and the interaction between the two. Our laboratory incubation experiments also identified this same interaction, where we found that CH₄ emissions increased at warmer temperature in all of the vegetation communities, but the increase was much greater in the grazing lawn community (Figure 6). This interaction is likely a result of the complex drivers of CH₄ production (methanogenesis) and consumption (methanotrophy) within the soil column, which determine net CH₄ emissions to the atmosphere.

Methanogenesis is an anaerobic process that primarily occurs in saturated soils or in anaerobic microsites, whereas methanotrophy occurs within oxic surface soils, and can be responsible for consuming much of the CH₄ produced at depth. The presence of wetland vegetation can affect CH₄ flux by facilitating the transport of CH₄ through aerenchymous tissue (air channels present in the plant stem) that allows CH₄ to reach the atmosphere without coming in contact with oxidizing soil conditions [Neue *et al.*, 1997; Kutzbach *et al.*, 2004]. Wetland plants can also facilitate methanogenesis by serving as a source of labile carbon through the production of high-quality root exudates [Shannon *et al.*, 1996; Bellisario *et al.*, 1999; Jobsson *et al.*, 1999]. Herbivory in wetland environments can potentially increase methane flux to the atmosphere through plant aerenchymous tissue by reducing diffusive resistance (by shortening the plant stem) and thus increasing diffusive flux to the atmosphere [Dingemans *et al.*, 2011]. Additionally, grazing can also limit the oxygen returning to the soil through the plant stem after clipping [Ding *et al.*, 2005], and thereby reducing the potential for CH₄ oxidation within the soil and increasing flux to the atmosphere [Cheng *et al.*, 2007].

Changes to diffusive resistance and oxygen transport due to grazing may help explain the interaction we observe between temperature and vegetation community type. At warmer temperatures, both methanogenesis and methanotrophy will increase, but in grazed vegetation where CH₄ can travel most easily from the soil to the atmosphere without coming in contact with oxidizing soil environment, increased methanogenesis will have the larger effect and the net result would be an increase in CH₄ emissions to the atmosphere. However, the fact that we observe this interaction in both the field data and the incubation data suggests that there could potentially be another driver. A similar interaction between goose grazing and temperature is observed for CO₂ flux in Sjögersten *et al.* [2008] and could be the result of a change in the microbial community due to nutrient input from fecal matter or a result of compensatory production of plant biomass as a result of grazing [Hik and Jefferies, 1990]. Whether the interaction between temperature and grazing is a result more efficient physical transport or changes in microbial community, our results suggest that future climate changes that result in higher temperature would increase CH₄ flux most from the GL landscapes. Furthermore, changes in the area of grazing lawn, produced as a function of goose population dynamics, would affect regional CH₄ emissions by changing the extent of the area that is most responsive to future temperature change.

4.3. Nitrous Oxide Emissions

Nitrous oxide emissions were negligible through the entire season, even from the GL plots where geese contribute high rates of organic N through fecal input. Nitrous oxide emissions at the soil surface are the net result of production and consumption within the soil. There are two primary pathways of N₂O production in high-latitude systems; nitrification, the process of converting NH₄ to NO₂⁻ and NO₃⁻, or denitrification, the reduction of NO₂⁻ or NO₃⁻ to N₂ via the intermediate stages of NO and N₂O [Braker and Conrad, 2011; Stewart *et al.*, 2014]. Cold temperatures can limit nitrification and N mineralization which produce inorganic N [Gersper *et al.*, 1980; Nadelhoffer *et al.*, 1991], but we can rule out temperature as the dominant constraint on N cycling at our site because we found that N₂O emissions were still negligible under warming conditions produced during the laboratory incubations. Similarly, the lack of emissions from the incubation experiments also suggest that N₂O emissions are likely not limited by the complete reduction of N₂O to N₂ during denitrification, which can occur in low-oxygen conditions when N₂O itself is used as an electron acceptor and reduced to N₂ [Veldkamp *et al.*, 1998; Chapuis-lardy *et al.*, 2007]. Low rates of N₂O emissions could be a result of low availability of inorganic N, which can occur in arctic soils even when the microbial communities responsible for denitrification are present [Christensen *et al.*, 1999; Buckeridge *et al.*, 2010]. Finally, inorganic N may be limited due to high demand by plant and microbial biomass. Previous research at our study site indicates that soil microbial biomass is a strong nutrient sink in this ecosystem, and further that direct uptake of amino acids by *C. ramenskii* may also be an important component of N cycling [Ruess *et al.*, 1997]. If this is the case, then inorganic N may be limiting in the soil environment because plants and soil microbes quickly take up available N.

4.4. Uncertainties and Future Work

This study presents compelling results regarding the interacting factors governing GHG fluxes in subarctic regions affected by migratory grazers and also highlights opportunities for future work. The results of our study suggest that the drivers of NEE, GPP, and CH₄ flux are best explained when vegetation community,

which is driven in part by grazing, is explicitly included. Furthermore, we identify an interaction between vegetation community and temperature that indicates that CH₄ emissions in grazed areas will be the most responsive to future temperature change.

Our study also has some limitations. First, due to challenges of measuring GHG fluxes in this remote location, our sample size is fairly small. The small sample size may be one reason our study did not identify statistical differences in GHG emissions between grazed and ungrazed *Carex* vegetation (except for GPP). Our analysis of the drivers of GHG exchange indicates that grazing is important, so it is possible that differences in GHG flux would be apparent with a larger sample size. Second, the effects of herbivory are confounded by the influence of microtopography in our study region, because microtopography is largely responsible for determining the regions most heavily grazed by geese. Because our observational study was designed to measure the variability in GHG emissions in response to ecologically relevant gradients of herbivory, it allows a somewhat limited interpretation of the influence of geese herbivory relative to the effects of microtopography on environmental factors that control GHG flux. Future work could build on the processes and interactions outlined in this paper by quantifying the relative importance of herbivory as a driver of GHG flux relative to microtopography and other environmental factors and by furthering our understanding of the mechanisms by which herbivory influences CO₂, CH₄, and N₂O fluxes in subarctic regions.

4.5. Changes in Response to Future Climate

Gas exchange between terrestrial ecosystems and the atmosphere in the YK Delta is driven by interacting factors of environmental conditions and vegetation characteristics that may be affected by future climate and global change. This region has experienced the largest increases in summer season temperatures of the entire circumpolar region [Bhatt *et al.*, 2010], and along with continued decreases in the length of the sea ice season [Serreze *et al.*, 2007; Stroeve *et al.*, 2012], and associated increases in coastal erosion [Jones *et al.*, 2009], these trends may result in further change to arctic and subarctic coastal regions. In vegetation communities with active sedimentation, such as the SL community, the elevation will likely remain in equilibrium with sea level, and therefore, ecosystem composition and productivity may remain constant [Jorgenson and Ely, 2001]. But in other regions of the YK Delta, increased deposition on slough levees may expand the area of the basins and ponds behind the levees [Jorgenson and Ely, 2001]. Such changes would alter the relative area of pond margins, grazing lawns, and *Carex* meadows, and therefore regional gas fluxes.

The relative area of different vegetation communities in this region may also be determined by changes in the number of geese that return to this colony in the summer to breed. Person *et al.* [2003] observed that area of grazing lawn at this site was proportional to the number of breeding pairs of one goose species that returned to the colony between 1987 and 2000. Further, they found that increase in grazing lawn area came at the expense of the *Carex* meadows. These authors suggest a positive feedback between the number of geese broods and the amount of grazing lawn: more grazing produces more grazing lawn, which then increases the ability of the system to support more geese broods. Based on the greenhouse gas fluxes measured in our study, we estimate that change in areal extent of vegetation communities that occurred following an increase in the number of geese broods from ~1000 to ~5000 in the 1990s [Person *et al.*, 2003], may have increased the global warming potential of the net GHG emissions from this site by ~150%. Changes in goose population and in areas used by geese are occurring elsewhere in coastal Alaska as a result of climate and other environmental changes [Flint *et al.*, 2008, 2014; Tape *et al.*, 2013], and our results suggest that such changes could have substantial implications for GHG fluxes from these regions.

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