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The Effects of Temperature, Flooding, and Goose Feces Addition on Greenhouse Gas Emissions and Ammonification in Four High-Latitude Soils from Western Alaska

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THE EFFECTS OF TEMPERATURE, FLOODING, AND GOOSE FECES ADDITION ON GREENHOUSE GAS EMISSIONS AND AMMONIFICATION IN FOUR HIGH-LATITUDE SOILS FROM WESTERN ALASKA

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THESIS ACCEPTANCE PAGE

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This thesis is approved as a creditable and independent investigation by a candidate for the master's degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ABSTRACT

THE EFFECTS OF TEMPERATURE, FLOODING, AND GOOSE FECES ADDITION ON GREENHOUSE GAS EMISSIONS AND AMMONIFICATION IN FOUR HIGH-LATITUDE SOILS FROM WESTERN ALASKA

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The large carbon (C) stock of wetlands is vulnerable to climate change, especially in high latitudes that are warming at a disproportional rate. Likewise, low-elevation Arctic coastal areas will flood more frequently under climate change and sea-level rise, which may alter goose herbivory and fecal deposition patterns if geese move inland. While temperature, flooding, and feces impact soil C emissions, their interactive effects have been rarely studied. Here, I explore the impact of these interactions on CO_2 and CH_4 emissions and nitrogen (N) mineralization (ammonification) in soils collected from four plant communities in the Yukon-Kuskokwim (Y-K) Delta, a high latitude coastal wetland in western Alaska. Plant communities follow an elevational gradient and vary in their flooding and grazing susceptibility. These communities include an intensely grazed and susceptible to flooding grazing lawn ("Grazing Lawn"), two wetlands that experience moderate grazing and frequent ("Lowland Wetland") and less frequent ("Upland Wetland") flooding, and a rarely grazed and flooded upland tundra community ("Tundra") located at the highest elevation. Soils were incubated for 16 weeks at 8°C or 18°C in microcosms and subjected to flooding and feces addition treatments with no-flood and no-feces controls. I quantified C emissions weekly and ammonification over the course of the experiment. I found that warming, which favors maintenance respiration

over growth, increased ammonification, reflecting increased microbial demand for C relative to N in the Lowland Wetland. While warming always increased CO_2 and CH_4 emissions, interactions with flooding complicated warming impacts on C emissions in the Grazing Lawn and Tundra. In the Grazing Lawn, flooding increased CH_4 emissions at 8°C and 18 °C, but in the Tundra, flooding suppressed CH_4 emissions at 18°C. Flooding alone reduced CO_2 emissions in the Upland Wetland. Feces addition increased CO_2 emissions in all communities, but feces impacts on CH_4 emissions and ammonification were minimal. When feces and flooding occurred together in the Lowland Wetland, CH_4 emissions decreased compared to when feces was added without concomitant flood. Feces decreased the immobilization of ammonium ($N\text{-}NH_4^+$) and therefore microbial N demand in the Tundra only. My results suggest that flooding could partially offset C emissions from warming in less frequently flooded, higher elevation communities, but this offset could be negligible if flooding and warming drastically increase C emissions in more flooded lowland areas.

INTRODUCTION

While wetlands play an important role in moderating climate change by sequestrating and storing large amounts of carbon (C), the bulk of which is in their soils, wetland ecosystems are particularly vulnerable to climate change and resulting alterations to C processes (reviewed by: Moomaw et al. 2018). High latitude wetlands may be especially vulnerable to warming under climate change, as high latitude areas are warming three to four times faster than the rest of the globe (Rantanen et al. 2022). In addition, rapid loss of ice and sea-level rise and resulting increases in storm-surges (Vermaire et al. 2013) make low-lying Arctic ecosystems susceptible to more intense and frequent coastal flooding and erosion under climate change (Jones et al. 2009; Arp et al. 2010). Geese are important herbivores in coastal Arctic systems (Kerbes et al. 1990; Gauthier et al. 2004). Climate-induced changes to forage and habitat are likely contributors to changes in geese abundance and distribution (Flint et al. 2008; Flint et al. 2014; Tape et al. 2013). Altered goose abundance and distribution and changes in patterns of grazing and fecal deposition can further alter nutrient dynamics and biogeochemical processes in high latitude wetlands. Therefore, it is important to identify how C cycling in high latitude coastal wetlands will be impacted by warming, increased flooding, and altered grazing patterns under climate change.

Warming can have substantial impacts on rates of decomposition and emissions of greenhouse gases such as carbon dioxide (CO_2) and methane (CH_4) because decomposition is a temperature sensitive microbial process (Davidson and Janssens 2006). Frozen soils constrain decomposition in high latitude ecosystems (Davidson and Janssens 2006), which allows substantial amounts of soil organic carbon (SOC) to

accumulate, much of which is in permafrost (Hugelius et al. 2014). However, the Arctic will warm on average 2° C to 9° C by 2100 (Anisimov et al. 2007). Elevated temperatures accelerate microbial decomposition, and thaw permafrost, promoting microbial decomposition of this permafrost C stock (Schuur et al. 2008) and other soil C. Therefore, projected increases in temperatures will likely increase C emissions from soils (Lloyd and Taylor 1994; Inglett et al. 2012; Williams and Crawford 1984). However, offsets from increased productivity under warming conditions will further complicate C dynamics and emissions. A warming climate may result in enhanced productivity, vegetation changes, and a longer growing season, which could increase plant uptake of C (reviewed by: Treat et al. 2024). At the same time, warming and vegetation changes can also alter the soil microclimate in complex ways, which could increase C emissions (reviewed by: Treat et al. 2024). Studies have demonstrated that the permafrost region is likely a wetland CH_4 source and a small terrestrial CO_2 sink, with sink strength decreasing towards higher latitudes (Treat et al. 2024). Yet, there is high spatial and temporal variability in the C balance of this region, and variability among studies (Treat et al. 2024). This demonstrates a continuing need to quantify C emissions from high latitude soils under warming.

Warming will likely also increase N mineralization (Rustad et al. 2001). Decomposition results in microbes breaking down organic matter (OM), which contains both C and N, and using these nutrients for metabolic processes and growth. Microbial mineralization of organic nutrients to inorganic compounds during this process depends on the nutrient content of OM, as well as the microbial demand of C compared to the nutrient in question (Mooshammer et al. 2014). In the case of N mineralization, when

C:N ratios of litter are lower, microbes will uptake C for growth, maximizing their C use efficiency as C is limiting (reviewed by: Mooshammer et al. 2014). They will have to reduce their N efficiency, excreting N that exceeds demand (reviewed by: Mooshammer et al. 2014). This leads to the mineralization of N, where it can accumulate in the soil. Contrarily, when C:N ratios of litter are high, microbial C use efficiency is low and microbes respire large amounts of C per unit of N used for growth (reviewed by: Mooshammer et al. 2014). This will lead to the immobilization of N as N is limiting to growth. Increases in temperature promotes maintenance respiration more than microbial growth (reviewed by: Chapin et al. 2011). As a result, C limitation increases under elevated temperatures, leading to the excretion of ammonium (NH_4^+) and N mineralization (reviewed by: Chapin et al. 2011). Therefore, quantifying N mineralization can provide insight on microbial nutrient demands during the mineralization of OM compounds during decomposition.

Sea level rise, which could be ~65 cm by 2100 globally (Nerem et al. 2018), and increased flooding will likely have complex effects on C emissions from soils and N mineralization. Flooding may promote N mineralization by increasing pH to a level that favors microbial activity (Ono 1991), but can also slow down NH_4^+ production, as the breakdown of soil organic matter may occur slower in anaerobic conditions (Reddy and Patrick 1984). Anaerobic conditions in flooded soils result in methanogenesis, or CH_4 production, the typical end product of anerobic decomposition (Ponnamperuma 1972). However, methanogenesis can also influence soil CO_2 efflux depending on the pathway of methanogenesis. CH_4 is produced primarily through two pathways in anaerobic conditions. These pathways include acetoclastic methanogenesis, which produces CO_2

and CH_4, and/or hydrogenotrophic methanogenesis, that uses CO_2 and H_2 to produce CH_4 (Conrad 2020a). While low temperatures may favor acetoclastic methanogenesis (Conrad 2020a), Arctic and permafrost soils contain methanogens using both pathways (Ganzert et al. 2007). Flooding effects on CO_2 and CH_4 can also be complicated by the presence of other terminal electron acceptors, such as NO_3^- (nitrate) in wetland soils or SO_4^{2-} (sulfate) in floodwater. Exposing freshwater soils to increased salinity suppresses CH_4 production through the introduction of sulfate, a more energetically favored electron acceptor, that can promote sulfate reduction by sulfate reducing bacteria that outcompete methanogens (Weston et al. 2006; Chambers et al. 2013). Therefore, soil and floodwater conditions, including salinity, need to be considered when examining flooding impacts on soil C emissions.

Fecal deposition by herbivores is an important grazing component that impacts C cycling, so alterations to the distribution of geese and where they deposit feces could result in substantial changes in nutrient dynamics across high latitude landscapes. Feces and urine from vertebrates contain labile carbon, nitrogen, and phosphorus, much of which is soluble, that can alleviate some nutrient limitations to microbial growth (Ruess and McNaughton 1987). Feces and urine are also directly incorporated into the soil, where they are more readily mineralized than plant tissues (McNaughton 1985). Fertilization from herbivory can impact N mineralization (Ruess and McNaughton 1987; Seagle et al. 1992), which is influenced by quality of feces input (Seagle et al. 1992) and microbial nutrient demand. Nutrient additions can stimulate C emissions from ecosystems through alleviation of microbial nutrient limitations and changes to microbial community structure (Lund et al. 2009; Cleveland et al. 2007). This suggests that

herbivore feces can play a similar role in influencing C emissions. In high latitude ecosystems, goose feces has variable impacts on C emissions. In laboratory-incubated soils from grazing lawns and ungrazed meadows, feces addition stimulates CO_2 emissions (Foley et al. 2022; Saunders et al. 2023). In the field with ambient fecal density, feces removal, and double ambient fecal density (fecal addition) plots, fecal addition does not increase CO_2 emissions (Beard et al. 2023). Feces removal, however, increases CO_2 emissions due to less productivity and root biomass in removal plots (Beard et al. 2023). The effects of goose feces on CH_4 emissions have also been mixed, with feces addition stimulating CH_4 emissions in the laboratory (Foley et al. 2022) but there being no observed differences in CH_4 emissions between ambient fecal density, feces removal, and feces addition plots in the field (Beard et al. 2023). Fecal addition impacts therefore warrant further investigation.

While warming, flooding, and feces addition have impacts on soil C cycling individually, it is much more likely that these climate change variables will interact to influence soil C emissions in high latitude ecosystems under a changing climate. For example, given that warming and the addition of labile nutrients from feces can both stimulate C emissions, it is possible that warming may amplify the effect of feces on C emissions from soils. Studies have demonstrated increases in CO_2 and CH_4 emissions from feces addition and warming individually in grazing lawn and ungrazed meadow communities, with three-way interactions between temperature, feces addition, and grazing (Foley et al. 2022). However, flooding may alleviate some of these emissions. In high latitude ecosystems, flooding can wash away feces (Choi et al. 2020; Beard et al. 2023), which could limit the effect that nutrient additions from herbivores have on C

emissions by leaching and removing nutrients. Despite the potential of these variables to influence one another, interactions between warming, flooding, and feces addition remain largely unexplored.

The Yukon-Kuskokwim (Y-K) Delta is a high-latitude coastal wetland that will likely experience accelerated warming, changes in flooding frequency and intensity, and potentially altered fecal addition patterns under climate change. This makes it a key area to study interactions between these variables. The majority of the Y-K Delta is within 3 m of sea level, with only a ca. 2 m rise in elevation within 10 km of the coast, making the region susceptible to tidal flooding and sedimentation, which shapes communities along an elevational gradient (Jorgenson 2000; Jorgenson and Ely 2001; Jorgenson et al. 2018). Low elevation also makes the area susceptible to storm surges that can reach 27-32 km inland (Terenzi et al. 2014). Increased storm frequency and sea-level rise will likely flood lowlands for longer and flood upland areas more frequently (Terenzi et al. 2014). In addition, a variety of migratory goose species, including cackling Canada geese (*Branta hutchinsii minima*), greater white-fronted geese (*Anser albifrons*), emperor geese (*Anser canagicus*), and especially pacific black brant (*Branta bernicla nigricans*) graze in the Y-K Delta (Ruess et al. 1997). Grazing occurs most often in salt-tolerant *Carex ramenskii* meadows and monospecific *Carex subspathacea* grazing lawns located close to the coast on low elevation coastal mudflats or inland on pond and slough margins (Ruess et al. 1997). Geese move inland to feed on berries in upland communities later during the brood-rearing and growing season (Babcock and Ely 1994; Sedinger and Raveling 1984). However, climate change and increased flooding of the lowlands and salt-tolerant

transitions of upland communities may push geese and feces deposition inland and upland, causing more frequent grazing in these areas.

In this lab study, I performed a fully factorial manipulation of temperature, flooding, and feces addition in microcosms consisting of soil from four Y-K Delta plant communities. The goal of this study was to determine the interactive impacts these variables have on CO_2 and CH_4 emissions and ammonification in each community, and to understand which variables are important in each community. Communities differed in 1) position on the landscape and therefore susceptibility to flooding and grazing and 2) background nutrient content. Performing a lab study allowed me to keep temperature and quantities of flood water and feces added across microcosms during treatments consistent. Others have demonstrated the usefulness of using soil-only microcosms in understanding the underlying mechanisms driving C emissions in the Y-K Delta (Foley et al. 2022; Saunders et al. 2023). I expected that (H1) individually, warming and feces addition would increase CH_4 and CO_2 emissions in all communities by speeding up decomposition and providing nutrients to microbes. I anticipated that feces would have large impacts in communities with lower background nutrients. I also expected temperature and feces addition to increase ammonification, through the promotion of maintenance respiration and alleviation of microbial N demand. Flooding, I expected, would increase CH_4 production, especially in more frequently flooded lower elevation communities that are more acclimated to salt exposure and anoxia than more upland communities. However, flooding would decrease ammonification because methanogenesis is a slower decomposition pathway than those requiring oxygen. Interactively, I hypothesized that (H2) warming would amplify the effects of feces

deposition, synergistically increasing CH_4 and CO_2 emissions, but flooding would mitigate feces addition impacts by leaching nutrients.

MATERIALS AND METHODS

Study Site

Soil and feces used in this experiment were collected near the Keoklevic and Kashunik Rivers at Old Chevak, Alaska (61.42797°N, -165.45162°W, Figure 1) in the Y-K Delta. The Bering Sea influences climate in the Y-K Delta, with 30-year mean (1991–2020) winter daily temperatures of −12.2 °C and mean summer daily temperatures of 12.5 °C (Palecki et al. 2021 as cited in: Saunders et al. 2023). Old Chevak is approximately 16 km inland from the Bering Sea (Holmes 1971), and tidal influence extends 39-55 km from the coast (Tande and Jennings 1986 as cited in: Kincheloe and Stehn 1991). The average salinity of tidal water at the study site for 2022 and 2023 field seasons was 2.5 ppt ± 1.9 (mean ± sd) in 2022 and 0.87 ppt ± 0.84 in 2023 (Appendix 1). Being slightly inland, the study site overlays inactive and abandoned floodplain deposits, where frequency of sedimentation and inundation are relatively low compared to more coastal areas (Jorgenson 2000; Jorgenson et al. 2018), and soils are organic.

Variable microtopography creates a variety of ecotypes regionally and at the field site (Jorgenson 2000). Grazing lawns are found occasionally in small patches along pond margins. Common ecotypes include graminoid-dominated meadows and wetlands located in depressions or on or near slough edges and river banks. These wetlands may be flooded during tidal cycles, and are habitat for geese nesting and grazing. The highest elevations contain moist low scrub communities located on permafrost plateaus, dominated by mosses, lichens, and shrubs (Jorgenson 2000). This is a common ecotype near the field site. Geese have been observed grazing on berries and depositing feces here usually later in the summer.

Soil Collection and Bulk Density

The vegetation communities investigated here include a grazing lawn ("Grazing Lawn"), two wetlands ("Lowland Wetland", "Upland Wetland"), and a moist low scrub community ("Tundra"). The Grazing Lawn is located ca. 6-7 km downstream of Old Chevak on the Kashunik River (61.37155°N, -165.45908°W, Figure 1). The Grazing Lawn is located on a pond-margin not far from the river, suggesting it is susceptible to flooding, and is comprised of short-stature *Carex*, high fecal deposition, high sulfate (Table 1) and mineral soils. The Lowland Wetland is the wettest of all of the communities and is frequently saturated with occasional standing water. This community is located directly next to a slough that flooded this community approximately monthly in summer 2022 and 2023. *Carex rariflora* and *Salix fuscescens* dominate this community, but other common plants include graminoids like *Eriophorum vaginatum*, *Calamagrostis deschampsioides*, and *Leymus mollis*; deciduous shrubs like *Salix ovalifolia* and *Betula nana*; evergreen shrubs like *Empetrum nigrim* and *Andromeda polifolia*; forbs like *Bistorta vivipara*, *Potentilla palustre,* and *Pedicularis sudetica*; and others. The Upland Wetland is drier than the Lowland Wetland. This community is located in a depression off the bank of a large slough, where higher upland topography on the side of this community near the riverbank may prevent it from flooding. However, a smaller slough on one side of this wetland that is unprotected by upland likely floods this community at least yearly, as this community contains moderate amounts of sulfate indicating it is flooded (Table 1). While this community contains similar species to the Lowland Wetland, it is dominated by more broadleaf sedges such as *Carex lyngbyei* and less by *Carex rariflora*, and contains species such as the forb *Cornus canadensis* that was rarely,

if ever, observed in the Lowland Wetland. Geese graze moderately in both wetlands. The Tundra is dominated by mosses like *Sphagnum spp*.; numerous species of lichen; evergreen shrubs like *Empetrum nigrim*, *Vaccinium vitis-idaea*, and *Ledum palustre*; the forb *Rubus chamaemorus*; and the deciduous shrub *Betula nana*. This most upland community historically only floods every few years.

I sampled soil from each community on August 10-12, 2022. In each community, I established a 15-m transect. At every 5 m along the transect, I collected four 15 x 15 cm soil turfs, one meter from the transect in each cardinal direction. This resulted in 12 soil turfs per community. Turfs were excavated to a depth of 15 cm below dead plant material, and vegetation was removed using a knife. In the moss-dominated Tundra community, turfs were excavated below the transition from live to dead moss (top ~2cm) (Hobbie et al. 2002; Neff and Hooper 2002; O'Donnell et al. 2009). Turfs were air-dried for ca. two to four days, transported to South Dakota State University, and then further air-dried completely in a greenhouse. I then homogenized them by community and sieved them to 2 mm to remove large roots for use in my incubation experiment. Soil pH, soluble salts (mmho/cm), OM (%), nitrate-nitrogen (ppm), potassium (ppm), sulfur (or sulfate-S) (ppm), sodium (ppm), phosphorus (ppm), and C:N was quantified in five dry subsamples of each soil type (Ward Laboratories in Kearney, Nebraska, Table 1, Appendix 2). The majority of the sulfur quantified is sulfate (sulfate-S), so I refer to sulfate-S as sulfate.

Soil bulk density for each community was determined by excavating 8 cm x 8 cm soil turfs to 15 cm every 5 m along the transect line (Table 2), resulting in three turfs per community. Turfs for bulk density measurements were sampled directly on the transect

line. The volume of the remaining hole where each bulk density soil sample was excavated from was measured using a plastic bag and water. The water was then weighed to determine the volume of the sample. Bulk density soil samples were allowed to air-dry prior to transport. Once at South Dakota State University, they were oven-dried at 60 °C and weighed. Bulk density was determined by dividing the dry weight of the soil by its volume.

Microcosm Experiment Design

I manipulated temperature, flooding, and feces in microcosms by subjecting them to incubation at 8°C or 18°C, flooding or no flooding, and feces addition or no feces addition in a fully-factorial design (Figure 2). The experimental design resulted in eight treatment combinations and seven replications for each of the four communities (n=224). Microcosms included 20 g (± 0.5 g) of air-dried, sieved soil inside 120 mL plastic cups placed inside 473 mL mason jars. Jar lids had septum to allow for sampling of headspace gas. Soil containment in plastic cups was necessary for submergence of soil during flooding treatments, and small holes in the bottom of plastic cups allowed for drainage. A filter was used on the bottom of plastic cups to minimize soil loss. Field capacity for each soil type was determined by adding distilled water to five subsamples of fresh soil from each community until they could no longer hold water (Table 2). Distilled water was added to dry soil in each microcosm to bring samples to field capacity based on soil community.

I incubated microcosms either at 8°C in a refrigerator, or at 18°C in an incubator for 16 weeks. The lower temperature represents early season soil temperatures, while the

warmed temperature represents approximately the maximum soil temperatures experienced in the region (Kelsey et al. 2016). Microcosms were removed from their temperature regimes only for flooding and feces addition treatments and gas sampling. Their position within their respective incubator or refrigerator was randomized approximately weekly. Two microloggers (iButton, Maxim Integrated Products, Inc., Sunnyvale, California) recorded hourly temperature data throughout the majority of the experiment. I-button data from the evening of October 24th 2022 until mid-December showed that actual incubation temperatures were 10.2 ± 1.34 (mean ± sd) and 18.6 ± 0.278 in the refrigerator and incubator, respectively. Five blank jars were incubated at each temperature to make sure there were no observed emissions from equipment.

Feces addition treatments occurred in weeks two, four and six of the experiment. In mid-August 2022, as fresh as possible goose feces were collected from areas surrounding soil sampling sites and was frozen until use. Feces were then thawed, homogenized, oven dried at 60°C, and grinded using a mortar and pestle (Foley et al. 2022). Five subsamples of ground feces were analyzed for nutrient concentration (Ward Laboratories in Kearney, Nebraska). Feces contained 1.79 organic N ± 0.0179 (mean ± sd) (% N), 37.4 total C ± 1.15 (% C), 1.92 total N (TKN) ± 0.0212 (% N), and 0.726 P ± 0.0573 (% P_2O_5) (Table 3, Appendix 2). During each feces addition treatment, 0.0410 g (± 0.0020 g) of feces was added to each grazed microcosm and pressed approximately 1 cm into the soil in five random spots to mimic goose trampling. This trampling technique was performed on all microcosms regardless of if they received feces addition or not for consistency. I calculated feces addition using average daily fecal deposition rates of 0.437 m^{-2} day^{-1} for the 2014, 2015, and 2016 field seasons (Beard et al. 2023).

Flooding treatments also occurred in weeks two, four, and six approximately 48 hours after feces addition treatments to analyze the role flooding has in leaching nutrients. During each treatment, soil cups from flooded microcosms were removed from jars and submerged in 225 mL of 3.5 ppt salinity water for 3 hours (Instant Ocean Sea Salt, Spectrum Brands, Blacksburg, VA, USA). This salinity represents the upper end of salinity observations at Old Chevak during high tide in early to mid-summer 2022 (Appendix 1). The tops of soil cups were covered with Saran wrap with holes that allowed water to flow in but which minimized soil loss. It is likely that the Saran wrap prevented the majority of feces from being washed away, but this was a necessary procedure to prevent substantial soil loss. After three hours, soil cups were allowed to drain and flood leachate was collected in vials and eventually frozen for future quantification of $N\text{-}NH_4^+$ concentration. Distilled water was added to non-flooded microcosms to replace evaporative water loss and maintain field capacity. After the final flood, distilled water was added to all microcosms to maintain field capacity biweekly until the end of the experiment.

C Emissions and Ammonium Content Quantification

I quantified the change in CO_2 and CH_4 concentrations over a 24-h period in each microcosm approximately weekly. Microcosms were removed from their incubation locations, immediately capped tightly, and 10 ml of headspace gas was removed through the septum using a needle and syringe. The headspace gas was then injected into a closed-loop system attached to a CO_2/CH_4 gas analyzer (model 7810, Li-Cor Inc., Lincoln, NE). Capped microcosms were returned to their respective temperatures for 24-

h. After this time, each microcosm was sampled again. CO_2 and CH_4 emissions were calculated as the difference between the two sampling events taking into account instrument, jar and tubing volumes, as well as temperature and pressure. A known volume of zero air was injected into the instrument approximately every ten samples to clear the system and to calculate the effective volume of the instrument for calculation of headspace gas concentrations. Microcosms were left loosely capped when they were not being sampled.

Ammonification (μg $N\text{-}NH_4^+ g^{-1} d^{-1}$) was determined in each microcosm over the duration of the incubation experiment. In the two weeks following the last gas sampling event, I added 100 mL of 2 M KCl (potassium chloride) to each microcosm and agitated them for two hours to extract exchangeable NH_4^+. I centrifuged the extract to further separate liquid from soil that remained when necessary. Extracted liquid was then filtered through a funnel lined with 15 cm diameter, fine porosity filter paper. I also performed KCl extractions on four 20 g (± 0.5 g) subsamples of fresh soil from each community to determine pre-incubation concentrations of $N\text{-}NH_4^+$ in each soil community. Net ammonification for each microcosm was quantified as the difference between the amount of exchangeable $N\text{-}NH_4^+$ in the soils at the end of the experiment and the average amount of exchangeable $N\text{-}NH_4^+$ in fresh soils of the respective community divided by the number of days since the microcosm was wetted (i.e., when ammonification began). All extracted liquid was frozen until analysis. I also attempted to quantify $N\text{-}NO_3^-$ in soil extracts but concentrations were below detection. Therefore, my study's N mineralization includes ammonification only.

The concentration of $N\text{-}NH_4^+$ in flood leachate and soil extracts was analyzed using colorimetric microplate assays, specifically using the Berthelot reaction and associated reagents (Forster 1995; Rhine et al. 1998). A visible light spectrophotometer (model V-1200, VWR Inc., Radnor, Pennsylvania, USA) was used to read absorbance at 650 nm against a blank reagent. $N\text{-}NH_4^+$ was quantified by fitting absorbances to a curve of known standards. I forced the 0-intercept for all curves in order to estimate low concentrations of $N\text{-}NH_4^+$ in floodwater and soil extracts that were below the lowest known standard. There were a few instances where concentrations in floodwater were negative, so I included these values as "0". A few of the KCl extracts were removed from the study due to broken vials during the freezing process and too high of absorbances to accurately predict ammonification. $N\text{-}NO_3^-$ in flood leachate was also below detection.

Statistical Analyses

I used analysis of variance (ANOVA) in the R statistical program (R Core Team 2023) to analyze main effects and all two-way interactions between flooding, temperature, and feces addition on CO_2 emissions, CH_4 emissions, ammonification and $N\text{-}NH_4^+$ in floodwater leachate. ANOVAs were performed for each community separately since I am looking at which variables are important in each community and not how these variables differ in their impacts across communities. Given that C emissions and $N\text{-}NH_4^+$ in floodwater were quantified from microcosms multiple times over the course of the experiment, I used a repeated measures ANOVA to analyze treatment effects on these variables, where microcosm jar was the repeatedly sampled experimental unit. I did not use flooding as a predictor in the floodwater leachate analysis since this

only included flooded microcosms, and therefore results can only provide information on how feces addition and temperature effected $N\text{-}NH_4^+$ in flood leachate.

I modeled estimated marginal means following each ANOVA using the emmeans package in R (Lenth 2023). Pairwise comparisons were performed using the multcomp package in R (Hothorn et al. 2008), where letters represent significantly different groupings based on a sidak adjustment. All residuals were checked for assumptions of normality. Percent changes in my results for CO_2 emissions, CH_4 emissions, ammonification and $N\text{-}NH_4^+$ in flood leachate were calculated using estimated marginal means of treatments, while temporal data for CO_2, CH_4, and flood leachate are from raw data. I removed the first gas sampling event on day 7 from my analysis due to exceptionally high variance compared to subsequent measurements.

RESULTS

CO_2 Emissions

Warming increased soil CO_2 emissions in all communities but interacted with flooding in the Tundra to complicate warming impacts. Temperature main effects (based on marginal means of the model result) showed that warming increased CO_2 emissions by 37.6, 75.5, and 73.5%, in the Grazing Lawn, the Lowland Wetland, and the Upland Wetland, respectively, regardless of flooding or feces addition treatments (Table 4, Figure 3). In the Tundra, temperature and flooding interacted such that flooding suppressed soil respiration by 30.2% at 8 ˚C, and by 25.3% at 18 ˚C during most of the experiment (Figure 3).

Flood and feces addition also had significant main effects. Flooding altered CO_2 emissions in the Upland Wetland, decreasing CO_2 emissions by 6.1% regardless of grazing and temperature treatment (Table 4, Figure 3). Flooding did not alter any CO_2 emissions in the Grazing Lawn and Lowland Wetland communities. Feces addition effects on CO_2 emissions were present in all communities. Feces addition increased CO_2 emissions by 40.1% in the Grazing Lawn, 12% in the Lowland Wetland, 15.5% in the Upland Wetland, and 14.3% in the Tundra (Table 4, Figure 3). No interactive effects between feces with flooding or warming on CO_2 emissions were observed.

Emissions of CO_2 varied considerably throughout the experiment in each community and depended on temperature. In the Grazing Lawn, at 8 ˚C, soil respiration gradually increased until ca. day 60. However, at 18 ˚C, soil respiration peaked earlier, declining through the majority of the experiment. Soil respiration in the Lowland Wetland was relatively consistent throughout the experiment at 8 ˚C, gradually increasing

until and slightly peaking around day 30, and then decreasing thereafter. At 18 ˚C, soil respiration began high, decreased, but then increased again just after day 40. In the Upland Wetland, soil respiration was consistent at 8 ˚C. At 18°C in this community, it peaked slightly before ca. day 60. The Tundra had consistent CO_2 emissions at both temperatures.

CH_4 Emissions

Temperature increased CH_4 emissions in all communities, but again interacted with flooding to complicate warming effects. In the wetland communities, warming independently increased CH_4 emissions by 789% in the Lowland Wetland and by 3830% in the Upland Wetland (Table 5, Figure 4). In general, CH_4 emissions were highest in these wetland communities (Figure 4). Similar to CO_2 emissions in the Tundra, flooding worked in tandem with temperature to influence CH_4 emissions in the Grazing Lawn and Tundra communities. However, the response of methanogenesis to flooding differed within each of these communities. In the Grazing Lawn, flooding increased CH_4 emissions by 1,470% at 8 ˚C, and 156% at 18 ˚C (Table 5, Figure 4). Contrarily, in the Tundra, at 8˚C there was a switch from slight consumption of CH_4 without flooding to slight production of CH_4 with flooding, while at 18 °C, flooding suppressed methanogenesis by 86.6%. Although CH_4 emissions were lowest in this community, the suppression of methanogenesis at the higher temperature by flooding is evident ca. day 60 and beyond (Figure 4).

Unlike feces impacts on CO_2, feces addition affected CH_4 emissions only in the Lowland Wetland where fecal impact depended on flooding. This interaction

demonstrated that when feces and flooding occurred together, there was a 40.4% decrease in CH_4 emissions compared to when feces was present without flooding (Table 5, Figure 4). Feces did not cause any effects on CH_4 emissions in any of the other communities.

Methanogenesis also varied throughout the course of experiment in each community and temperature regime (Figure 4). At 8 °C in the Grazing Lawn, CH_4 emissions were low and CH_4 consumption was observed for some treatments early to mid-experiment. However, just before ca. day 60, CH_4 emissions from flooded microcosms drastically increased. At 18°C in the Grazing lawn, methanogenesis peaked ca. day 40. Flooded microcosms emitted higher CH_4 in this community for the majority of the experiment. In the Lowland Wetland, methanogenesis was low for most of the experiment at 8 °C, increasing toward the end of the experiment, and peaking ca. day 40 at 18 °C. The Upland Wetland followed very similar patterns at 8 °C and 18 °C as the Lowland Wetland, except CH_4 emissions from some treatments slightly increased during the last sampling event. Some CH_4 consumption was observed at lower temperatures. CH_4 production was very low in the Tundra community at 8 °C throughout the experiment, and CH_4 consumption was common in this community at 8°C in the first half of the experiment up to and including day 55, and for some treatments at 18 °C. At 18 °C, methanogenesis increased dramatically right before day 60, especially for non-flooded microcosms (Figure 4). Overall, there was a lag in the onset of substantial CH_4 production in all communities, indicated by low CH_4 production in the first several weeks of the experiment relative to peak CH_4 emissions. The highest CH_4 emissions measured happened ca. day 90 for all communities in the experiment at 8 °C, and just after ca. day 40 at 18°C, besides in the Tundra where peak emissions happened ca. day 90 at 18°C.

Ammonification

Temperature had a main effect on ammonification only in the Upland Wetland, where warming increased ammonification by 222% (Table 6, Figure 5). In general, I observed high ammonification in the wetland communities. However, no significant treatment effects were present in the Lowland Wetland.

Flooding impacted ammonification in the Grazing Lawn community and in the highest elevation Tundra community, where in the Grazing Lawn, flooding impacts were influenced by temperature. In the Grazing Lawn, flooding reduced ammonification by 68.7% at 8 °C, and switched ammonification from net positive to net negative at 18 °C (Table 6, Figure 5). In the Tundra, net ammonification was negative, indicating the immobilization of NH_4^+, and flooding reduced the immobilization of $N\text{-}NH_4^+$ (or increased ammonification) by 81.5% regardless of flooding or temperature treatment (Table 6). Feces addition effects were observed only in the Tundra, where feces addition reduced N immobilization or $N\text{-}NH_4^+$ by 24.6% (Table 6, Figure 5).

$N\text{-}NH_4^+$ in Flood Leachate

Leaching of $N\text{-}NH_4^+$ in floodwater was observed from all communities. However, only temperature significantly affected the concentration of $N\text{-}NH_4^+$ in flood leachate, not feces addition. Temperature impacts on the concentration of $N\text{-}NH_4^+$ in flood leachate were present in all communities but the Tundra. In the Grazing Lawn, the Lowland Wetland, and the Upland Wetland, temperature reduced the concentration of $N\text{-}NH_4^+$ leached by 27.3, 33.2, and 22.5%, respectively (Table 7, Figure 6). Overall, there were also no noticeable trends observed with the amount of $N\text{-}NH_4^+$ leached from one flooding

event to another (Figure 7). However, in general, the most $N\text{-}NH_4^+$ tended to be leached from the Upland Wetland community, and the least from the Tundra community (Figure 6).

DISCUSSION

I manipulated temperature, flooding, and feces addition to understand how these climate change variables will influence C emissions and ammonification across a high latitude wetland. Warming and feces addition independently increased greenhouse gas emissions, likely due to effects on decomposition and nutrient availability that impacted microbial demand for C and N in some communities. However, flooding impacts were more complicated, especially in the flooding susceptible Grazing Lawn, where flooding increased CH_4 emissions, and the rarely flooded, highest elevation Tundra ecosystem, where flooding decreased emissions of both greenhouse gases. The response to each climate change variable within a community, as well as the magnitude of this response, may reflect how well adapted the microbial community is to the variable. Responses also may reflect soil characteristics, substrate quantity or quality, and vegetation type within each community.

Greater CO_2 and CH_4 emissions from warming in the communities was likely a result of increased microbial decomposition. These findings are supported by others who observed increases in soil respiration (Lloyd and Taylor 1994) and methanogenesis (Williams and Crawford 1984; Dunfield et al. 1993, Inglett et al. 2012) with increasing temperatures. Since CO_2 and CH_4 production can be influenced by C substrate quantity and quality (Inglett et al. 2012; Bridgham and Richardson 1992; Valentine et al. 1994), C quality and quantity may explain differences in soil respiration and methanogenesis among communities. The lowest soil respiration in the Grazing Lawn compared to other soils, and lower methanogenesis compared to the Lowland Wetland and Upland Wetland, could result from low OM and C availability in this community (Table 1). Low OM and

C availability in the Grazing Lawn may be due to less litter input from frequent grazing, which may limit decomposition. Likewise, despite the Tundra having the highest amounts of C (Table 1) and similar rates of soil respiration to the wetland communities, it produced orders of magnitude less CH_4 than the other communities (Figure 4). This could partially be due to poor substrate quality or limited quantities of labile C. The Tundra is dominated by mosses, which contain lignin-like recalcitrant C compounds and antibacterial compounds that contribute to their slow decomposition (Chapin et al. 1986; Verhoeven and Toth 1995; Hobbie et al. 2000). Shrubs are also dominant in this community, which generally have high lignin concentrations (Hobbie 1996) that make them harder to decompose. Labile C especially limits methanogenesis at the fermentation step, where complex carbon compounds are broken into usable products for methanogenesis (Valentine et al. 1994). However, how much a role C quality plays in CH_4 emissions in the Tundra community requires further attention.

Differences in methanogenesis among communities could also result from differences in the abundances of methanogens. For example, in mineral soils, numbers of methanogenetic archaea in desert soil crusts and dry upland soils were typically low compared to wetter soil types such as lake sediments that had large populations of methanogens that only require the correct conditions and substrate to become active (Conrad 2020b). Under increased flooding, numbers of methanogenic archaea increased in drier soils, but abundances remained relatively unchanged in wetter soils (Conrad 2020b). The wetland areas of the study site, especially the Lowland Wetland, are frequently wet and therefore may support an abundant methanogen community compared to the rarely flooded Tundra. Frequent saturation of these organic soils, which hold onto

water, might also be the reason CH_4 production was not significantly impacted in the Lowland Wetland and Upland Wetland by flooding if abundances of methanogens did not change under increased flooding.

The suppression of soil respiration from flooding in the Tundra and Upland Wetland, regardless of temperature, suggests that flooding may have an impact on microbial communities in these soils. Flooding could have induced osmotic stress by adding salt, which can cause lysis, reductions in microbial growth rates, soil respiration, and other microbial activity (reviewed by: Yan et al. 2015; Rath et al. 2016). Saltwater treatments of only 5 ppt reduced microbial biomass and respiration in soils that had been protected from saltwater exposure for 20 years (Ardón et al. 2018), and other authors suggest salinity can have negative impacts on microbial processes in communities that are not adapted to higher levels of salinity (Rath and Rousk 2015). Although the salinity in my experiment was only ~3.5 ppt, it is possible that the Tundra and Upland Wetland communities, that are less frequently flooded and that contain less soluble salts, lack salinity adaptations. Flooding could have also altered microbial community composition, leading to the suppression of soil respiration, especially in the Tundra where suppressed CH_4 production at 18 °C from flooding was also observed. Cyclical flooding and draining may inhibit the establishment of a predominantly aerobic or anerobic population (Randle-Boggis et al. 2018). This could explain the reduction in both CH_4 production and soil respiration in the Tundra if neither population was able to establish. It is also possible that after the three flooding events, which introduced sulfate, anaerobic decomposition was dominated by sulfate reducers in flooded microcosms in the Tundra, in which increased sulfate reduction could have suppressed methanogenesis (Weston et al. 2006; Chambers

et al. 2013). Increases in sulfate-reducing bacteria have been observed after three two-week flooding events followed by two weeks of draining (Randle-Boggis et al. 2018). The Tundra community contained the lowest sulfate concentrations, which could suggest it originally lacked sulfate reducing bacteria. Over the course of the flooding treatments in my experiment, sulfate reducer abundance could have increased. This could have led to the continuous suppression of methanogenesis in flooded microcosms in the Tundra throughout the second half of the experiment as sulfate reduction occurred upon the increase of the sulfate reducer population. This would explain why flooded microcosms in the Tundra never produced substantial methane, at least at 18°C.

While flooding may offset some of the increases in CH_4 from warming in the Tundra, a key finding is the difference in the role flooding plays in the Grazing Lawn, as results suggest flooding and warming will interact to increase CH_4 production. One attribute of the Grazing Lawn that may favor anoxia and CH_4 production under flooding is its high bulk density (Table 2) and likely low porosity. This also may be why less CH_4 production in unflooded Grazing Lawn soils was observed. In addition, the high concentrations of soluble salts and sulfate in the Grazing Lawn (Table 1) suggest it may be frequently flooded from seawater, and therefore could have microbial communities more adapted to salinity than the Tundra.

Given its high sulfate concentration, it is surprising that substantial CH_4 production was observed in the Grazing Lawn. One possible explanation is that substantial CH_4 production was inhibited until sulfate was depleted. Unlike the Tundra, the Grazing Lawn contains high concentrations of sulfate. Therefore, sulfate reducers may have already been present early on in this community. The lag or low CH_4

production in all communities in the beginning of the experiment could show the suppression of CH_4 production by alternative electron acceptors, such as sulfate, competing for substrates early on and the growth of methanogenic biomass during this time (Segers and Kengen 1998; van Hulzen et al. 1999; Conrad 2020b). Fermentation occurs quickly after flooding, and hydrogenotrophic methanogens regain activity quickly before sulfate reducers following flooding, with acetotrophic (acetoclastic) methanogens not becoming active until later (reviewed by: Conrad 2007). When sulfate reducers eventually become active, they compete for fermentation products to the point that hydrogenotrophic methanogenesis is no longer thermodynamically possible (reviewed by: Conrad 2007). Once sulfate is depleted, both types of methanogenesis are thermodynamically feasible (reviewed by: Conrad 2007). The shorter lag time for all communities at the higher temperature, besides the Tundra, could be due to more C substrate becoming available under increased anaerobic C mineralization, which depletes the alternative electron pool faster (van Hulzen et al. 1999). Along with the cycling of electron acceptors, anaerobic C-mineralization is a driver of methane production (Segers 1998) that is directly coupled to the production of C substrate (e.g. acetetate) (Segers and Kengen 1998).

Feces addition increased CO_2 emissions in all communities, which is supported by other Y-K Delta soil incubation studies (Foley et al. 2022; Saunders et al. 2023). Feces addition partially alleviates nutrient limitations on microbes (Ruess and McNaughton 1987), stimulating C emissions. Although field studies demonstrated no effects of double ambient fecal density (fecal addition) on CO_2 emissions, but increased CO_2 emissions under feces removal (Beard et al. 2023), this was due to impacts of feces on plant

productivity which I do not consider in my lab incubation experiment. The greatest increase in CO_2 from feces in my experiment was observed in the Grazing Lawn. This may suggest that feces provide an important C substrate here, where decreased litter inputs from heavy grazing may result in low OM and C (Table 1). In a feces addition study using more coastal Y-K Delta soils, higher CO_2 emissions were found in unamended grazing lawn soils vs. unamended ungrazed meadow soils (Foley et al. 2022). This could be due to the fact grazing lawns contain less C efficient copiotrophic bacteria that may be favored by feces addition (Saunders et al. 2023). Foley et al. (2022) also found greater feces addition effects in ungrazed meadow soils vs. grazing lawn soils, which they attributed to lower stocks of P and K in ungrazed meadow soils. However, although K stocks in the Grazing Lawn in my study were highest of all the soils, P stocks in the Grazing Lawn were slightly lower than the Upland Wetland and Tundra communities, but higher than the Lowland Wetland (Table 1). Therefore, differences in nutrient dynamics in my study's communities, which also vary in species composition compared to this coastal study (Foley et al. 2022), could explain the difference in findings between our two studies.

The only feces addition impact on CH_4 emissions observed was a reduction in CH_4 emissions in the Lowland Wetland when feces and flooding occurred together compared to when feces was present alone, which could be due to flooding leaching nutrients in feces. Contrary to my expectations, I did not observe increases in CH_4 emissions from feces addition. It is important to note that feces addition treatments occurred in the first six weeks of my experiment, much of which was during the lag time in CH_4 production (Figure 4). Therefore, the opportunity for enhanced CH_4 production

likely did not exist. Overall, results from nutrient and fertilizer addition experiments examining CO_2 and CH_4 emissions have been mixed (Wu et al. 2023; Lund et al. 2009; Keller et al. 2005), especially effects of feces addition on CH_4 in Y-K Delta studies (Foley et al. 2022; Beard et al. 2023). While Foley et al. (2022) found that feces addition increased CH_4 emissions in incubated soils, double ambient fecal density (fecal addition) did not increase CH_4 emissions compared to feces removal and ambient fecal control plots in a field study (Beard et al. 2023). Again, this could be due to effects of feces addition of plant growth or oxygen-transport processes (Beard et al. 2023) that are not accounted for in soil-only lab experiments. Overall, the role of feces addition and nutrient inputs and how they relate to C emissions, especially methanogenesis, locally and globally warrants further investigation.

While the mineralization of nutrients such as N partially depends on C:N ratios of OM (Mooshammer et al. 2014), in the case of ammonification in my study, it does not appear that C:N ratios of soil explain my findings. Similar C:N ratios were observed in the Lower-Midland Meadow and Tundra, despite seeing high net ammonification in the Lower-Midland Meadow and net immobilization in the Tundra. Ammonification and immobilization of $N\text{-}NH_4^+$ in my study therefore likely reflect microbial demand for C vs. N, providing information on which nutrients were limiting during microbial growth within each community. In the Tundra, net immobilization of $N\text{-}NH_4^+$ with high CO_2 emissions indicates N limitation to microbial growth and therefore N demand by microbes. Microbes therefore likely had to reduce their C efficiency to obtain more N. Tundra sites and their vegetation are well known for being N-limited (Shaver and Chapin 1980; Shaver et al. 1986), and microbes immobilize and may even compete among plants

for N during the growing season (reviewed by: Jonasson et al. 2001). Therefore, this may explain overall immobilization of $N\text{-}NH_4^+$ in the Tundra. Contrarily, ammonification in the Lowland Wetland and Upland Wetland suggest C-limitation to microbial growth and C demand by microbes in these more productive communities. These more productive communities likely have OM inputs composing of readily available N due to the presence of large amounts of fresh graminoid and forb biomass that satisfies N-demand and is rapidly broken down. High C emissions here even along with high ammonification indicate that there must also be a relatively labile source of C. Lastly, low but net ammonification, at least for the majority of the treatments, in the Grazing Lawn suggest C limitation and demand for C during microbial growth. In addition, low ammonification in the Grazing Lawn corresponds with the lowest soil respiration in this study, likely reflecting low OM content in this mineral soil.

Increase ammonification in the Upland Wetland under warming likely reflects increased microbial demand for C as warming temperature promotes maintenance respiration over growth, leading to C limitation for growth and increased demand for C (Reviewed by: Chapin et al. 2011). This was accompanied by increased soil respiration under warming. This is supported by a global meta-analysis where N mineralization and soil respiration following 2-9 years of experimental warming increased across all sites and years, despite variable responses at individual sites (Rustad et al. 2001). Likewise, the flooding and feces addition effects on ammonification in the Tundra may reflect changes in C vs. N demand of microbes. If flooding negatively impacted microbial growth in this community, indicated by reduced soil respiration, then microbial demand for N also likely decreased leading to reduced immobilization of $N\text{-}NH_4^+$. In this

community, feces addition also reduced immobilization of $N\text{-}NH_4^+$ and stimulated soil respiration. Feces contains NH_4^+ and soluble N (Bazely and Jefferies 1985) which may have become directly available to microbes for decomposition, alleviating demand for N (McNaughton 1985) and reducing immobilization of $N\text{-}NH_4^+$ and N limitations. At the same time, feces added C, which provided C substrate for soil respiration. The fact feces addition impacts on ammonification were observed only in the Tundra may show that the translocation of nutrients from more productive communities to this ecosystem through grazing is important to C and N cycling.

In the Grazing Lawn, there were no observed effects of flooding on soil respiration that would reflect microbial nutrient demands or that could explain the reduction in ammonification at both temperatures from flooding. While flooding can promote N mineralization due to increased pH that may favor microbial activity (Ono 1991), the breakdown of soil organic matter, and mineralization may slow in anaerobic environments (Reddy and Patrick 1984). Flooding increased methanogenesis in both temperature treatments, indicating anaerobic conditions and a possible reduction in N demand.

Finally, the reduction of $N\text{-}NH_4^+$ leached during flooding in the Grazing Lawn, Lower Wetland, and Higher Wetland at the higher temperature could reflect more $N\text{-}NH_4^+$ tied up in microbial biomass as decomposition was accelerated at the higher temperature, resulting in less being leached. This may especially be true in the Grazing Lawn, where observed net immobilization of $N\text{-}NH_4^+$ under flooding at 18 °C. While I expected floodwater $N\text{-}NH_4^+$ to relate to ammonification, ammonification was calculated over the course of the experiment, while $N\text{-}NH_4^+$ in flood leachate may only offer insight

on the first six weeks of the experiment, when flooding events occurred. This could be why there were decreases in $N\text{-}NH_4^+$ in leachate under warming in the Lower Wetland and Upland Wetland, despite warming increasing ammonification in the Upland Wetland and having no effect on ammonification in the Lower Wetland.

CONCLUSION

Using the Y-K Delta, a high-latitude coastal wetland as a case study, this study provides evidence that temperature, flooding, and feces addition from grazing work independently and synergistically to influence C and N microbial processes related to greenhouse gas emissions and ammonification in soils. High latitude coastal wetland systems like the Y-K Delta reside in a region that is warming at a disproportionate rate (Rantanen et al. 2022). Likewise, these low-lying Arctic ecosystems are susceptible to more intense and frequent coastal flooding under climate change (Jones et al. 2009; Arp et al. 2010), which may cause upland areas to become more salt-tolerant over time. The abundance and distribution of geese will also likely change due to climate-induced changes to goose forage and habitat (Flint et al. 2008; Flint et al. 2014; Tape et al. 2013). Since geese graze on salt-tolerant plants in high latitude coastal systems (Ruess et al. 1997; Bazely and Jefferies 1985) and deposit N-rich feces (Bazely and Jefferies 1985), increased coastal flooding may push grazers inland as these salt-tolerant lowlands become flooded more frequently, altering nutrient dynamics. Therefore, warming, flooding, and grazing are likely to be large drivers of alterations to C cycling in high latitude coastal ecosystems under a changing climate.

However, it is important to think about these climate change variables and C cycling on the broader Y-K Delta scale. Increased coastal flooding in the Y-K Delta will likely inundate lowlands for longer and possibly flood upland tundra areas annually (Terenzi et al. 2014). In regards to grazing, I saw the greatest increases in CO_2 emissions from feces addition in the frequently grazed Grazing Lawn that is susceptible to flooding due because it is located on a pond margin not far from the riverbank. As this community

type becomes more frequently flooded and loses herbivores that move inland, which is happening in real time, my findings suggest that CH_4 emissions will likely increase from flooding in these areas, which may be reinforced by warming. Herbivory will likely continue to increase CO_2 emissions in higher elevation ecosystems as they slowly transition into more-salt tolerant communities. Although greenhouse gas emissions from warming may be partially offset by flooding in higher elevation ecosystems, warming caused large emissions of both greenhouse gasses in the Lowland Wetland and Upland Wetland, where CH_4 emissions are highest and which are commonly found community types across the Y-K Delta ecosystem. However, while there is potential for these wetland areas to be large C sources under a warming climate, my study only takes into consideration C emissions from soil. To understand the true greenhouse gas potential of the Y-K Delta under climate change, C sinks such as offsets from biomass and changes to vegetation community composition under warming will need to be considered. In addition, C quality in addition to C quantity of soils will need to be considered to understand the magnitude of soil emissions. Since my flooding and grazing treatments all happened within two-weeks of one another and all consisted of the same magnitude of flooding and feces addition, future studies could manipulate frequency and intensity of flooding and grazing. This would allow for a better understanding of how temporal differences and differences in magnitude of these climate change variables will interact with warming to alter the greenhouse gas potential of this high latitude wetland, especially in regard to feces addition impacts on CH_4.

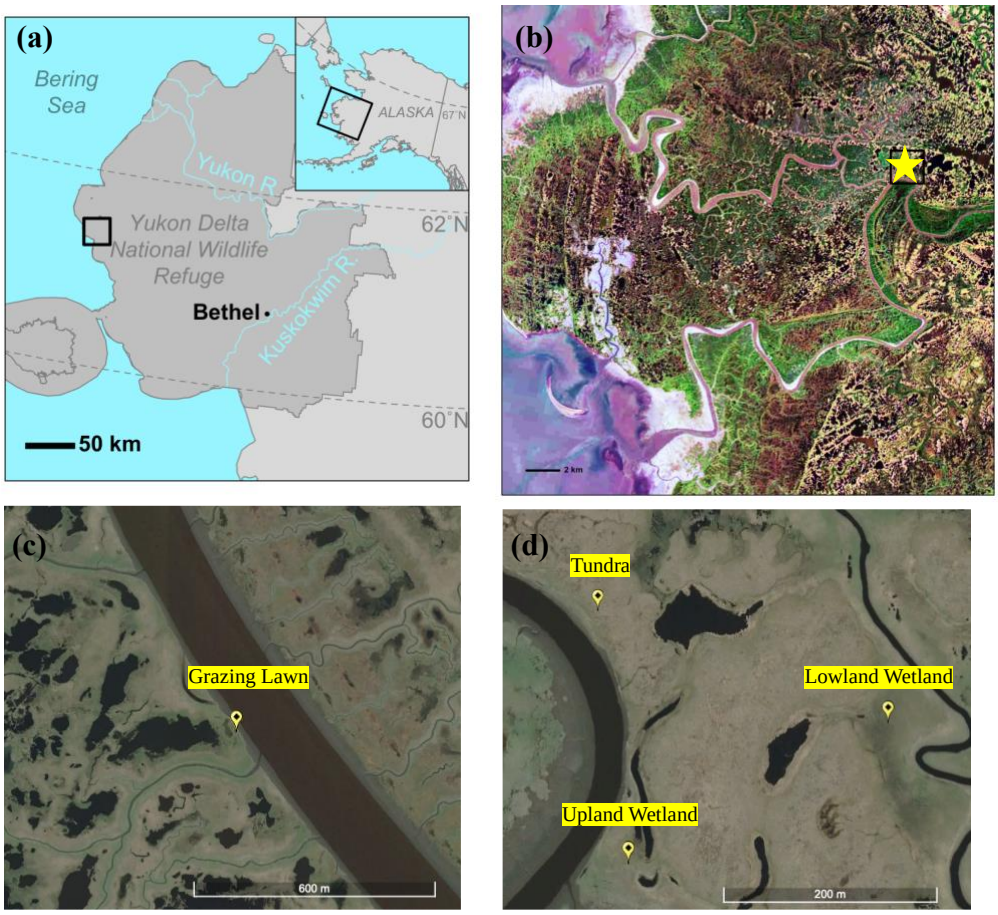


Figure 1. Regional and local maps of the Y-K Delta and the study site. Figure panels are: (a) a map of the Y-K Delta showing the location of the field site near Old Chevak within the region, denoted by the smaller black square on the left of the panel, (b) a regional map showing rivers and a star indicating Old Chevak, (c) the location of the Grazing Lawn community relative to the local landscape, and (d) the location of the Lowland Wetland, Upland Wetland, and Tundra communities relative to the local landscape.

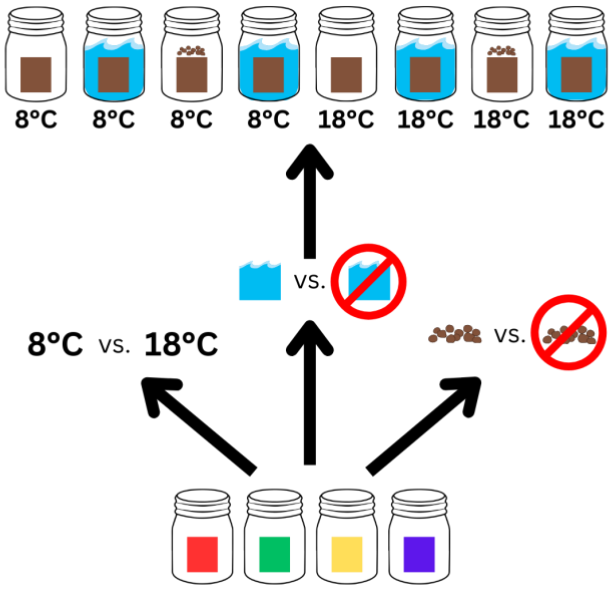


Figure 2. The full-factorial experimental design of my study. Microcosms consisted of soil from four communities and were subjected to incubation at 8°C or 18°C, flooding or no flooding, and feces addition or no feces addition. For each soil type, this resulted in 8 unique treatment combinations and 7 replications per community. N=56 per community, N=224 total.

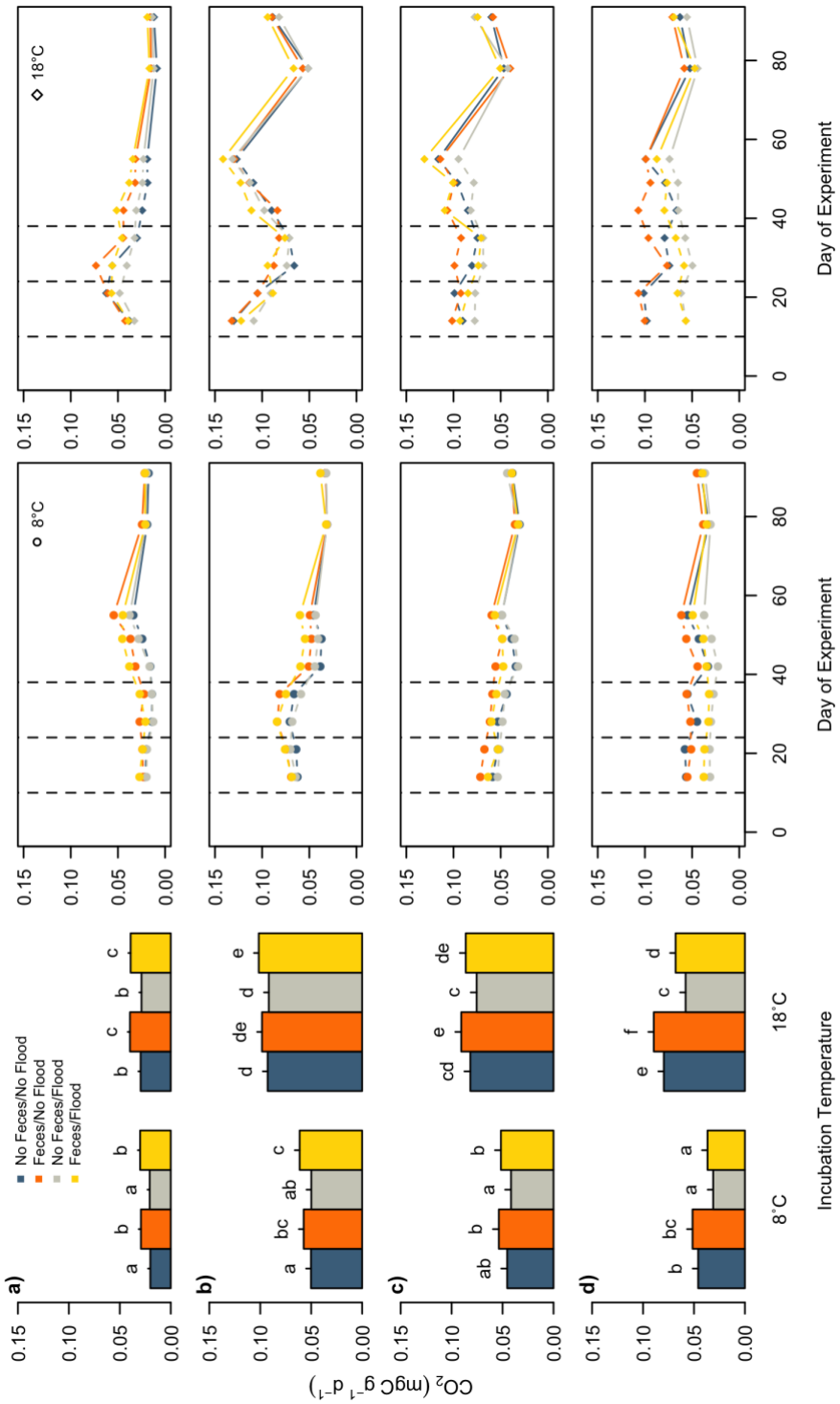


Figure 3. Estimated marginal means (±95% CI) for CO_2 emissions for each treatment in each community at 8°C and 18°C following the repeated measures ANOVA. Letters represent significant groupings based on a sidak adjustment. Line graphs show raw data means for each treatment at each temperature on each day of measurement. Vertical dotted lines show when feces addition treatments occurred, with flooding treatments happening 48 hours after. Figure panes are: (a) Grazing Lawn, (b) Lowland Wetland, (c) Upland Wetland, and (d) Tundra community.

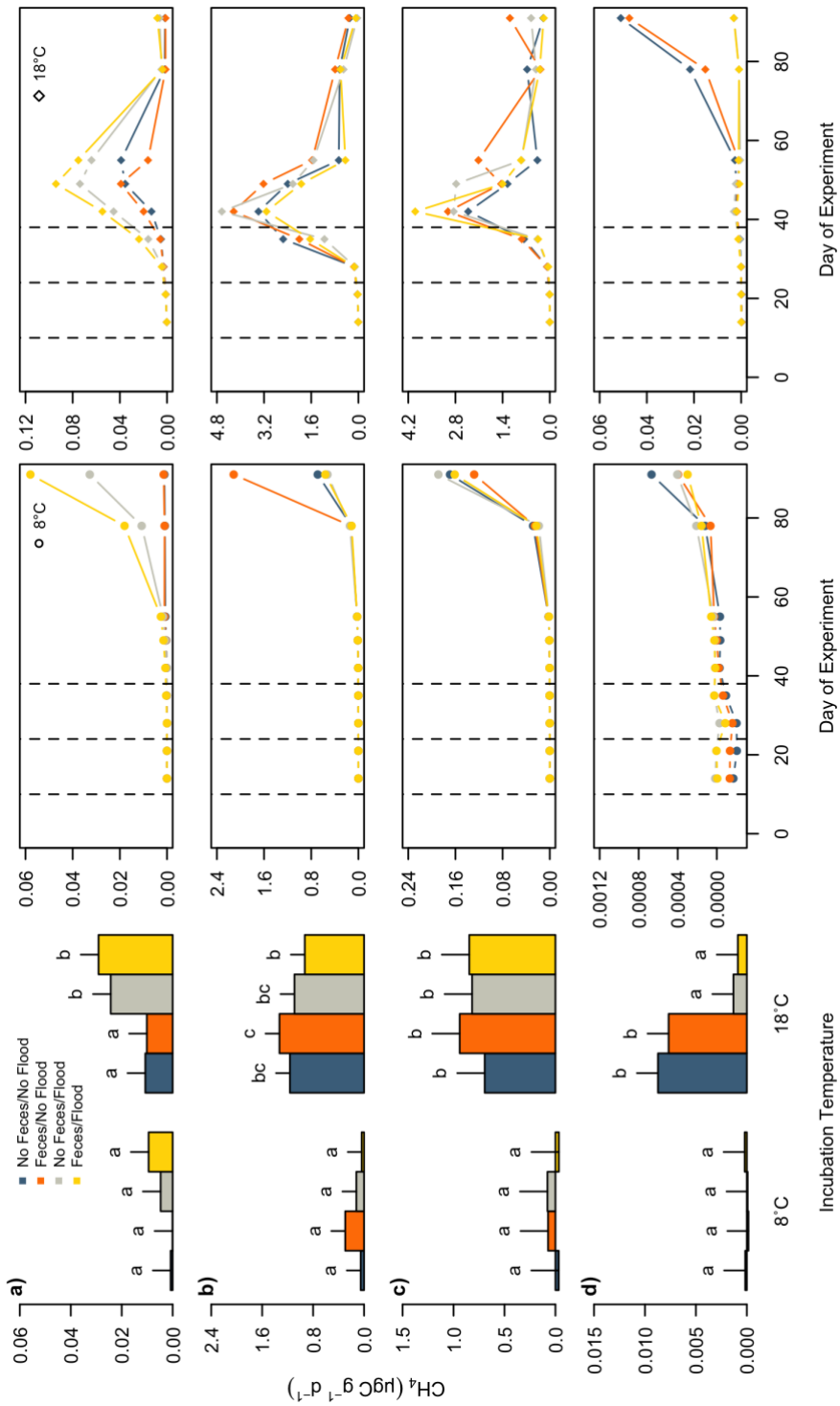


Figure 4. Estimated marginal means (±95% CI) for CH_4 emissions for each treatment in each community at 8°C and 18°C following the repeated measures ANOVA. Letters represent significant groupings based on a sidak adjustment. Line graphs show raw data means for each treatment at each temperature on each day of measurement. Vertical dotted lines show when feces addition treatments occurred, with flooding treatments happening 48 hours after Figure panes are: (a) Grazing Lawn, (b) Lowland Wetland, (c) Upland Wetland, and (d) Tundra community.

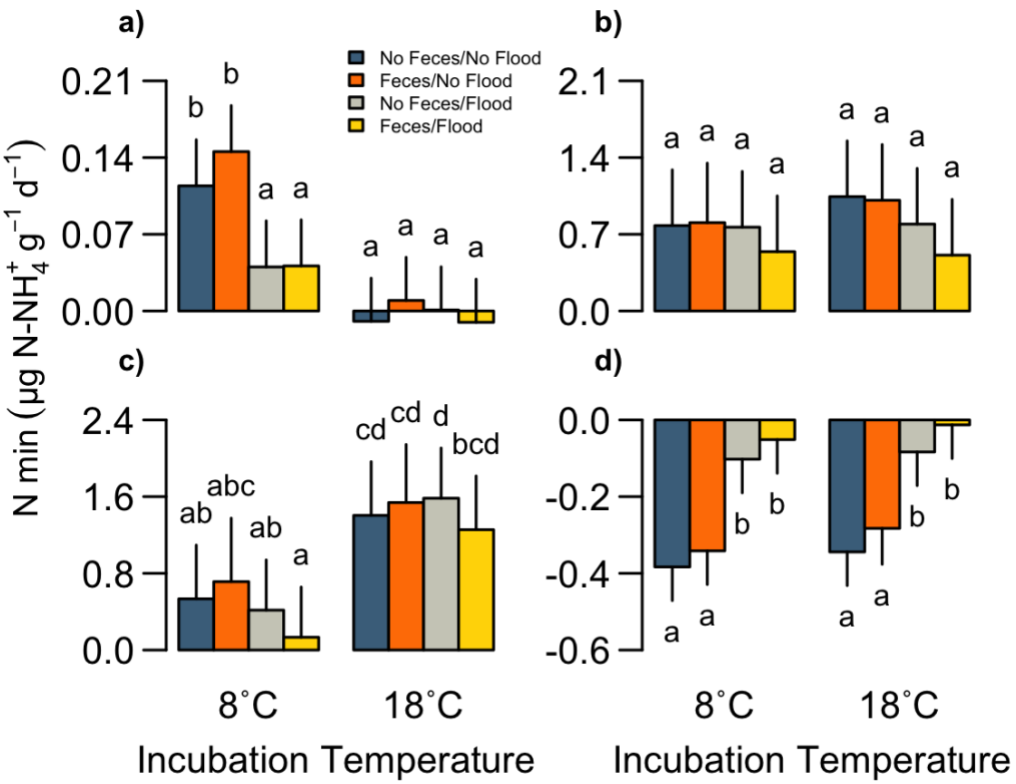


Figure 5. Estimated marginal means (±95% CI) for ammonification for each treatment in each community at 8°C and 18°C following the ANOVA. Letters represent significant groupings based on a sidak adjustment. Figure panes are: (a) Grazing Lawn, (b) Lowland Upland, (c) Upland Wetland, and (d) Tundra community.

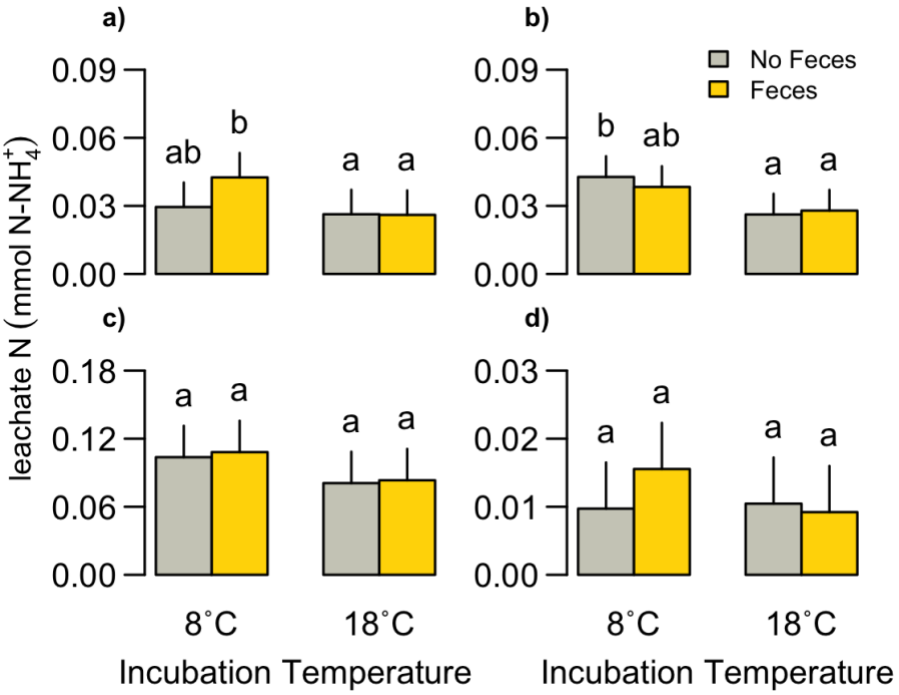


Figure 6. Estimated marginal means (±95% CI) for the concentration of $N\text{-}NH_4^+$ in flood leachate for each treatment in each community at 8°C and 18°C following the repeated measures ANOVA. Letters represent significant groupings based on a sidak adjustment. Figure panes are: (a) Grazing Lawn, (b) Lowland Upland, (c) Upland Wetland, and (d) Tundra community.

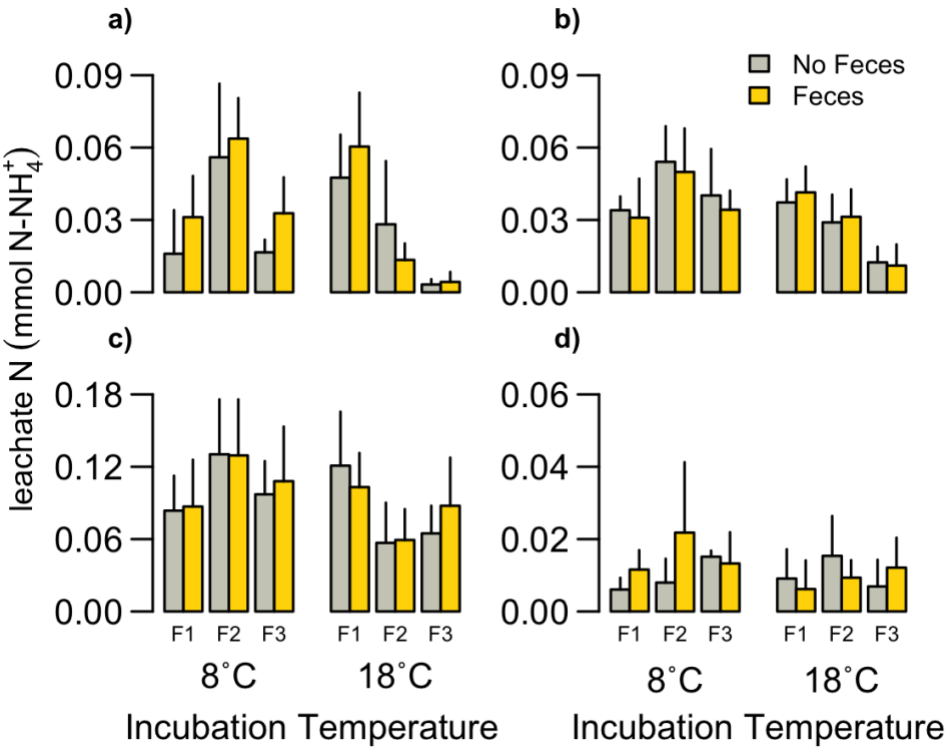


Figure 7. Bar graphs displaying raw data means of the concentration of $N\text{-}NH_4^+$ in flood leachate for each treatment in each community at 8°C and 18 °C during each of the three flooding events. Error bars represent standard deviation values. F1=flooding event one, F2= flooding event 2, and F3= flooding event 3. Figure panes are: (a) Grazing Lawn, (b) Lowland Upland, (c) Upland Wetland, and (d) Tundra community.

Table 1. Mean and standard deviation of soil characteristics of each community. Units are in mmho/cm for Soluble Salts, % for Organic Matter (OM), ppm of N for Nitrate-N, ppm for phosphorus (P), ppm for potassium (K), ppm of S for Sulfate-S, and ppm for sodium (Na). Mean and standard deviation are rounded to three significant figures when possible.

	Grazing Lawn	Lowland Wetland	Upland Wetland	Tundra
Soil pH	5.18 ± 0.0837	5.24 ± 0.114	5.62 ± 0.0447	4.20 ± 0.141
Soluble Salts	3.42 ± 0.700	0.830 ± 0.131	0.482 ± 0.0295	0.112 ± 0.0110
OM	5.08 ± 0.217	57.8 ± 1.63	39.7 ± 1.45	60.3 ± 1.62
Nitrate-N	0.18 ± 0.0837	0.18 ± 0.0837	0.10 ± 0.00	0.10 ± 0.00
K	136 ± 5.13	60.6 ± 7.30	69.4 ± 6.19	34.8 ± 1.48
Sulfate-S	644 ± 25.9	134 ± 18.0	69.9 ± 6.29	31.0 ± 1.80
Na	1412 ± 59.2	692± 67.0	330 ± 25.4	70.8 ± 5.12
P	12.8 ± 0.837	9.8 ± 0.447	13.8 ± 0.447	13.2 ± 0.837
Total C:N	13.7 ± 0.237	24.5 ± 1.36	21.0 ± 0.271	26.9 ± 0.244

Table 2. Mean and standard deviation of the bulk density and field capacity of each community. Units are g/mL for bulk density and g water/g dry soil for field capacity. Mean and standard deviation are rounded to three significant figures when possible.

Community	Bulk Density	Field Capacity
Grazing Lawn	0.843 ± 0.0408	1.05 ± 0.0194
Lowland Wetland	0.0637 ± 0.0142	5.58 ± 0.118
Upland Wetland	0.144 ± 0.0309	4.12 ± 0.315
Tundra	0.0890 ± 0.0397	4.79 ± 0.275

Table 3. Mean and standard deviation of characteristics of dried goose feces. Units are in % N for organic N, ammonium, and total N (TKN), % P_2O_5 for phosphorus (P), % K_2O for potassium (K), % Na for sodium (Na), mmho/cm for Soluble Salts, and % C for total carbon. Mean and standard deviation are rounded to three significant figures when possible.

	Feces
Organic N	1.79 ± 0.0179
Ammonium	0.128 ± 0.00602
Total N (TKN)	1.92 ± 0.0212
P	0.726 ± 0.0573
K	1.99 ± 0.0550
Na	0.95 ± 0.0495
Soluble Salts	64.8 ± 5.96
pH	5.8 ± 0
TC	37.4 ± 1.15
Total C:N	19.5 ± 0.449

Table 4. F-values and P-values (F-Value over P-Value) from the results of the repeated measures ANOVA for CO_2 emissions for soils in each community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=224, (56 for each community). P-values that are bolded are significant at $p<0.05$.

Factor	df	Grazing Lawn	Lowland Wetland	Upland Wetland	Tundra
Graze	1	296	45.9	37.4	29.1
		<0.001	**<0.001**	**<0.001**	**<0.001**
Flood	1	0.00179	1.26	7.12	161
		0.966	0.267	**0.0103**	**<0.001**
Temp	1	265	1080	524	522
		<0.001	**<0.001**	**<0.001**	**<0.001**
Graze*Flood	1	0.0454	2.95	0.335	<0.00001
		0.832	0.0922	0.565	0.999
Flood*Temp	1	1.51	0.0955	0.617	5.50
		0.225	0.759	0.436	**0.0231**
Graze*Temp	1	1.09	0.403	0.0576	2.27
		0.302	0.529	0.811	0.138

Table 5. F-values and P-values (F-Value over P-Value) from the results of the repeated measures ANOVA for CH_4 emissions for soils in each community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=224, (56 for each community). P-values that are bolded are significant at $p<0.05$.

Factor	df	Grazing Lawn	Lowland Wetland	Upland Wetland	Tundra
Graze	1	1.23 0.273	0.486 0.489	0.862 0.358	0.471 0.496
Flood	1	38.4 **<0.001**	8.08 **0.00651**	0.0140 0.906	41.1 **<0.001**
Temp	1	64.2 **<0.001**	299 **<0.001**	126 **<0.001**	70.8 **<0.001**
Graze*Flood	1	2.15 0.149	7.97 **0.00687**	2.32 0.134	0.309 0.581
Flood*Temp	1	6.78 **0.0121**	1.45 0.235	0.00767 0.931	42.7 **<0.001**
Graze*Temp	1	6.80E-04 0.979	0.461 0.500	0.962 0.332	0.436 0.512

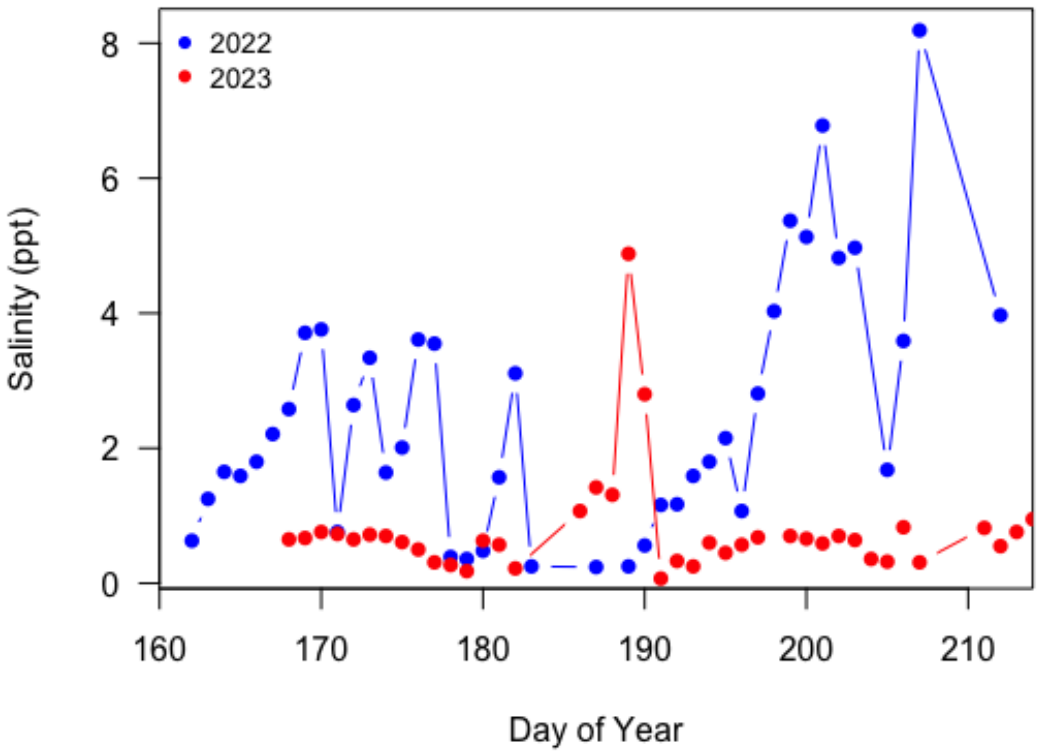
Table 6. F-values and P-values (F-Value over P-Value) from the results of the ANOVA for ammonification for soils in each community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=52 for the Grazing Lawn, N=55 for the Lowland Wetland, N=48 for the Upland Wetland, and N=55 for the Tundra. P-values that are bolded are significant at $p<0.05$.

Factor	df	Grazing Lawn	Lowland Wetland	Upland Wetland	Tundra
Graze	1	0.785	0.939	0.679	6.63
		0.380	0.338	0.415	**0.0132**
Flood	1	16.6	3.64	2.16	139
		<0.001	0.0625	0.149	**<0.001**
Temp	1	66.0	0.739	48.7	2.69
		<0.001	0.394	**<0.001**	0.108
Graze*Flood	1	1.99	0.869	2.33	0.0454
		0.165	0.356	0.135	0.832
Flood*Temp	1	15.3	0.761	0.983	0.179
		<0.001	0.387	0.327	0.674
Graze*Temp	1	0.319	0.0485	0.0231	0.173
		0.575	0.827	0.880	0.679

Table 7. F-values and P-values (F-Value over P-Value) from the results of the repeated measures ANOVA for $N\text{-}NH_4^+$ concentration in flood leachate from soils that were flooded in each community under two feces addition treatments (feces addition vs. no feces addition) and two incubation temperatures (8°C and 18°C). N=112 per flood (28 for each community). P-values that are bolded are significant at $p<0.05$.

Factor	df	Grazing Lawn	Lowland Wetland	Upland Wetland	Tundra
Graze	1	2.54 0.124	0.158 0.694	0.114 0.738	0.824 0.373
Temp	1	6.05 **0.0215**	15.8 **<0.001**	5.37 **0.0293**	1.23 0.277
Graze*Temp	1	2.76 0.110	0.814 0.376	0.00903 0.925	1.96 0.174

APPENDIX



Appendix 1: Salinity of daily tidal samples taken near high tide for the 2022 and 2023 field seasons.

Appendix 2. Soil and feces samples were analyzed for nutrient content by Ward Laboratories in Kearney, Nebraska. For soil, pH and soluble salts were determined using a 1:1 water pH. Organic matter (OM) was determined using loss on ignition (LOI). Nitrate-nitrogen was quantified by extracting nitrate using KCl solution and then using flow injection analysis (FIA) to analyze nitrate. Cations such as potassium (K) and sodium (Na) were quantified using ammonium acetate as an extractant and then using Inductively Coupled Argon Plasma (ICAP) to measure the cations in the extract. Phosphorus (P) was quantified using Mehlich 3 solution as an extractant. Soluble and available sulfur (S) was also quantified using Mehlich 3 solution, a majority of which is sulfate. ICAP was then used to analyze S. For feces, total N represents Total Kjeldahl nitrogen (TKN) (Ward Laboratories in Kearney, Nebraska).

Appendix 3. Complete repeated measures analysis of variance (ANOVA) table for CO_2 emissions for the Grazing Lawn community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	0.0124	0.0124	296	**<0.001**
Flood	1	7.52E-08	7.52E-08	0.00179	0.966
Temp	1	0.0111	0.0111	265	**<0.001**
Graze*Flood	1	1.91E-06	1.91E-06	0.0454	0.832
Flood*Temp	1	6.35E-05	6.35E-05	1.51	0.225
Graze*Temp	1	4.57E-05	4.57E-05	1.09	0.302
Residuals	49	0.00206	4.20E-05		
Error: Within					
Before Date	8	0.0276	0.00345	67.6	**<0.001**
Graze*Before Date	8	0.00374	4.68E-04	9.16	**<0.001**
Flood*Before Date	8	0.00275	3.44E-04	6.73	**<0.001**
Temp*Before Date	8	0.0417	0.00522	102	**<0.001**
Graze*Flood*Before Date	8	4.84E-04	6.06E-05	1.19	0.306
Flood*Temp*Before Date	8	0.00110	1.38E-04	2.70	**0.00674**
Graze*Temp*Before Date	8	1.73E-04	2.16E-05	0.424	0.907
Residuals	392	0.0200	5.11E-05		

Appendix 4. Complete repeated measures analysis of variance (ANOVA) table for CO_2 emissions for the Lowland Wetland community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	0.00915	0.00915	45.9	**<0.001**
Flood	1	2.51E-04	2.51E-04	1.26	0.267
Temp	1	0.215	0.215	1080	**<0.001**
Graze*Flood	1	5.88E-04	5.88E-04	2.95	0.0922
Flood*Temp	1	1.90E-05	1.90E-05	0.0955	0.759
Graze*Temp	1	8.02E-05	8.02E-05	0.403	0.529
Residuals	49	0.00976	1.99E-04		
Error: Within					
Before Date	8	0.108	0.0135	82.4	**<0.001**
Graze*Before Date	8	0.00210	2.62E-04	1.60	0.122
Flood*Before Date	8	0.00479	5.98E-04	3.65	**<0.001**
Temp*Before Date	8	0.0874	0.0109	66.7	**<0.001**
Graze*Flood*Before Date	8	7.81E-04	9.76E-05	0.596	0.781
Flood*Temp*Before Date	8	0.00299	3.73E-04	2.28	**0.0216**
Graze*Temp*Before Date	8	0.00148	1.85E-04	1.13	0.344
Residuals	392	0.0642	1.64E-04		

Appendix 5. Complete repeated measures analysis of variance (ANOVA) table for CO_2 emissions for the Upland Wetland community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	0.0112	0.0112	37.4	**<0.001**
Flood	1	0.00214	0.00214	7.12	**0.0103**
Temp	1	0.157	0.157	524	**<0.001**
Graze*Flood	1	1.01E-04	1.01E-04	0.335	0.565
Flood*Temp	1	1.85E-04	1.85E-04	0.617	0.436
Graze*Temp	1	1.73E-05	1.73E-05	0.0576	0.811
Residuals	49	0.0147	3.00E-04		
Error: Within					
Before Date	8	0.0782	0.00977	46.7	**<0.001**
Graze*Before Date	8	0.00567	7.08E-04	3.38	**<0.001**
Flood*Before Date	8	0.00506	6.33E-04	3.02	**0.00263**
Temp*Before Date	8	0.0281	0.00352	16.8	**<0.001**
Graze*Flood*Before Date	8	0.00201	2.51E-04	1.20	0.298
Flood*Temp*Before Date	8	0.00244	3.05E-04	1.46	0.171
Graze*Temp*Before Date	8	5.87E-04	7.34E-05	0.351	0.945
Residuals	392	0.0820	2.09E-04		

Appendix 6. Complete repeated measures analysis of variance (ANOVA) table for CO_2 emissions for the Tundra community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	0.00744	0.00744	29.1	**<0.001**
Flood	1	0.0410	0.0410	161	**<0.001**
Temp	1	0.133	0.133	522	**<0.001**
Graze*Flood	1	2.26E-10	2.26E-10	<0.00001	0.999
Flood*Temp	1	0.00140	0.00140	5.50	**0.0231**
Graze*Temp	1	5.80E-04	5.80E-04	2.27	0.138
Residuals	49	0.0125	2.55E-04		
Error: Within					
Before Date	8	0.0291	0.00363	37.1	**<0.001**
Graze*Before Date	8	0.00339	4.23E-04	4.33	**<0.001**
Flood*Before Date	8	0.0106	0.00132	13.6	**<0.001**
Temp*Before Date	8	0.00935	0.00117	11.9	**<0.001**
Graze*Flood*Before Date	8	0.00108	1.35E-04	1.38	0.204
Flood*Temp*Before Date	8	0.00196	2.45E-04	2.51	**0.0115**
Graze*Temp*Before Date	8	0.00109	1.36E-04	1.39	0.201
Residuals	392	0.0384	9.78E-05		

Appendix 7. Complete repeated measures analysis of variance (ANOVA) table for CH_4 emissions for the Grazing Lawn community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	5.29E-04	5.29E-04	1.23	0.273
Flood	1	0.0165	0.0165	38.4	**<0.001**
Temp	1	0.0276	0.0276	64.2	**<0.001**
Graze*Flood	1	9.25E-04	9.25E-04	2.15	0.149
Flood*Temp	1	0.00292	0.00292	6.78	**0.0121**
Graze*Temp	1	2.92E-07	2.92E-07	6.80E-04	0.979
Residuals	49	0.0211	4.30E-04		
Error: Within					
Before Date	8	0.0556	0.00695	19.9	**<0.001**
Graze*Before Date	8	0.00109	1.36E-04	0.389	0.926
Flood*Before Date	8	0.0122	0.00153	4.37	**<0.001**
Temp*Before Date	8	0.0764	0.00954	27.3	**<0.001**
Graze*Flood*Before Date	8	0.00113	1.41E-04	0.403	0.919
Flood*Temp*Before Date	8	0.0205	0.00256	7.33	**<0.001**
Graze*Temp*Before Date	8	0.00146	1.82E-04	0.522	0.840
Residuals	392	0.137	3.49E-04		

Appendix 8. Complete repeated measures analysis of variance (ANOVA) table for CH_4 emissions for the Lowland Wetland community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	0.205	0.205	0.486	0.489
Flood	1	3.42	3.42	8.08	**0.00651**
Temp	1	127	127	299	**<0.001**
Graze*Flood	1	3.37	3.37	7.97	**0.00687**
Flood*Temp	1	0.611	0.611	1.45	0.235
Graze*Temp	1	0.195	0.195	0.461	0.500
Residuals	49	20.7	0.423		
Error: Within					
Before Date	8	183	22.9	35.7	**<0.001**
Graze*Before Date	8	2.66	0.332	0.517	0.844
Flood*Before Date	8	5.64	0.705	1.10	0.363
Temp*Before Date	8	237	29.6	46.2	**<0.001**
Graze*Flood*Before Date	8	8.61	1.08	1.68	0.102
Flood*Temp*Before Date	8	5.43	0.678	1.06	0.393
Graze*Temp*Before Date	8	2.19	0.273	0.426	0.905
Residuals	392	252	0.642		

Appendix 9. Complete repeated measures analysis of variance (ANOVA) table for CH_4 emissions for the Upland Wetland community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	0.555	0.555	0.862	0.358
Flood	1	0.00902	0.00902	0.0140	0.906
Temp	1	81.3	81.3	126	**<0.001**
Graze*Flood	1	1.49	1.49	2.32	0.134
Flood*Temp	1	0.00495	0.00495	0.00767	0.931
Graze*Temp	1	0.620	0.620	0.962	0.332
Residuals	49	31.6	0.645		
Error: Within					
Before Date	8	113	14.1	20.2	**<0.001**
Graze*Before Date	8	6.55	0.818	1.17	0.314
Flood*Before Date	8	5.22	0.653	0.936	0.486
Temp*Before Date	8	116	14.5	20.8	**<0.001**
Graze*Flood*Before Date	8	5.24	0.655	0.939	0.484
Flood*Temp*Before Date	8	5.34	0.667	0.956	0.470
Graze*Temp*Before Date	8	6.63	0.829	1.19	0.304
Residuals	392	273	0.697		

Appendix 10. Complete repeated measures analysis of variance (ANOVA) table for CH_4 emissions for the Tundra community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=56. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	1.78E-05	1.78E-05	0.471	0.496
Flood	1	0.00156	0.00156	41.1	**<0.001**
Temp	1	0.00268	0.00268	70.8	**<0.001**
Graze*Flood	1	1.17E-05	1.17E-05	0.309	0.581
Flood*Temp	1	0.00162	0.00162	42.7	**<0.001**
Graze*Temp	1	1.65E-05	1.65E-05	0.436	0.512
Residuals	49	0.00186	3.79E-05		
Error: Within					
Before Date	8	0.00864	0.00108	48.0	**<0.001**
Graze*Before Date	8	4.03E-05	5.03E-06	0.224	0.987
Flood*Before Date	8	0.00702	8.78E-04	39.0	**<0.001**
Temp*Before Date	8	0.00799	9.99E-04	44.4	**<0.001**
Graze*Flood*Before Date	8	4.36E-05	5.46E-06	0.242	0.983
Flood*Temp*Before Date	8	0.00687	8.58E-04	38.1	**<0.001**
Graze*Temp*Before Date	8	3.50E-05	4.38E-06	0.195	0.992
Residuals	392	0.00882	2.25E-05		

Appendix 11. Complete analysis of variance (ANOVA) table for ammonification for the Grazing Lawn community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=52. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Graze	1	0.00118	0.00118	0.785	0.380
Flood	1	0.0249	0.0249	16.6	**<0.001**
Temp	1	0.0990	0.0990	66.0	**<0.001**
Graze*Flood	1	0.00299	0.00299	1.99	0.165
Flood*Temp	1	0.0230	0.0230	15.3	**<0.001**
Graze*Temp	1	4.79E-04	4.79E-04	0.319	0.575
Residuals	45	0.0675	0.00150		

Appendix 12. Complete analysis of variance (ANOVA) table for ammonification for the Lowland Wetland community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=55. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Graze	1	0.238	0.238	0.939	0.338
Flood	1	0.923	0.923	3.64	0.0625
Temp	1	0.187	0.187	0.739	0.394
Graze*Flood	1	0.220	0.220	0.869	0.356
Flood*Temp	1	0.193	0.193	0.761	0.387
Graze*Temp	1	0.0123	0.0123	0.0485	0.827
Residuals	48	12.2	0.254		

Appendix 13. Complete analysis of variance (ANOVA) table for ammonification for the Upland Wetland community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=48. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Graze	1	0.176	0.176	0.679	0.415
Flood	1	0.561	0.561	2.16	0.149
Temp	1	12.6	12.6	48.7	**<0.001**
Graze*Flood	1	0.604	0.604	2.33	0.135
Flood*Temp	1	0.255	0.255	0.983	0.327
Graze*Temp	1	0.00600	0.00600	0.0231	0.880
Residuals	41	10.6	0.259		

Appendix 14. Complete analysis of variance (ANOVA) table for ammonification for the Tundra community under two feces addition treatments (feces addition vs. no feces addition), two flooding treatments (flooding vs. no flooding), and two incubation temperatures (8°C and 18°C). N=55. P-values and factors that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Graze	1	0.0500	0.0500	6.63	**0.0132**
Flood	1	1.05	1.05	139	**<0.001**
Temp	1	0.0203	0.0203	2.69	0.108
Graze*Flood	1	3.43E-04	3.43E-04	0.0454	0.832
Flood*Temp	1	0.00135	0.00135	0.179	0.674
Graze*Temp	1	0.00131	0.00131	0.173	0.679
Residuals	48	0.362	0.00755		

Appendix 15. Complete repeated measures analysis of variance (ANOVA) table for N-NH_4^+ concentration in floodwater leachate for the Grazing Lawn community from soils that were flooded in each community under two feces addition treatments (feces addition vs. no feces addition) and two incubation temperatures (8°C and 18°C). N=28. P-values and treatments that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	8.55E-04	8.55E-04	2.54	0.124
Temp	1	0.00204	0.00204	6.05	**0.0215**
Graze*Temp	1	9.31E-04	9.31E-04	2.76	0.110
Residuals	24	0.00809	3.37E-04		
Error: Within					
Flood Date	2	0.0120	0.00601	20.8	**<0.001**
Graze*Flood Date	2	0.00113	5.66E-04	1.96	0.152
Temp*Flood Date	2	0.0182	0.00908	31.4	**<0.001**
Graze*Temp*Flood Date	2	3.68E-04	1.84E-04	0.636	0.534
Residuals	48	0.0139	2.89E-04		

Appendix 16. Repeated measures analysis of variance (ANOVA) table for $N\text{-}NH_4^+$ concentration in floodwater leachate for the Lowland Wetland community from soils that were flooded in each community under two feces addition treatments (feces addition vs. no feces addition) and two incubation temperatures (8°C and 18°C). N=28. P-values and treatments that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	3.83E-05	3.83E-05	0.158	0.694
Temp	1	0.00382	0.00382	15.8	**<0.001**
Graze*Temp	1	1.97E-04	1.97E-04	0.814	0.376
Residuals	24	0.00580	2.42E-04		
Error: Within					
Flood Date	2	0.00404	0.00202	18.0	**<0.001**
Graze*Flood Date	2	6.29E-05	3.15E-05	0.281	0.757
Temp*Flood Date	2	0.00439	0.00219	19.6	**<0.001**
Graze*Temp*Flood Date	2	6.56E-06	3.28E-06	0.0293	0.971
Residuals	48	0.00538	1.12E-04		

Appendix 17. Repeated measures analysis of variance (ANOVA) table for $N\text{-}NH_4^+$ concentration in floodwater leachate for the Upland Wetland community from soils that were flooded in each community under two feces addition treatments (feces addition vs. no feces addition) and two incubation temperatures (8°C and 18°C). N=28. P-values and treatments that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	2.53E-04	2.53E-04	0.114	0.738
Temp	1	0.0119	0.0119	5.37	**0.0293**
Graze*Temp	1	2.01E-05	2.01E-05	0.00903	0.925
Residuals	24	0.0533	0.00222		
Error: Within					
Flood Date	2	0.00120	6.01E-04	0.666	0.518
Graze*Flood Date	2	0.00211	0.00105	1.17	0.320
Temp*Flood Date	2	0.0340	0.0170	18.8	**<0.001**
Graze*Temp*Flood Date	2	0.00104	5.18E-04	0.574	0.567
Residuals	48	0.0433	9.03E-04		

Appendix 18. Repeated measures analysis of variance (ANOVA) table for $N\text{-}NH_4^+$ concentration in floodwater leachate for the Tundra community from soils that were flooded in each community under two feces addition treatments (feces addition vs. no feces addition) and two incubation temperatures (8°C and 18°C). N=28. P-values and treatments that are bolded are significant at $p<0.05$.

Source of Variation	df	SS	MS	F-value	P-value
Error: Microcosm Number					
Graze	1	1.10E-04	1.10E-04	0.824	0.373
Temp	1	1.65E-04	1.65E-04	1.23	0.277
Graze*Temp	1	2.62E-04	2.62E-04	1.96	0.174
Residuals	24	3.20E-03	1.33E-04		
Error: Within					
Flood Date	2	4.22E-04	2.11E-04	4.19	**0.0210**
Graze*Flood Date	2	2.76E-05	1.38E-05	0.274	0.761
Temp*Flood Date	2	4.38E-05	2.19E-05	0.435	0.650
Graze*Temp*Flood Date	2	6.39E-04	3.19E-04	6.34	**0.00359**
Residuals	48	0.00242	5.03E-05		

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