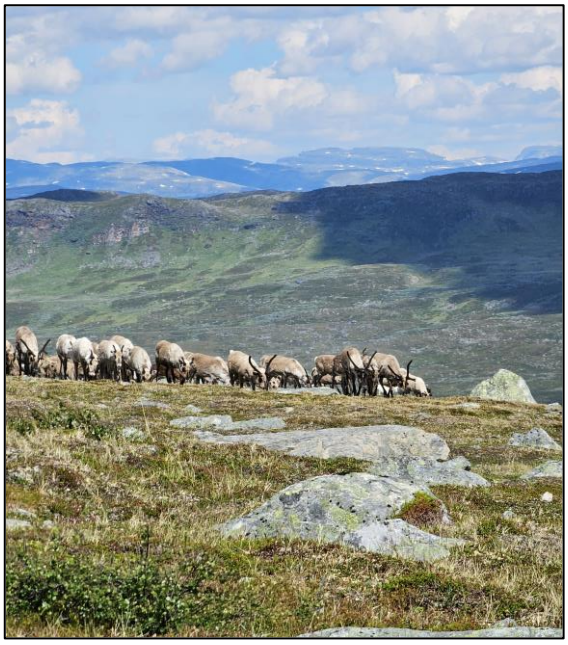
UNIVERSITY OF GOTHENBURG

DEPARTMENT OF EARTH SCIENCES

INFLUENCE OF REINDEER ON METHANE FLUXES IN ARCTIC TUNDRA ECOSYSTEMS



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Abstract

Atmospheric methane (CH_4) contributes to global warming and Arctic amplification. CH_4 fluxes are important in the Arctic, since approximately 50 % of the global soil organic carbon is stored in the Arctic. Soil moisture and soil temperature are key factors for CH_4 fluxes as they regulate microbial activity and redox state, while other factors such as plant functional types and isotopic signature (e.g. $\delta^{13}C$) are also important. Large mammalian herbivores, mostly reindeer in the Swedish Arctic, can change vegetation communities, soil microclimate and soil physico-chemical properties due to trampling, nutrient input and grazing/browsing. This thesis aims to determine the difference in net CH_4 fluxes of wet and dry Oro-arctic vegetation between reindeer herbivory excluded areas and ambient areas. Two sites, a wet grass meadow and a dry shrub heath, near Ritsem, Sweden, were investigated. CH_4 fluxes were measured six times during the snow free season at reindeer herbivory excluded and ambient areas at both sites. It was measured over two focal shrubs: deciduous shrubs (*Betula nana*) and evergreen shrubs (*Empetrum nigrum*). The results showed an overall uptake of CH_4 at both the grass meadow and the shrub heath. At the grass meadow this could be due to high quality carbon, while the shrub heath acts like a typical upland habitat. The grass meadow showed no impact of reindeer herbivory on the CH_4 fluxes or soil moisture. Variations in the fluxes at the grass meadow were instead affected by soil moisture, soil temperature, surface temperature, $\delta^{13}C$ and seasonality. At the shrub heath, reindeer exclusion had an impact on the CH_4 fluxes by increasing the uptake under *Betula nana*. Soil moisture was also lower at the same plots. There was an increase in *Betula nana* cover at herbivory excluded areas at both study sites, with the biggest difference being at the shrub heath. These findings point towards increased evapotranspiration that dry the shrub heath soil and consequently increase the CH_4 uptake under *Betula nana* at these herbivory excluded areas. In conclusion, there is a larger reindeer herbivory effect at the dry shrub heath than the wet grass meadow.

Sammanfattning

Atmosfärisk metan (CH_4) bidrar till global uppvärmning och arktisk amplifiering. CH_4-flöden är viktiga i Arktis, eftersom cirka 50 % av allt globalt organiskt kol i marken lagras i Arktis. Markfuktighet och marktemperatur är nyckelfaktorer för CH_4-flöden eftersom de regulerar mikrobiell aktivitet och redoxtillstånd, medan andra faktorer som växtfunktionstyper och isotopisk signatur (t.ex. $\delta^{13}C$) också är viktiga. Stora däggdjursväxtätare, mestadels renar i svenska Arktis, kan förändra vegetationssamhällens, markmikroklimat och markegenskaper genom trampning, tillförsel av näringsämnen och bete. Denna uppsats syftar till att fastställa skillnaden i netto-CH_4-flöden av våt och torr oroarktisk vegetation mellan områden uteslutna från renar och omgivande områden. Två platser, en våt gräsäng och en torr buskhed, nära Ritsem, Sverige, undersöktes. CH_4-flöden mättes vid sex tillfällen under hela växtsäsongen i områden uteslutet från renar och omgivande områden på både gräsängen och buskheden. Det mättes över två fokusbuskar: lövfällande buskar (*Betula nana*) och vintergröna buskar (*Empetrum nigrum*). Resultaten visade ett totalt upptag av CH_4 både på gräsängen och buskheden. På gräsängen kan detta bero på kol av hög kvalitet, medan buskheden fungerar som en typisk höglandsmiljö. Gräsängen visade ingen påverkan av renarnas bete på CH_4-flödena eller markfuktigheten. Variationer i flödena på gräsängen påverkades istället av markfuktighet, marktemperatur, ytemperatur, $\delta^{13}C$ och säsongsvariation. Vid buskheden påverkade uteslutning av renar CH_4-flödena genom att öka upptaget under *Betula nana*. Markfuktigheten var också lägre vid samma plotter. Det fanns en ökning av täckningen av *Betula nana* i områden som utesluter renar på båda studieplatserna, med den största skillnaden på buskheden. Dessa fynd pekar mot ökad evapotranspiration som torkar jorden vid buskheden och konsekvent ökar CH_4-upptaget under *Betula nana* vid dessa områden som utesluter renar. Sammanfattningsvis finns det en större effekt av renarnas bete på den torra buskheden än på den våta gräsängen.

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1. Introduction

The Arctic is warming faster than the global average due to Arctic amplification, and one of the contributors to the warming is increased methane (CH_4) in the atmosphere (Rantanen et al., 2022). CH_4 is the second most abundant, after carbon dioxide (CO_2), and one of the most efficient greenhouse gases in the atmosphere (Masson-Delmotte et al., 2021; Pachauri et al., 2014). It is 28 times more efficient as a greenhouse gas than CO_2 under a 100-year period, but it has a shorter atmospheric lifetime of around 12 years (Pachauri et al., 2014). CH_4 fluxes, especially in the Arctic, is important since approximately 50 % of the global soil organic carbon is stored in the Arctic (Hugelius et al., 2014). Wet tundra habitats tend to have emissions of CH_4, while more upland and dry tundra habitats tend to have uptake of CH_4 (Emmerton et al., 2014; St Pierre et al., 2019).

CH_4 in the soil is determined by two competing processes, methanogenesis (CH_4 production) and methanotrophy (CH_4 consumption) (Keuschnig et al., 2022). Methanogenesis is performed by methanogenic archaea under anoxic conditions deeper in the soil (Hedderich & Whitman, 2006). The CH_4 produced rises and reaches higher up in the soil where methanotrophic bacteria exist. They perform methanotrophy, CH_4 oxidation, under mostly oxygen rich (some anoxic) conditions (Keuschnig et al., 2022). CH_4 flux is the net flux of the production and consumption.

Many things in the soil contribute to uptake or emission of CH_4, such as soil moisture, soil temperature, vegetation and soil physico-chemical properties (Christensen et al., 2003; Rinne et al., 2022; Voigt et al., 2017; Voigt et al., 2019). The most important factors for CH_4 flux are soil moisture and soil temperature (Christensen et al., 2003; Olefeldt et al., 2013; Voigt et al., 2019; Voigt et al., 2023). Soil moisture controls CH_4 fluxes by making the soil anaerobic with high soil moisture, giving advantage to methanogenic archaea, and making the soil aerobic with low soil moisture, giving advantage to methanotrophic bacteria (Keuschnig et al., 2022). Soil moisture is highly dependent on intake and outtake of water in a system, as well as evapotranspiration (Bring et al., 2016). Higher soil temperature stimulates microbial activity, which would lead to CH_4 emission or uptake depending on if there is more aerobic or anaerobic activity (Van Hulzen et al., 1999). Different plant species or functional types can affect the CH_4 differently, for example some sedges have aerenchyma, which are air channels in the roots that can efficiently transport CH_4 directly from the soil to the atmosphere (Hodgkins et al., 2018; Noyce et al., 2014; Sachs, 1875). Shrubs however, which grow more in drier areas, contribute

to more aerobic decomposition, which will decrease the CH_4 emissions (Hodgkins et al., 2018; Keuschnig et al., 2022). Soil physico-chemical properties such as isotopic signature (e.g. $\delta^{13}C$) can give insight in the turnover of soil organic matter, which is a substrate for methanogenesis and methanotrophy (Soldatova et al., 2024).

The soil and the vegetation in Arctic tundra can be altered by large mammalian herbivores, such as reindeer, moose and muskoxen (Falk et al., 2015; Mathisen et al., 2010; Ylänne et al., 2018). In the Swedish Arctic, reindeer graze large parts of the land (Sametinget, 2024). Large mammalian herbivores can change vegetation communities, soil microclimate (defined as soil moisture and soil temperature) and soil physico-chemical properties (Fischer et al., 2022; Vowles et al., 2017a; Ylänne et al., 2018). The vegetation communities can shift from shrubs to grasses and sedges through trampling and browsing, and there could be less deciduous tall shrubs (Falk et al., 2015; Mathisen et al., 2010; Vowles et al., 2017a; Ylänne et al., 2018). The herbivores can increase nutrient availability from fertilization, accelerate nutrient cycling, reduce plant litter which results in increased evapotranspiration and decreased above ground biomass (Fischer et al., 2022; Magliano et al., 2017; Olofsson et al., 2004; Raillard & Svoboda, 1999). Trampling and grazing compacts the soil resulting in it being less aerated, decreases soil moisture and increases soil temperature (Fischer et al., 2022; Olofsson et al., 2004; Ylänne et al., 2018). Few studies investigating CH_4 fluxes in connection to reindeer herbivory in the Arctic, highlighting a need for further research.

The aim of this thesis is to determine the difference in net CH_4 fluxes of a wet (grass meadow) and dry (shrub heath) Oro-arctic vegetation between large mammalian herbivory excluded areas and ambient areas. This study hypothesizes that:

(a) the wet site will have overall emission of CH_4 while the dry site will have overall uptake of CH_4, because wet sites in the Arctic usually emit CH_4 while drier sites can have uptake of CH_4 (Emmerton et al., 2014; St Pierre et al., 2019).
(b) The ambient areas will have stronger uptake of CH_4 than the herbivory excluded areas at both the wet and the dry site, because soil moisture will be reduced through soil compaction (Fischer et al., 2022; Wang et al., 2023).
(c) The soil moisture in the ambient areas will be reduced compared to the herbivory excluded areas for both sites, largest at the wet site. This is due to increased evapotranspiration from reduced plant cover and compaction of soil. The compaction

can also reduce infiltration of water into the soil (Cournane et al., 2011; Hassan et al., 2024).

(d) The cover of the deciduous tall shrub *Betula nana* will increase at the herbivory excluded areas compared to the ambient, with the biggest difference being at the wet site. The wet herbivory excluded areas will be able to grow more and larger deciduous shrubs. They also have more palatable plants than the dry, such as deciduous shrubs, which means that the herbivory effect will be higher at the wet site than the dry (Vowles & Björk, 2019; Ylänne et al., 2015).

2. Methods

2.1 Study sites

The study was conducted at two Arctic tundra sites north of Ritsem in the Swedish Scandes, Norrbotten county, in Sweden (figure 1). These sites have previously been studied, but never for CH_4 fluxes (Brachmann et al., 2023; Vowles et al., 2017a; Vowles et al., 2017b). One of the sites is a shrub heath (67°46'33" N, 17°32'22" E; 719 m.a.s.l), hereon referred to as RIRI, and the other a grass meadow (67°46'33" N, 17°32'22" E; 853 m.a.s.l), hereon referred to as RIGA (figure 1). RIRI is 6.5 km north of Ritsem and RIGA 15.5 km northeast, while they sites are 9.5 km from each other. RIRI is in the Unna Tjerusj Sami village and RIGA the Baste Čearru Sami village. The normal air temperature for Ritsem during the snow free months (June-September) ranges from 6-12 °C, and the normal precipitation ranges from 39-62 mm/month (figure 2). Reindeer (*Rangifer tarandus tarandus*) are the most prominent large mammalian herbivore at both sites. The density of reindeer, reported for Unna Tjerusj near RIGA are 2.2 km^{-2} and 1.4 km^{-2} for Baste Čearru near RIRI (Vowles et al., 2017a; Vowles et al., 2017b).

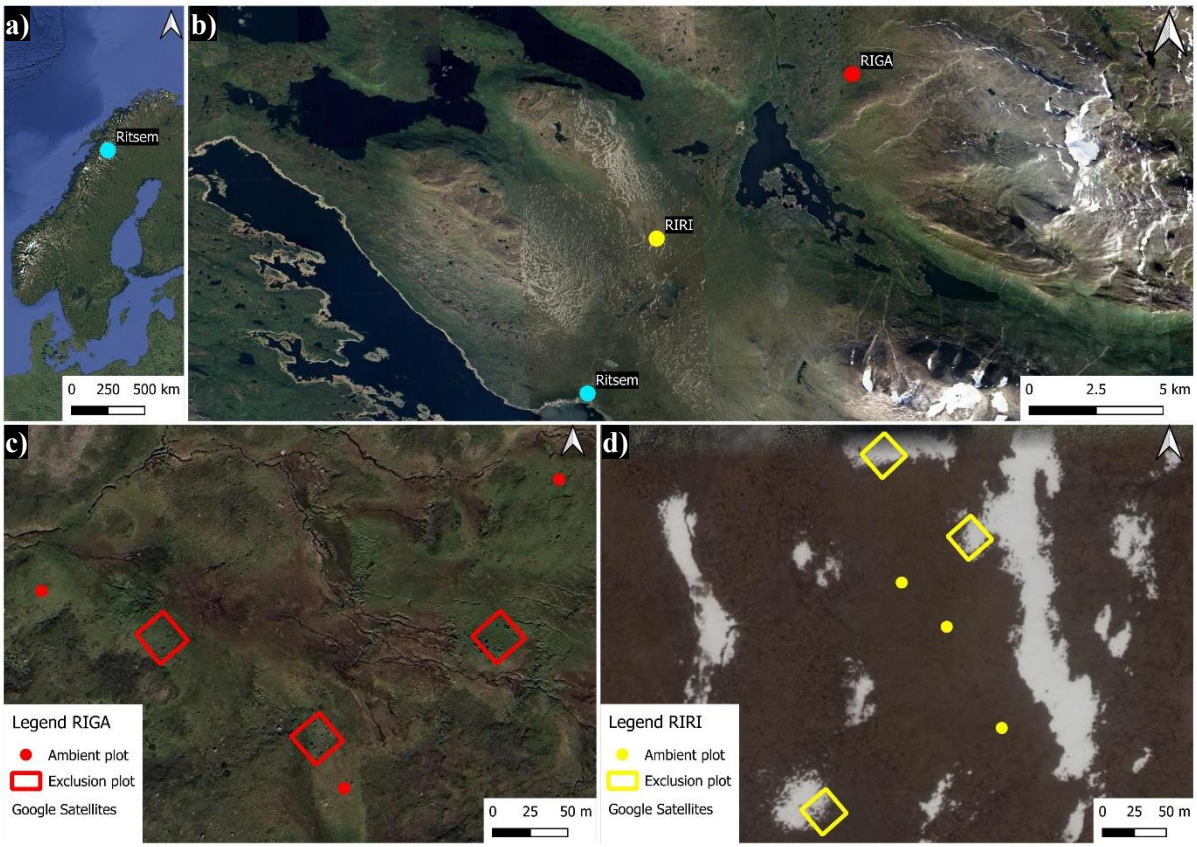

Figure 1. a) Where Ritsem is situated in Sweden. b) Where the study sites are related to Ritsem and each other. c) Where the ambient and exclusion plots are situated at RIGA. d) where the ambient and exclusion plots are situated at RIRI.

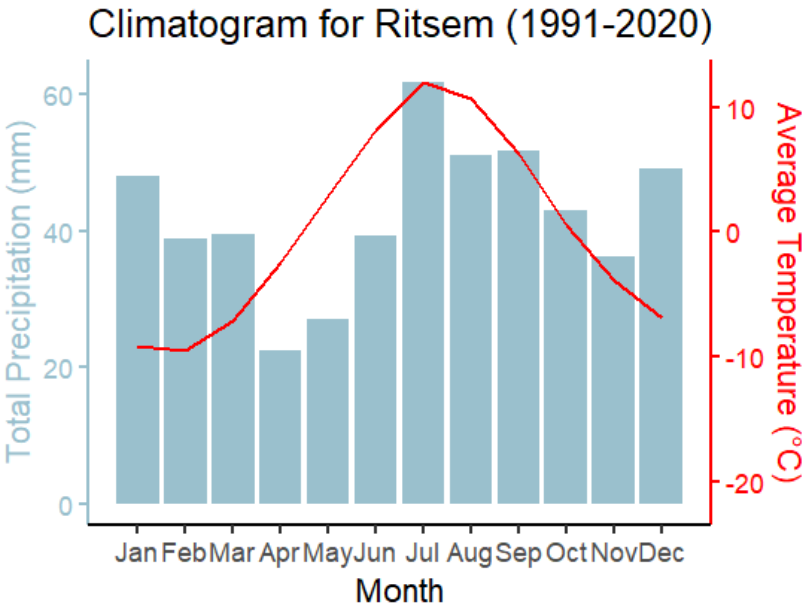

Figure 2. Normal precipitation and normal temperature for Ritsem during the period 1991-2020 (SMHI, 2024).

Two study sites were investigated, a grass meadow and a shrub heath, and at each site there were six plots investigated, three fenced plots excluding reindeers and other large mammalian herbivores, and three ambient control plots where reindeer and other large mammalian herbivores were not excluded (figure 1). The plots were installed in 1995, measure 25 x 25 m, and the fences are a wire mesh 1.7 m high. Measurements were taken 6 times during the growing (snow free) season of 2024. Period 1 on 27-28/6, period 2 on 10-11/7, period 3 on 25-26/7, period 4 on 6-7/8, period 5 on 21-22/8, and period 6 on 5-6/9.

In each plot there were four subplots, two including an evergreen (dwarf) shrub represented by *Empetrum nigrum*, further mentioned as Empetrum, and two including a deciduous (tall) shrub represented by *Betula nana*, further mentioned as Betula (figure 3). One evergreen shrub subplot and one deciduous shrub subplot were grouped together at each side of each plot.

Figure 3. Examples of subplots of a) *Empetrum nigrum* and b) *Betula nana*.

2.1.1 RIGA & RIRI

RIGA is a grass meadow that is representing a wet site for this project (figure 4a-b). It is located in a valley on quite a flat west facing area. The dominating plant species in the area are shrubs *Betula nana*, and *Salix* spp., forbs *Viola biflora*, *Thalictrum alpinum*, and *Saussurea alpina*, grasses *Deschampsia cespitosa* and *Deschampsia flexuosa,* and the sedge *Carex aquatilis* (Vowles et al., 2017b). RIRI is a shrub heath representing a dry environment compared to the

grass meadow (figure 4c-d). It is located higher up on a mountain on a flat area facing south-east. Here the dominating plant species are *Empetrum nigrum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calluna vulgaris*, and *Betula nana*. But there are also more species making it a very species rich shrub heath: *Calamagrostis lapponica*, *Carex bigelowii*, *Bistorta vivipara* and *Hieracium* L. sect. *Alpina* (Vowles et al., 2017a). At both sites the bedrock is locally calciferous and consist of relatively easy weathered mica schist that affects the vegetation (Eriksson et al., 2007).

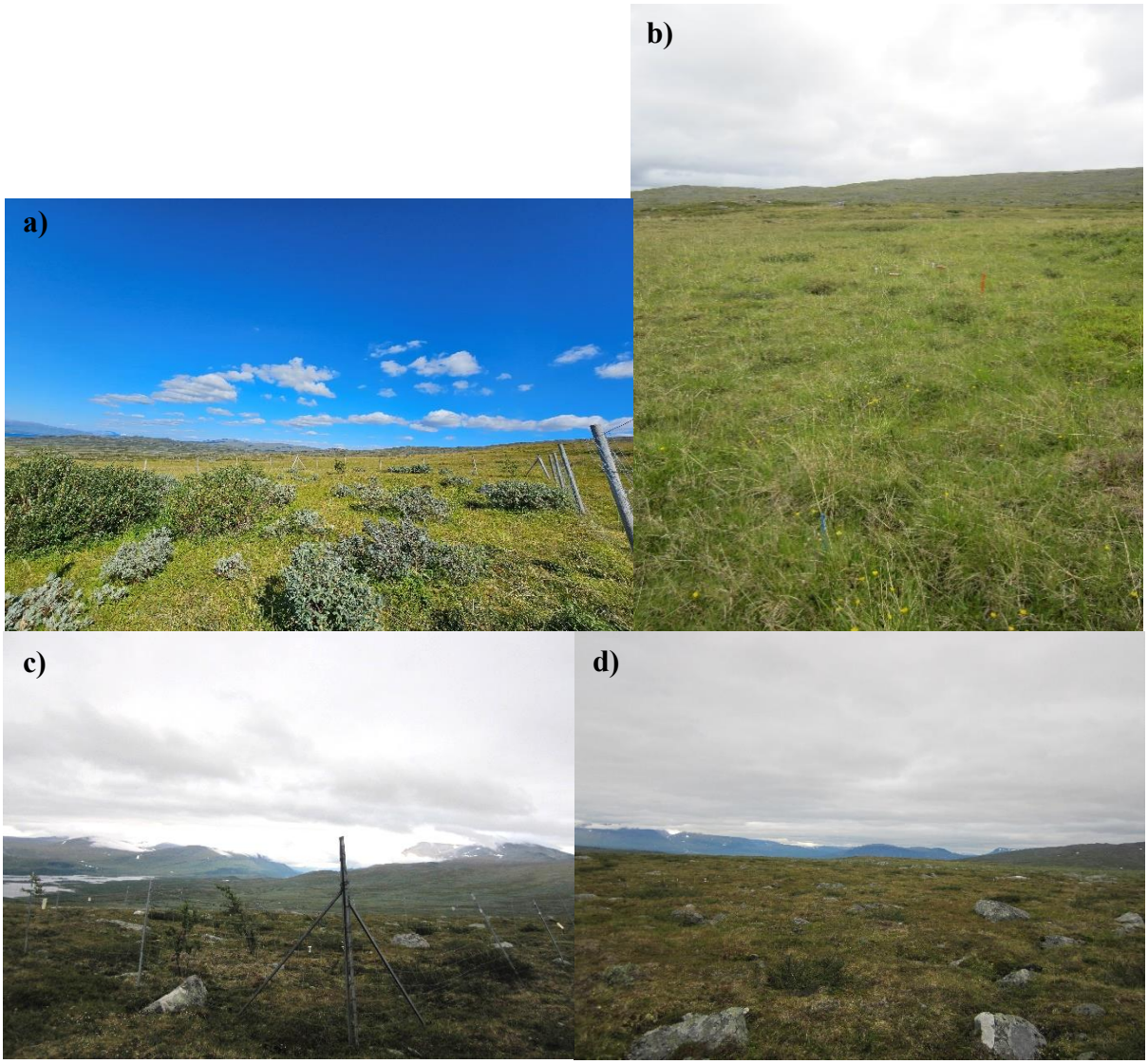

Figure 4. a) Exclosure plot RIGA, b) ambient plot RIGA, c) exclosure plot RIRI, d) ambient plot RIRI.

2.2 CH_4 fluxes

CH_4 flux measurements were completed with an Ultra-portable Greenhouse Gas Analyzer (UGGA; Los Gatos Research, USA). This analyser measured CH_4 in ppm from the chamber

headspace and corrected for water vapour in the air. The technique used was a closed chamber system with a transparent chamber, that was covered with a hood to also take measurements with a dark chamber. This was done to enclose whole ecosystem plots with vegetation and underlying soil. There were collars with a size of Ø20 cm installed into the ground that the chamber placed over. The chamber fit over the base using a plastic tube with a silicon seal attached to the chamber, so when the chamber was placed on the collar, it formed an airtight seal. Each measurement lasted 4 minutes and the chamber was aired in between measurements to allow the CH_4 concentration to return to normal atmospheric concentrations.

To calculate the CH_4 flux, the "FluxCal" function from the *FluxCalR* package was used in R version 4.4.0 (R Core Team, 2024; Zhao, 2019). The flux rate (F) was calculated with the equation in equation 1.

$$F = vol/(R \times T_a \times area) \times dG/dt \quad (1)$$

Vol is the volume of the chamber measured in situ for each subplot, R is the gas constant, T_a is the ambient temperature (K), area is the area of the base of the chamber (m^2), and dG/dt is the rate of the measured gas concentration change over time t (ppm s^{-1}) measured by the UGGA. The air pressure data is from the SMHI's Ritsem A weather station, and it is located 541.214 m above sea level (SMHI, 2025).

The CH_4 flux was converted from µmol CH_4 m^{-2} s^{-1} to µg CH_4 m^{-2} h^{-1} using the equation in equation 2. The µmol is multiplied by the combined molar mass of the carbon (12.01 g mol^{-1}) and the hydrogen (4*1.01 g mol^{-1}). It is lastly multiplied by 3600 to get the flux per hour instead of per second.

$$\mu mol \times Molar\ mass(g\ mol^{-1}) \times 3600 \quad (2)$$

Interpolation was done for the N/A values in the measured CH_4 data. For the single N/A values there was an average made from the value before and after. At other places there were several N/A values in a row and therefore there was an even sequence of values made between the value before and after the N/A values. CH_4 flux measurements from transparent and dark chamber did not differ a lot (figure 5), and it was therefore decided to use both as replicates in the further analyses.

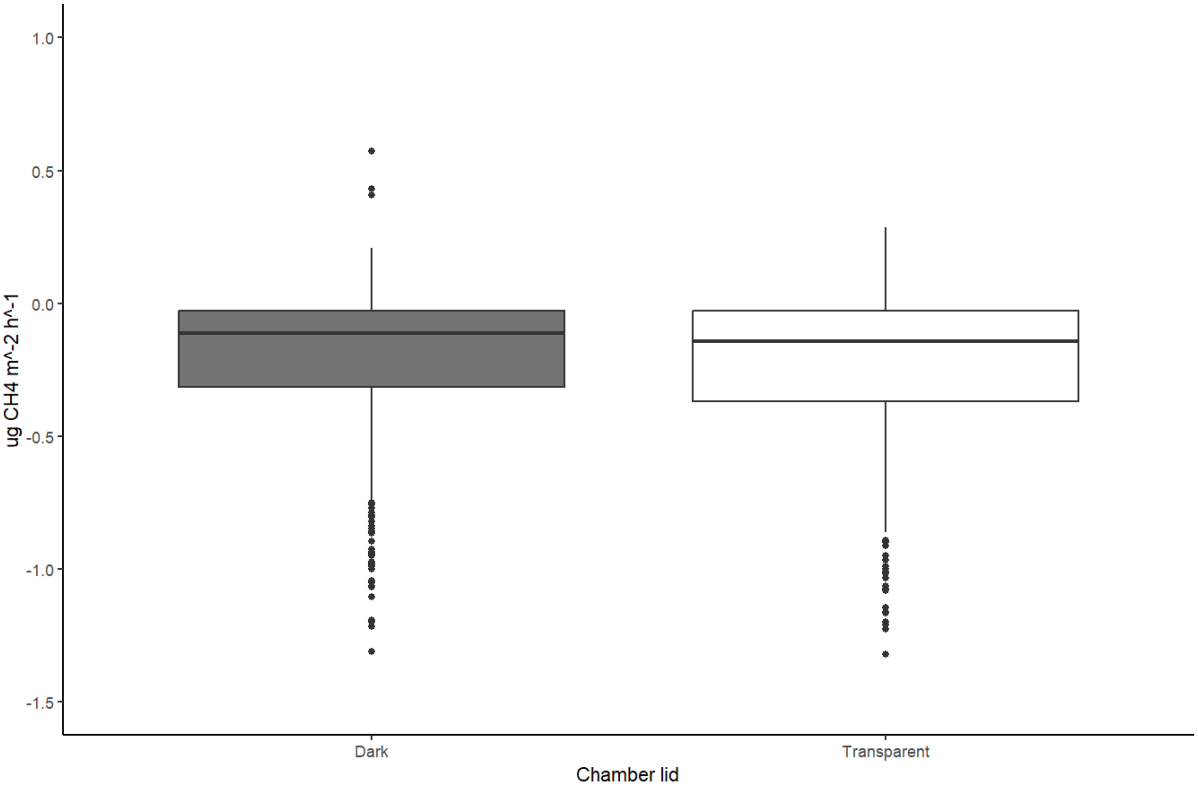

Figure 5. CH_4 fluxes between dark and transparent chamber lids.

2.3 Vegetation

The vegetation inventory was done using a point intercept technique with a 0.5 x 0.5 m point frame centred over the collar of each subplot. The frame had five lines along each axis producing 25 evenly spaced intersecting points, and the first species identified at every intersection was recorded.

The plant species identified during the inventory were sorted into plant functional types (appendix A). Namely, deciduous tall shrub, deciduous dwarf shrub, evergreen tall shrub, evergreen dwarf shrub, forb, grass and sedge. Based on Elmendorf et al. (2012), tall shrubs were categorized as shrubs > 50 cm and dwarf shrubs are shrubs measuring ≤ 50 cm height. The height classes are based on the highest average height for an adult plant (Mossberg & Stenberg, 2008). Rushes were grouped into the sedges since they are more similar to sedges than grasses, as they are both typically non-mycorrhizal. Ferns, Lycopodium and Selaginella were grouped with forbs. The percentage cover of the different plant species that were identified within the flux collar during the vegetation inventory for every subplot was calculated.

Thereafter all percentages for every functional type for every subplot was summed. There were no evergreen tall shrubs at either site, and therefore they were not included in further analyses.

2.4 Soil

Soil samples were taken at every subplot during period 1, 3, 4 and 6. Soil was not taken during all measurement periods as it was unnecessary for the variables of interest and to minimize the number of holes around the collars. The sampling times were selected to maximize any potential differences along the growing season. Two samples were taken on opposite sides of the subplots with a soil corer. Each sample was 2 cm in diameter and aimed to be 10 cm deep since that is where the bacteria and fungi is most productive and where most roots are (Björk et al., 2007). However, at some subplots in the shrub heath it was too rocky to take that deep of a sample and so maximum depth was taken. The cores were stored in freeze boxes during transportation, and in a freezer until lab work was done. All RIGA samples from period 1 and all samples from both site from period 6 were stored with silica gel.

The soil was sieved frozen in a 2 mm metal sieve, then stored in sample jars in a freezer until freeze dried. The samples were freeze dried using the VirTis benchtop K (Chemical Instruments AB) freeze drier. In the freeze drier they were covered with parafilm with a few holes poked through, and tape to secure it. The samples were in the freeze drier for circa 24 hours from that the condenser were at -40 to -50 °C and vacuum pressure <200 µBar. The ones that were not completely dried during the 24 hours were rewetted with water in a spray bottle and put through the machine again for 24 hours.

The soil organic matter (SOM) was calculated by weighing approximately 5 g of the soil samples in crucibles that was put in an Heraeus D-6450 Hanau muffle oven for 8 hours at 550 °C, at which temperature all the organic matter will combust. Each crucible was weighed, then the soil, and after taken out of the oven it was weighed again. With that the percentage of the weight lost in the oven was calculated, which represents the SOM. Some samples did not have enough soil left after taking 5 g or did not have 5 g in total, and therefore less soil was used for those samples (ranging from 0.2-4 g) and the samples noted.

pH was only measured for period 3 and 4 due to time constraints. To measure the pH, in general 5 g of soil was weighed out, and between 0.2-4 g for the ones that did not have enough. First

each 5 g sample was submerged in 25 ml deionized water, same ratio of soil to water for the ones with less soil. The samples where then shaken on a shake table for 30 minutes, then left for 24 hours. After that the pH was measured using a Metrohm 691 pH Meter. Then 2 molar KCl, with a 0.25 ml KCl to 5 g of soil (the amount used since the beginning) ratio to the soil to get 0.002 molar KCl, was put in the soil mixture, shaken on a shake table for 30 minutes, then left for another 24 hours. After which the pH was measured again. KCl is added to extract more nutrient than from only water (Kome et al., 2018).

Total nitrogen, total carbon, $\delta^{15}N$ and $\delta^{13}C$ was measured by first grinding the soil samples in a ball mill (MM 400 Mixer Mill, Retsch), then weighing approximately 15 mg soil in 8 x 5 mm tin capsules and folded into a compact puck, which was then measured using Elemental Analyzer – Isotope Ratio Mass Spectrometry (EA-IRMS; Thermo Scientific™) which flash combusts the puck and measures the nitrogen and carbon. A C:N ratio was calculated by dividing the total carbon by the total nitrogen.

Soil moisture and soil temperature was measured using TMS-4 loggers (TOMST®). They were installed next to each collar measuring at 8 cm depth, and in the ambient plots rebar was put over them to help keep the reindeer away. The loggers were installed during the beginning of the growing season (June/early July) 2022 at the shrub heath, and on 27/6 2024 at the grass meadow.

2.5 Statistical analysis

All the statistical analyses were performed in R version 4.4.0 for this project (R Core Team, 2024). To exclude outliers in the CH_4 flux data, all flux values with a R^2-value < 0.8 while also being three times the standard deviation or more were removed (figure 6). To further prepare the data for analysis of variance (ANOVA) and linear models, the normality and equal variance assumptions were investigated. The data was found to be not normally distributed or having equal variance. Arcsinh transformation, performed using the “arcsinh_x” function from the *bestNormalize* package, showed a relatively normal distribution and equal variance, whilst also giving the highest R^2 values for the linear models (Peterson, 2021). Therefore, that was used for all ANOVAs and linear models. The last step in the preparation of the data was to divide it

by site, since each site is going to be investigated separately. This is because a high variance between sites makes the within site effects more interesting as flux drivers.

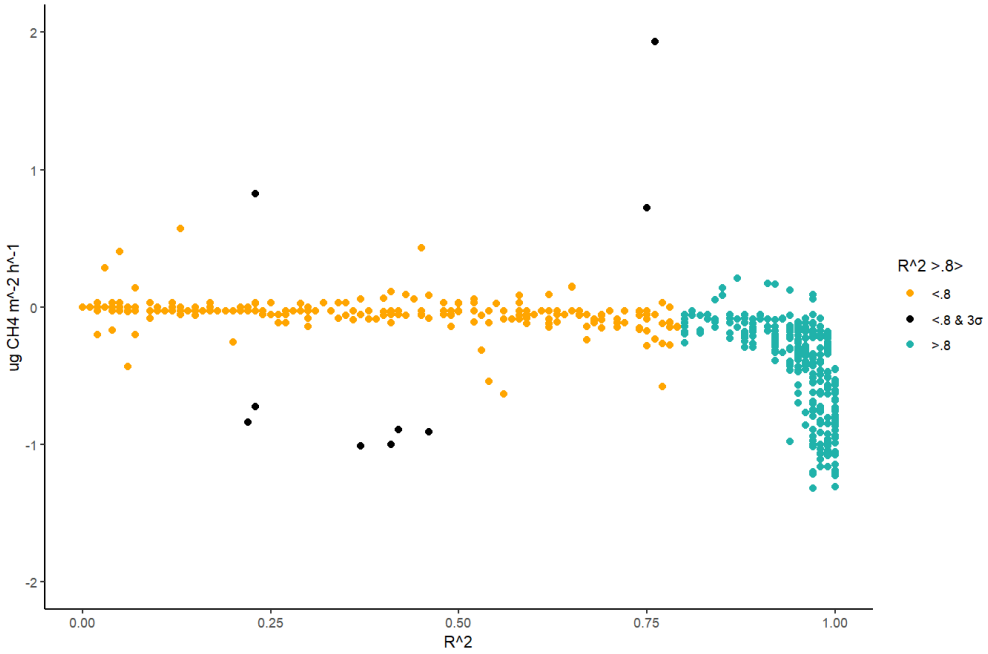

Figure 6. CH_4 fluxes against R^2. Showing flux values with a $R^2 > 0.8$, $R^2 < 0.8$, and three times the standard deviation or more for values with a $R^2 > 0.8$ (9 values). (σ = Standard deviation.)

All ANOVAs were performed with the "aov" function and post hoc tests with the "TukeyHSD" function from base R (R Core Team, 2024). A two-way ANOVA was made to look at if there was an overall difference in the CH_4 fluxes dependent on treatment type, focal shrub type or the interaction between them. Another identical three-way ANOVA was made but this one took time into consideration, represented by period as a factor. In the three-way ANOVA the treatment type compared the exclosure to a standard of ambient, the focal shrub type compared Empetrum to a standard of Betula, and the period compared each period individually to the standard of period 1. If the result from the ANOVA was significant, a Tukey's Honest Significant Difference (HSD) post hoc test was performed to compare the variables in more detail.

Linear mixed-effects models for both RIGA and RIRI were created to see which variables could best explain the variation in the CH_4 fluxes. The model was planned to be fitted with all variables, including: the percentage cover of all the plant functional types, pH without the KCl, pH with the KCl, SOM, soil moisture, soil temperature, surface temperature, air temperature (from the Tomst-logger), $\delta^{15}N$, $\delta^{13}C$, C:N ratio. To reduce multicollinearity between variables

they were assessed with a correlation matrix using "cormat" from base R and then a variance inflation factor (VIF) model using "VIF" from the *car* package to identify which variables to remove (Fox & Weisberg, 2019; R Core Team, 2024). Variables were removed singularly by removing the variable with the highest VIF and reassessing until all values in the VIF model were under 4. For RIGA the soil moisture was over 4, but since it is a key variable for CH_4 fluxes and still under 5, it was included in the model. The variables that were removed for RIGA were deciduous dwarf shrub, evergreen dwarf shrub, evergreen tall shrub and air temperature. For RIRI it was evergreen dwarf shrub, evergreen tall shrub and surface temperature. The remaining variables were plotted using the "lmer" function from the *lme4* package (Bates et al., 2015).

Only period 1, 3, 4 and 6 were analysed for the linear models since there were only soil samples for those periods. SOM was analysed to see if there could be a mean made for the two periods without soil samples. A linear model was made the see the variation in CH_4 fluxes with SOM and period as variables, and it showed that SOM-period interaction was significant. pH with only deionized water and pH with KCl was also analysed over time with a linear model with CH_4 as the formula and showed that period was not significant. A mean between data for the two measured periods was therefore made and used for period 1 and 6. Another linear model was made to see if the different pH variables, pH with only deionized water and pH with KCl, explained the variations in the CH_4, to see if there was a difference between the pH variables. The model showed no significant difference between them. Because pH with KCl is the scenario with most nutrients available, it was chosen for the linear models.

The final linear mixed-effects models (FLMM) were chosen by the Akaike information criterion (AIC) using the function "AIC" the *stats* package from base R (R Core Team, 2024). AIC shows how well a model explains variation in observed data while also penalizing the model for having a high number of variables. The lowest AIC value among the models compared is the most optimal model (Sakamoto et al., 1986). There were 16 linear mixed-effects models made for the CH_4 fluxes at RIGA, and the $FLMM_{RIGA}$ included the following variables: subplot as a random effect, period, soil temperature, surface temperature, soil moisture and $\delta^{13}C$. For the CH_4 fluxes at RIRI 17 mixed-effects models were made, and the $FLMM_{RIRI}$ included the following variables: subplot as a random effect, period and soil moisture.

There was a soil microclimate linear model (SMLM) made for each site to look at the differences in the CH_4 fluxes based on the soil microclimate. The SMLM included the following variables: treatment, shrub, period, soil moisture and soil temperature. This model was plotted with the function “lm” from base R for period 1to 6 (R Core Team, 2024).

A non-metric multidimensional scaling (NMDS) ordination was used to see the composition of the plant species between sites, treatment conditions and focal shrubs. First a Bray-Curtis distance matrix was made using the “distance” function in the *ecodist* package to calculate the dissimilarity between each site, treatment, and focal shrub combination in terms of plant community composition (Goslee & Urban, 2007). Then a two-dimensional NMDS with maximum 999 tries was calculated using the “metaMDS” function from the *vegan* package (Oksanen et al., 2024). The Bray-Curtis distance matrices were also used in a Permutational multivariate analysis of variance (PERMANOVA) with 999 permutations, using the “adonis2” function from the *vegan* package, to determine statistically how the plant species composition changed between the variables (Oksanen et al., 2024).

3. Results

3.1 CH_4 fluxes

The CH_4 fluxes at each focal shrub and treatment type at both RIGA and RIRI show an uptake (figure 7). An ANOVA showed that neither treatment, focal shrub, nor treatment-shrub interaction significantly changed the CH_4 fluxes at RIGA. At RIRI an ANOVA showed that the CH_4 fluxes varied significantly per treatment type ($F_{1,281}$=9.407, p=0.002), focal shrub ($F_{1,281}$=11.010, p=0.001) and treatment-shrub interaction ($F_{1,281}$=24.245, p<0.001). The post hoc test for RIRI showed that the exclosure Betula plots have significantly higher CH_4 uptake than the ambient Betula plot, while the Empetrum did not show a significant treatment effect (figure 7). It also showed a significantly higher uptake at Betula exclosure than Empetrum exclosure (figure 7).

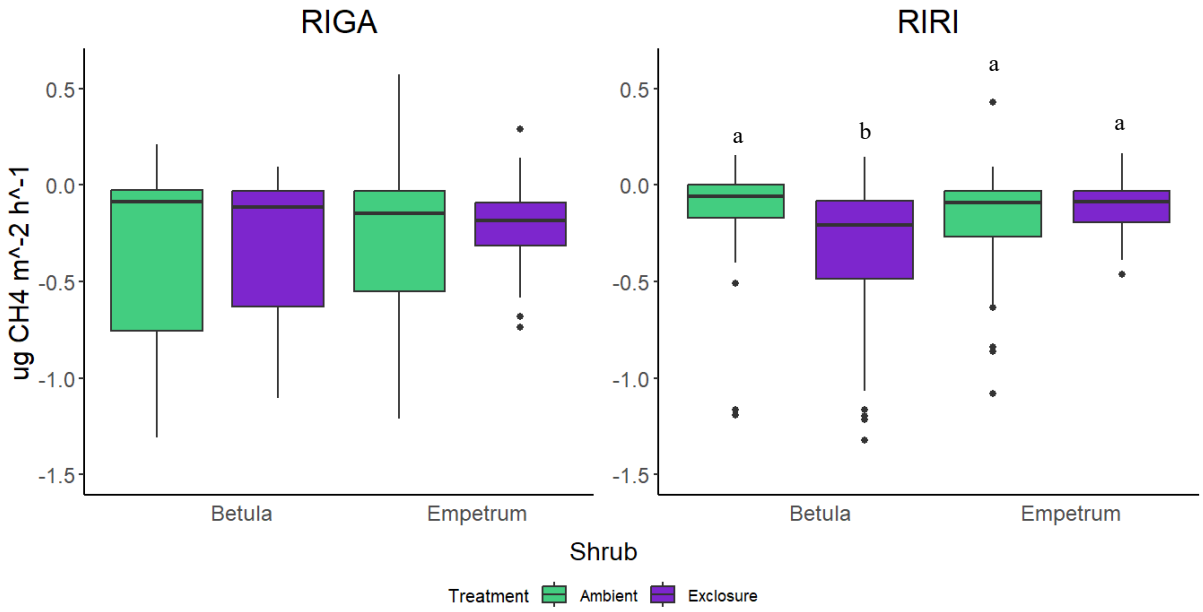

Figure 7. CH_4 fluxes per site, treatment and focal shrub. b = significant differences ($p<0.05$) in fluxes to all a's, a= not significant to each other.

3.2 CH_4 fluxes, soil properties, soil microclimate and vegetation

An ANOVA for CH_4 fluxes over time at RIGA showed a significant difference between periods ($F_{5,254}=4.371$, $p<0.001$). A further post hoc test showed that the difference in fluxes between period 3 and 2 ($p=0.014$), period 4 and 2 ($p<0.001$), and period 6 and 2 ($p=0.011$) were significant (figure 8c). An ANOVA for CH_4 fluxes over time at RIRI showed a significant difference between treatment type ($F_{1,161}=10.016$, $p=0.002$), focal shrub ($F_{1,161}=11.723$, $p<0.001$), period ($F_{5,161}=3.732$, $p=0.003$), and treatment-shrub interaction ($F_{1,161}=25.437$, $p<0.001$). A post hoc test showed that the difference in fluxes between period 5 and 1 ($p=0.011$), and period 5 and 3 ($p=0.004$) were significant (figure 8f).

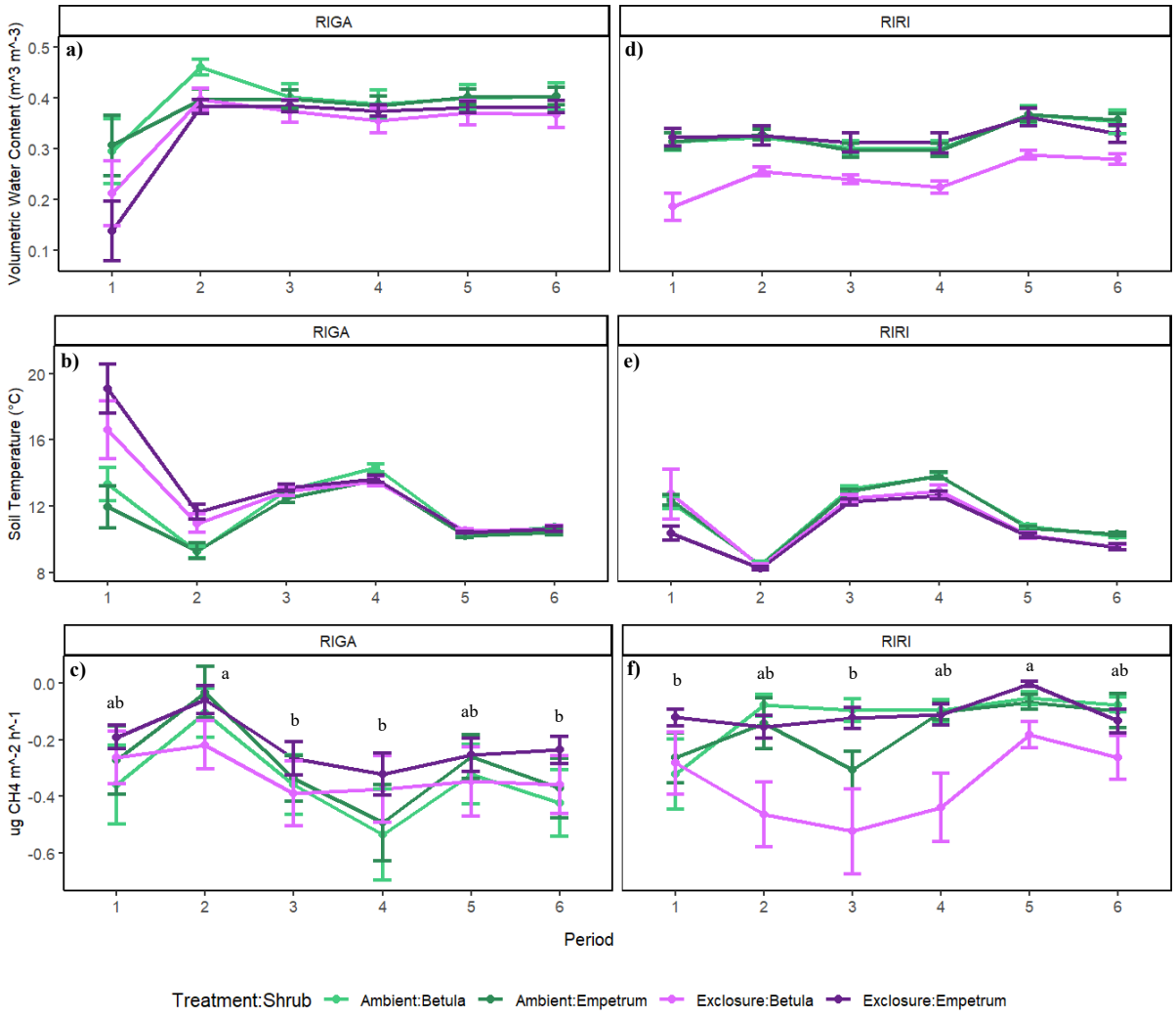

Figure 8. Mean and error bars for a) volumetric water content at RIGA, b) soil temperature at RIGA, c) CH_4 fluxes at RIGA where there is a significant difference ($p<0.05$) in fluxes between a and b, but not between b, and ab are not significantly different to anything, d) volumetric water content at RIRI, e) soil temperature at RIRI, f) and CH_4 fluxes at RIRI where there is a significant difference ($p<0.05$) in fluxes between a and b, but not between b, and ab are not significantly different to anything.

In the $FLMM_{RIGA}$ (AIC=210.077), period 4 compared to period 1 (t=-7.804, p<0.001), soil temperature (t=3.793, p<0.001), surface temperature (t=3.621, p<0.001), soil moisture (t=3.506, p<0.001) and $\delta^{13}C$ (t=-3.891, p<0.001) were found to be significant predictors for the CH_4 fluxes. In the $FLMM_{RIRI}$, period 4 compared to period 1 (t=3.249, p=0.001), and period 6 compared to period 1 (t=2.818, p=0.005) were found to be significant predictors for the CH_4 fluxes (AIC=333.011).

At RIGA the treatment-focal shrub interactions for the soil moisture, soil temperature, and CH_4 fluxes are consistent with each other (figure 8a-c). At RIRI the soil temperature is consistent

with each other, while there is lower soil moisture and higher CH_4 uptake for exclosure Betula (figure 8d-f). The $SMLM_{RIGA}$ explained approximately 52 % of the variance in the CH_4 fluxes ($F_{9,268}$=33.68, p<0.001, R^2_{adj}=0.515). In the model exclosure compared with ambient (t_{268}=3.565, p<0.001), Empetrum compared with Betula (t_{268}=3.110, p=0.002), soil moisture (t_{268}=14.856, p<0.001), soil temperature (t_{268}=4.973, p<0.001), period 3 compared with period 1 (t_{268}=-6.957, p<0.001), period 4 compared with period 1 (t_{268}=-8.489, p<0.001), period 5 compared with period 1 (t_{268}=-3.939, p<0.001), and period 6 compared with period 1 (t_{268}=-5.084, p<0.001) were found to be significant predictors for the flux. The $SMLM_{RIRI}$ explained approximately 15 % of the variance in the CH_4 fluxes ($F_{9,275}$=6.578, p<0.001, R^2_{adj}=0.150). In the model, exclosure compared with ambient (t_{275}=-3.156, p=0.00178), soil moisture (t_{275}=4.468, p<0.001) and period 5 compared with period 1 (t_{275}=2.256, p=0.025) were found to be significant predictors for the flux.

3.3 Vegetation (and CH_4 fluxes)

There was a difference between treatment type for grasses only, with a difference in CH_4 uptake between ambient and exclosure plots overall for increased grass cover (figure 9a). Increased forb, grass and sedge cover at RIRI corresponds with an increased uptake of CH_4 at one treatment type and decreased uptake at the other (figure 9b). Increased deciduous dwarf shrub, forb and grass cover corresponds with increased uptake of CH_4 under Betula at the exclosure plots (figure 9b). There is higher deciduous tall shrub cover at exclosure Betula compared to ambient Betula for both RIGA and RIRI (figure 9a-b).

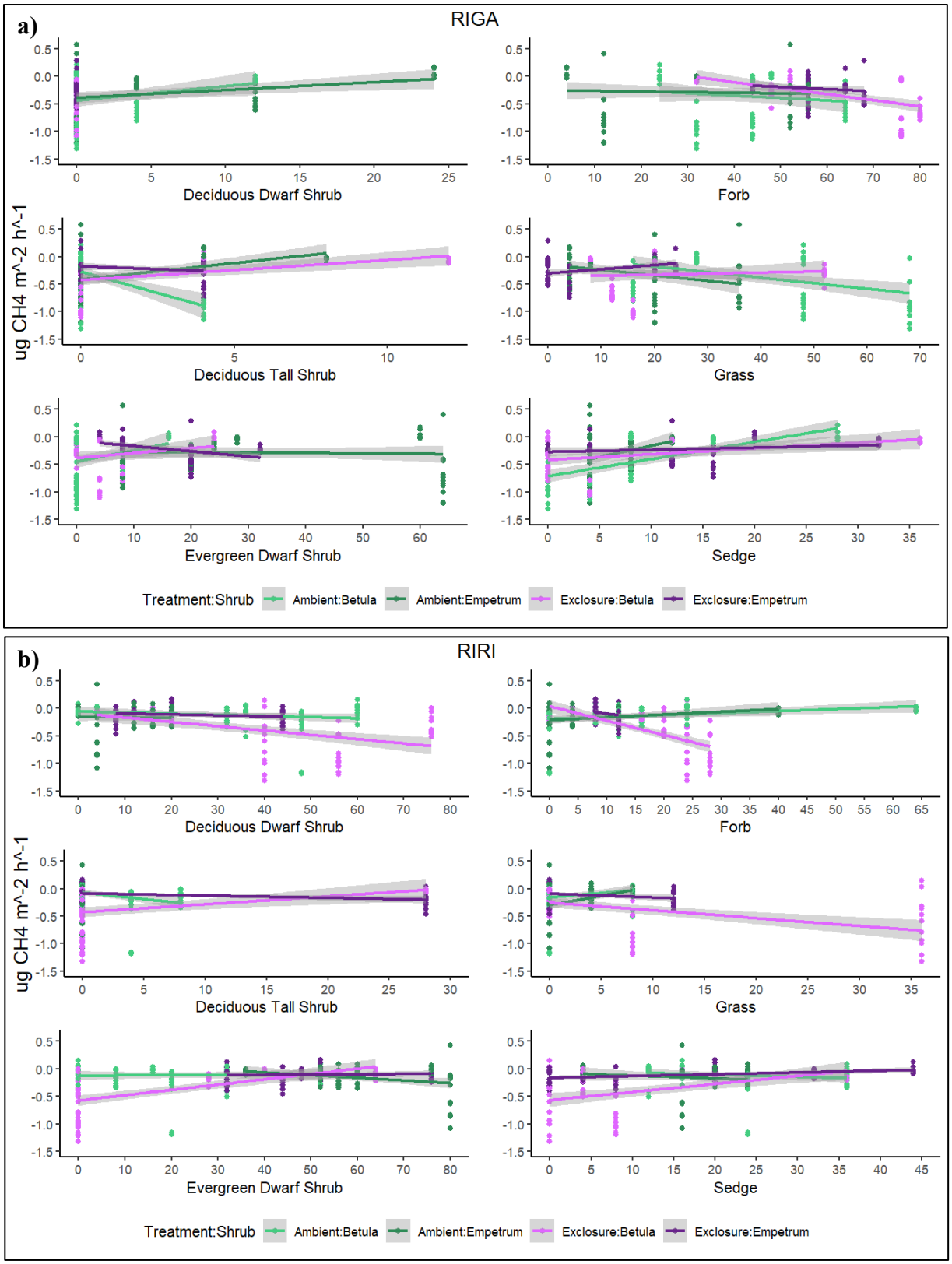

Figure 9. CH_4 fluxes per plant functional type cover (%) of deciduous dwarf shrub, deciduous tall shrub, evergreen dwarf shrub, forb, grass, and sedge at a) RIGA, b) and RIRI. Evergreen tall shrub was no included since there was none found at either sites.

The NMDS for RIGA shows a difference in plant community according to treatment type, while at RIRI the differences in plant community are more strongly related to shrub type (figure 10). For RIGA the PERMANOVA found a difference between both treatment type ($F_{1,20}$=2.171, p=0.022) and focal shrub ($F_{1,20}$=2.273, p=0.006) in the NMDS. For RIRI the PERMANOVA found a difference between focal shrub ($F_{1,20}$=5.732, p=0.001) in the NMDS.

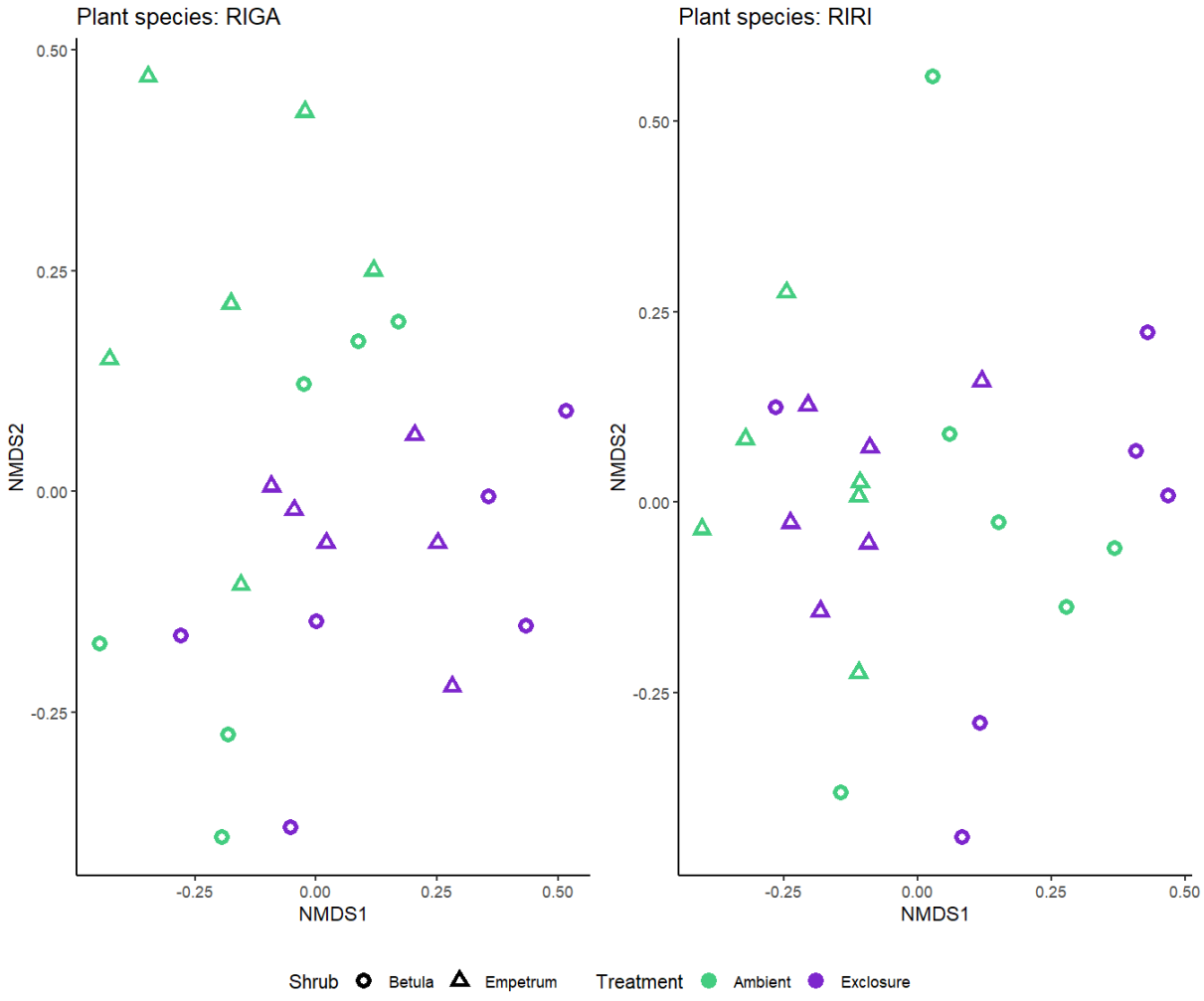

Figure 10. A non-metric multidimensional scaling (NMDS) ordination plot for plant species.

4. Discussion

4.1 CH_4 fluxes

Overall, there is an uptake of CH_4 at both RIGA and RIRI (figure 7), where RIGA does not differ between treatment type or focal shrub, while RIRI does differ between them and when interacting with each other. The first part support hypothesis a) for RIRI, but not for RIGA. Since the CH_4 fluxes do not show any variation for treatment or focal shrub, but RIRI does, it

implies that there are different processes at work resulting in uptake of CH_4 at both sites. Typical habitats with uptake of CH_4 in the Arctic are drier areas such as polar deserts, heaths and dwarf shrub tundra, which all are similar to the habitat at RIRI, a shrub heath (Christensen et al., 2000; Emmerton et al., 2014; Flessa et al., 2008; Hermesdorf et al., 2022; Pedersen et al., 2017; St Pierre et al., 2019; Wagner et al., 2019). RIGA, which is a wet grass meadow, does not correspond with the typical habitats with uptake of CH_4 in the Arctic. Habitats like RIGA usually have emission of CH_4, such as areas with dense sedge cover, wet meadow tundra, tussock tundra, fen, grassland, wet sedge and mesic tundra (Christensen et al., 2000; Emmerton et al., 2014; Keuschnig et al., 2022; Olefeldt et al., 2013; Schimel, 1995; Wagner et al., 2019). Comparing to the soil moisture and soil temperature at the mesic tundra and wet sedge investigated by Wagner et al. (2019), RIGA seems to be wet and warm enough to have emission of CH_4 (figure 8a-b). In conclusion, RIRI acts like a typical upland habitat by having uptake of CH_4, while RIGA does not act like a typical Arctic wet meadow by having uptake of CH_4.

Increased methanotrophy could be the reason for uptake of CH_4 at RIGA. At an alpine meadow investigated by Wang et al. (2023) type II methanotrophs were found to increase CH_4 uptake. Type II methanotrophs grow in CH_4 rich and high soil moisture environments, meaning that there could be high methanogenesis in the area, but that it could also be the best environment for type II methanotrophs resulting in higher methanotrophy (Chowdhury & Dick, 2013). A reason for higher abundance or efficiency of methanotrophs could be high quality carbon in the soil (Voigt et al., 2023). The C:N ratio at RIGA is between 10-20 (appendix B), which is a lot lower than RIRI. Lower C:N ratio means that the carbon in the soil is turned over fast, meaning that it has high quality (Ostrowska & Porębska, 2015; Soldatova et al., 2024). A lower ratio can result in higher availability of nutrients which can stimulate both methanogenic and methanotrophic communities, and it can also change the communities (Cao et al., 2022; Chen et al., 2024; Li et al., 2021). This could mean that type II methanotrophs have benefited most from the quality of carbon in the soil at RIGA, resulting in overall CH_4 uptake.

4.2 CH_4 fluxes and soil moisture by treatment type

The CH_4 fluxes at RIGA does not vary between treatment, focal shrub nor treatment-shrub interaction, but it does per period with period 2 varying from period 4 and 6 (figure 7; figure 8c). This does not support with hypothesis b). There is variation in the fluxes by soil temperature, surface temperature, soil moisture and $\delta^{13}C$, shown in the $FLMM_{RIGA}$ and the

$SMLM_{RIGA}$ explaining 52 % of the variation. This corresponds to the findings by Ford et al. (2012), that grazing of large herbivores at a temperate salt marsh (coastal wetland) neither increased nor decreased CH_4 uptake. But they did find that soil temperature, soil moisture, surface temperature and seasonal variability, with a peak in June, caused the variation in the CH_4. A subalpine grassland and high Arctic wet moss meadow also showed no increase or decrease in CH_4 fluxes from grazing by large herbivores (Sjögersten et al., 2012; Sjögersten et al., 2011). Low grazing intensity is a possible reason for the limited change in CH_4 fluxes in the subalpine grassland, which would need to be investigated further to see if it is a factor at RIGA as well (Sjögersten et al., 2012). Increased $\delta^{13}C$ leads to increased CH_4 uptake at RIGA. This coincides with other studies, that show it could be because of fractionation were methanotrophs will favor oxidizing the lighter ^{12}C-CH_4 before the heavier ^{13}C-CH_4, leaving behind more ^{13}C in the SOM (Liptay et al., 1998; Wu et al., 2018). There is a decreased CH_4 uptake at exclosure areas and increased uptake at ambient areas with increased grass cover at RIGA (figure 9a). This could be explained by increased forb and sedge cover at the exclosure (figure 9a), that can contribute to decreasing CH_4 uptake since some sedges have aerenchyma, roots create favourable environment for methanogens and productivity is increased (Cong et al., 2017; Hodgkins et al., 2018; Noyce et al., 2014; Strack et al., 2006; Waldo et al., 2022). As a whole, CH_4 fluxes at RIGA do not vary substantially due to reindeer herbivory, but predominantly by soil microclimate, surface temperature, $\delta^{13}C$ and period during the growing season.

At RIRI the CH_4 fluxes vary between treatment, focal shrub, treatment-shrub interaction and period, with the significant difference being between exclosure Betula and the other treatment-shrub interactions and period 5 having higher uptake than period 1 and 3 (figure 7; figure 8f). This does not support hypothesis b). The $FLMM_{RIRI}$ only showed period as a predictor for the variation in the fluxes. The $SMLM_{RIRI}$ shows soil moisture and soil temperature as significant predictors of the CH_4 fluxes, but the model only explains 15 % of the variation in the fluxes. There are several studies agreeing with the results, showing a decrease in CH_4 uptake at areas with herbivory compared to herbivory excluded areas, with many of the studies only finding a decrease during high grazing intensity (Mutschlechner et al., 2018; Pan et al., 2021; Tang et al., 2019a; Tang et al., 2019b; Tang et al., 2018). Grazing intensity is something that would need to be further investigated to see if it is a factor a RIRI. Furthermore, similar to the results in this study, increased soil moisture and/or soil temperature was found to decrease CH_4 uptake (Mutschlechner et al., 2018; Pan et al., 2021; Tang et al., 2019b; Tang et al., 2018). However, seasonal variability might explain the variation in the CH_4 fluxes more since the soil

microclimate did not explain a lot. A late growing season burst of CH_4 production can be found in Arctic ecosystems (Mastepanov et al., 2008). But since period was a variable in the $SMLM_{RIRI}$ that did not explain the variation in the fluxes well, there might be other underlying factors to the variation not investigated in this study, such as grazing intensity. There is an increase in CH_4 uptake at exclosure areas and decreased uptake at ambient areas with increased forb and grass cover, which might be because of decreased soil moisture at exclosure Betula (figure 8d; figure 9b) (Keuschnig et al., 2022). There is higher grass and sedge cover at the exclosure plots which would result in more aerenchyma and microbes benefiting from the roots, and therefore decrease CH_4 uptake with increased sedge cover (Cong et al., 2017; Hodgkins et al., 2018; Noyce et al., 2014; Strack et al., 2006; Waldo et al., 2022). These findings point toward reindeer herbivory having an impact on CH_4 fluxes at RIRI, with higher uptake at exclosure areas, with soil microclimate and seasonality having influence. However, more would need to be investigated, e.g. soil type at each plot, to find the driving factors of the variation in the fluxes.

For exclosure Betula at RIRI, compared with the other focal shrubs at each treatment type, there is higher CH_4 uptake that varies overall and over time (figure 7; figure 8f), lower soil moisture (figure 8d), increased deciduous dwarf shrub, forb and grass cover corresponding with increased CH_4 uptake, and higher deciduous tall shrub cover than ambient Betula (figure 9b). For RIGA there is no difference between any of the treatment-shrub interactions for the CH_4 fluxes or soil moisture. This does not support hypothesis b) or c) for either RIGA or RIRI. Evapotranspiration could increase for exclosure Betula at both sites. Deciduous shrubs have larger leaf area than other functional types which means that they can transpire more (Bonfils et al., 2012; Breil et al., 2023; Ladekarl et al., 2005; Nicholls & Carey, 2021; Te Beest et al., 2016). There might be high evapotranspiration at RIGA, but as Ladekarl et al. (2005) found, the soil moisture does not decrease when there is a constant inflow of water into the system. There is both precipitation and a high amount of runoff at RIGA since the site is on the downslope of a mountain. For RIRI the inflow of water from surface runoff might be less since the site is on a flat area higher up on a mountain. There could be higher rates of evaporation at RIRI as well, since it is more exposed to sunlight and has a rougher, blocky, terrain, which increases evaporation rates (Bonfils et al., 2012; Breil et al., 2023; Ladekarl et al., 2005; Nicholls & Carey, 2021; Te Beest et al., 2016). This is in agreement with findings that reindeer herbivory increases soil moisture and lowers evapotranspiration rates (Te Beest et al., 2016). In conclusion, exclosure Betula at RIGA is not significantly different in CH_4 fluxes likely due to

constant inflow of water from surface runoff, while for RIRI there is significantly higher uptake probably due to not as much inflow from surface runoff and higher evapotranspiration rate.

4.3 Vegetation (*Betula nana*)

There is higher deciduous tall shrub cover at exclosure Betula compared to ambient Betula for both RIGA and RIRI, with the largest difference at RIRI (figure 9a-b). At RIGA there is a difference in plant community between treatment and focal shrub, while at RIRI the difference is only between focal shrub (figure 10). Since the PERMANOVA for RIRI showed the highest F-value for the focal shrubs, there is a stronger relationship between the focal shrubs there than at RIGA. This supports hypothesis d) partly, since *Betula nana* is a deciduous tall shrub and is more abundant at the Betula focal shrub plots, but RIGA does not seem to have a larger difference in *Betula nana* cover than RIRI. *Betula nana* decreasing due to herbivory agrees with results from several studies (Scott, 2001; Te Beest et al., 2016; Vowles et al., 2017a). These results also coincide with previous studies in the Arctic, showing biggest change of *Betula nana* as an effect of reindeer herbivory occurring at unproductive heaths, compared to more productive environments (Moen & Oksanen, 1998; Pajunen et al., 2008; Vowles et al., 2017b). This could be because of increased competition with deciduous or evergreen dwarf shrubs (figure 9b). These findings point toward an effect of reindeer herbivory on *Betula nana*, with the biggest impact on RIRI.

4.4 Limitations

No repeated measures ANOVA were performed in this study, since time was limited on finding out a correct method. A repeated measures would take into consideration that there are repeated measures on the same area over a period (Park et al., 2009). However, this study has used the different periods measurements occurred as a variable in the ANOVA to still account for changes in CH_4 fluxes over time.

There were gaps in the data for CH_4 fluxes and pH which could limit the accuracy of the results of this study. Interpolation with equal intervals was done for the gaps in the CH_4 flux data, which could influence the results since there were fairly consistent N/A values. This could possibly be a reason for the low (15 %) explanation of the $SMLM_{RIRI}$ on the variation in the CH_4 fluxes. Having statistically significant variables in the model but having low R^2 can mean that there is a lot of noise around the estimated relationship (Spiess & Neumeyer, 2010). But it

would need to be further investigated to see if it is a contributing factor. For the pH however, a mean was performed over period 3 and 4 and filled in at period 1 and 6. Even though it could differ to the true values, it would not be completely inaccurate since pH was found to not vary over time.

Investigating methanogenic and methanotrophic communities would be a way to build on this study. With that knowledge, factors contributing to the overall uptake of CH_4 at RIGA and the impact of reindeer herbivory at RIRI, could be looked into deeper. Since a few of the results in this study corresponds with results from studies based on grazing intensity, it would be interesting to investigate it. It would also be interesting to investigate specific plant species, to see if there is any specific species competing with *Betula nana* at RIGA.

5. Conclusions

There is an overall uptake of CH_4 at both RIGA and RIRI, with only RIRI showing an effect of reindeer herbivory. RIGA does not act like a typical Arctic wet grass meadow which could be because of high quality carbon, while RIRI acts like a typical upland habitat. CH_4 fluxes at RIGA varies by soil microclimate, surface temperature, $\delta^{13}C$ and period during the growing season, coinciding with many studies in similar habitats. At RIRI reindeer herbivory have an impact on variation in CH_4 fluxes under the focal shrub *Betula nana* where herbivory was excluded. This is probably due to increased evapotranspiration. Reindeer herbivory did not have an effect on soil moisture at RIGA. It could be because of constant inflow of water from surface runoff into the soil, even through increased evaporation at herbivory exclusion. At RIRI, reindeer herbivory had a decreasing effect on soil moisture under the focal shrub *Betula nana* where herbivory was excluded, which could be a result of increased evapotranspiration and no large inflow of water into the soil from surface runoff. There is an increase in *Betula nana* cover at herbivory excluded areas at both RIGA and RIRI, with the biggest difference being at RIRI. This coincides with previous studies in the Artic, showing greater reindeer herbivory effect on *Betula nana* at unproductive heaths compared to more productive environments. In conclusion, there is only a reindeer herbivory effect on CH_4 fluxes at RIRI, while there is larger reindeer herbivory effect on vegetation at RIRI, a dry shrub heath, than RIGA, a wet grass meadow.

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Appendix

Appendix A

Plant species

The following table includes the plant species found during the vegetation inventory and both RIGA and RIRI. It also includes which plant functional type each species fall under.

Table A. Plant species per plant functional type for the study sites RIGA and RIRI

	RIGA	RIRI
Deciduous dwarf shrub	*Salix herbacea*	*Salix herbacea*
Deciduous tall shrub	*Betula nana* *Salix lanata* *Salix Lapponum* *Vaccinium uliginosum*	*Betula nana* *Vaccinium uliginosum*
Evergreen dwarf shrub	*Arctous alpina* *Empetrum nigrum* *Vaccinium myrtillus* *Vaccinium vitis idaea*	*Arctous alpina* *Empetrum nigrum* *Vaccinium myrtillus* *Vaccinium vitis idaea*
Evergreen tall shrub		
Forb	*Astragalus alpinus* *Bistorta vivipara* *Botrychium lunaria* *Campanula persicifolia* *Dryas octopetala* *Equisetum pratense* *Equisetum scirpoides* *Erigeron borealis* *Euphrasia wettsteinii* *Gentiana nivalis* *Gnaphalium norvegicum* *Gnaphalium supinum*	*Bistorta vivipara* *Dryas octopetala* *Equisetum scirpoides* *Gnaphalium supinum* *Hieracium sect Alpina* *Kalmia procumbens* *Lycopodium alpinum* *Lycopodium annotinum* *Lysimachia europaea* *Pedicularis lapponica* *Phyllodoce caerulea* *Ranunculus acris*

	Hieracium sect Alpina *Parnassia palustris* *Potentilla crantzii* *Potentilla nivea* *Pyrola minor* *Ranunculus acris* *Rhinanthus minor subsp groenlandicus* *Saussurea alpina* *Selaginella selaginoides* *Solidago virgaure* *Taraxacum croceum* *Trollius europaeus* *Viola biflora*	*Saussurea alpina* *Selaginella selaginoides* *Sibbaldia procumbens* *Solidago virgaure* *Taraxacum croceum* *Viola biflora*
Grass	*Agrostis mertensii* *Anthoxanthum alpinum* *Avenella flexuosa* *Deschampsia cespitosa* *Dryas octopetala* *Festuca rubra* *Phleum alpinum*	*Agrostis mertensii* *Avenella flexuosa* *Calamagrostis lapponica* *Dryas octopetala* *Festuca rubra subsp arctica* *Phleum alpinum*
Sedge	*Carex bigelowii* *Carex capillaris* *Carex nigra* *Carex saxatilis* *Carex vaginata* *Juncus castaneus* *Luzula spicata*	*Carex bigelowii* *Carex brunnescens* *Carex lachenalii* *Juncus trifidus*

Appendix B

C:N ratio

The following figure presents the C:N ratio for each focal shrub and treatment type at both RIGA and RIRI.

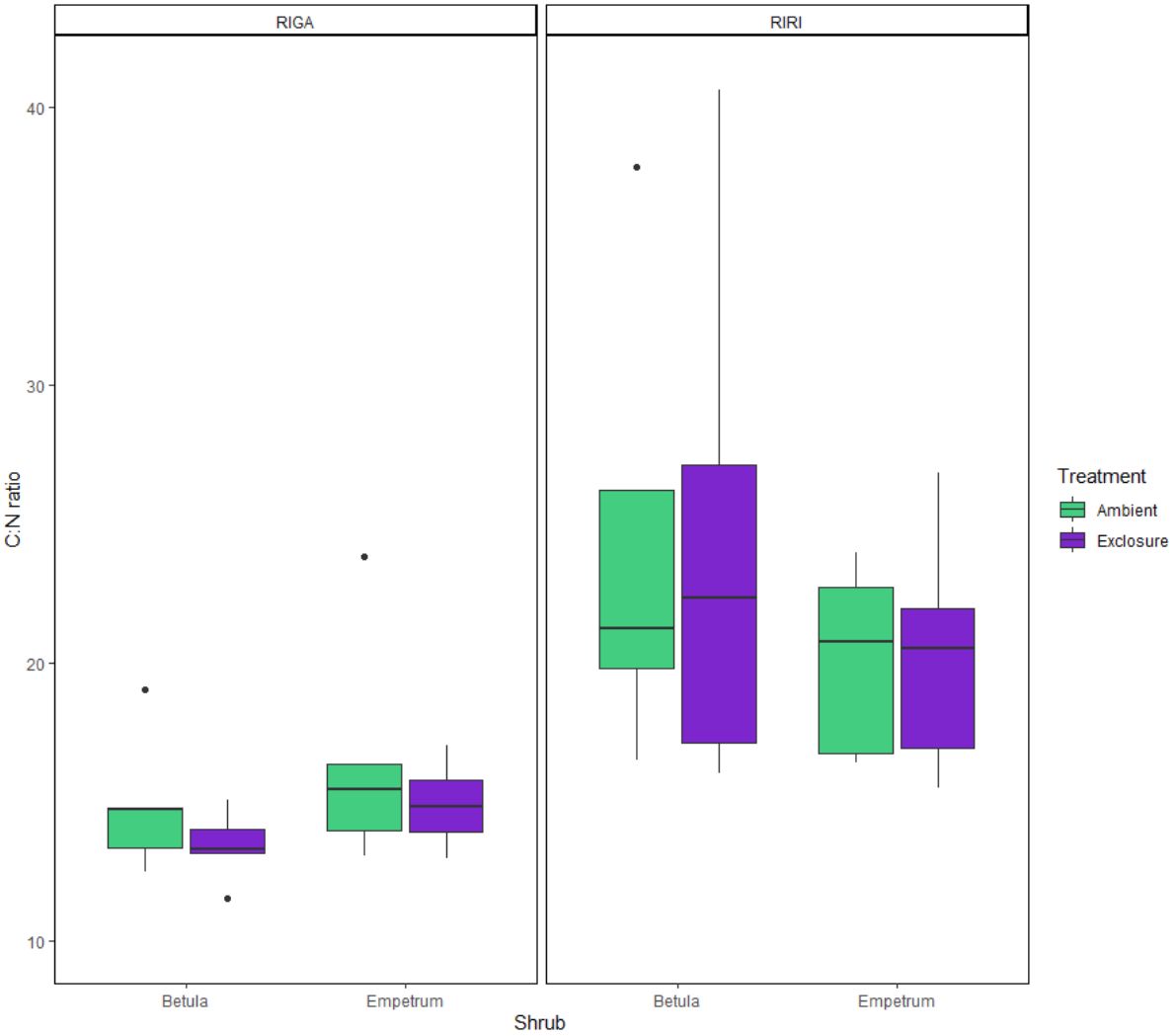

Figure A. C:N ratio per treatment type and focal shrub, at the study sites RIGA and RIRI.