Effects of sheep grazing on plants adapting to climate change and rising temperatures

Rán Finnsdóttir

Abstract

Global warming is expected to affect the arctic harsher than other regions of the globe. Many plant species will face conditions that contradict their adaptations in a warming climate. Changes in habitat can lead to drastic changes in biodiversity as well as exerting a strong selective pressure for plants to evolve and adapt quickly. Herbivore grazing in the arctic also affects plant ecosystems e.g. by lowering biodiversity and changing species composition and may influence their response to warming.

The aim of this study was to examine whether grazing influences plants' adaptation to rising temperatures. Geothermally warmed areas have been used as *in situ* proxy systems for effects of warming climates on ecosystems. Grændalur, a geothermally warmed valley in southwest Iceland, was used as a study site to explore the effects of warming and grazing on ecosystems. Three soil temperature gradient transects were established there and each transect has six fenced-off plots, at different soil temperatures (ambient +0, +1, +3, +5, +10 and +20°C), and paired plots outside the fence that were grazed by sheep. Species richness, evenness, Shannon-Wiener and Simpson's diversity, species cover, and composition as well as plant height were measured in these plots inside and outside the fence. In addition, flowering and vegetative *Ranunculus acris* (meadow buttercup) individuals were counted in each plot to assess grazing effects on flowering success.

Grazing did not influence the plant community response to warming. Rising temperature decreased species richness and both Shannon-Wiener and Simpson's diversity, and drove changes in community composition. Plant height increased with rising temperatures but decreased with grazing. Grazing also significantly reduced *R. acris flowering*. These results highlight the need for sustainable grazing management in Iceland, as well as the significance global warming has for plant communities.

Table of contents

List of figures

List of tables

Introduction

Sheep herbivory on Icelandic commons

Commonage, the age-old Icelandic tradition of letting sheep roam free on rangeland commons, has had adverse effects on the already vulnerable ecosystems of this volcanic island. Grazing of free roaming sheep is thought to be the main driver of soil and vegetative degradation in Iceland (Ó. Arnalds *et al.*, 2001; Thórhallsdóttir & Thorsteinsson, 1993). The negative effects of sheep are most prominent in the loss of vegetational cover, i.e. increase of bare ground, which in turn leads to increase in soil erosion (Marteinsdottir *et al.*, 2017). Today, many of the areas used for summer pastures are severely degraded, with the combination of herbivory, geological and meteorological activity halting their recovery (Ó. Arnalds & Barkarson, 2003; Marteinsdottir *et al.*, 2017). The grazing period generally ranges from June to September (Ó. Arnalds & Barkarson, 2003), although sheep may be released as early as May when weather conditions allow. In 2018 the number of sheep in Iceland was just over 430.000, outnumbering human inhabitants by more than 80.000 (Statistics Iceland, 2019a, 2019b).

Sheep are selective grazers. Not only do they prefer certain plant species, they also selectively feed on young succulent seedlings, thereby hindering their growth in barren areas (Marteinsdottir *et al.*, 2017). Plants favoured by Icelandic sheep are amongst others; *Festuca rubra* (red fescue), *Calamagrostis neglecta* (narrow small-reed), *Agrostis* spp., *Poa* spp., *Carex bigelowii* (Bigelow's sedge), *Salix callicarpea* (goat willow), *Bistorta vivipara* (alpine bistort), *Galium* spp., and *Equisetum* spp. They are also keen on available forbs, such as *Gentiana campestris* (field gentian), *Rubus saxatilis* (stone bramble), *Rhinanthus minor* (yellow rattle), and *Ranunculus acris* (meadow buttercup) (Perron, 2017; Thórhallsdóttir & Thorsteinsson, 1993; Þorsteinsson, 1980).

Sheep grazing affects plant communities in various ways

Heavy grazing can have adverse effects on plant species biodiversity and species composition. Species richness and diversity (Shannon-Wiener and Simpson's) can decrease with grazing (Allred *et al.*, 2012; Hanke *et al.*, 2014; Jing *et al.*, 2014; Louhaichi *et al.*, 2012). Grazing also significantly decreases average plant cover, height and density in rangelands (Deng *et al.*, 2014; Louhaichi *et al.*, 2012; Marteinsdottir *et al.*, 2017). As for species evenness herbivore exclusion can affect this community trait both negatively and positively (Deng *et al.*, 2014; Jing *et al.*, 2014). This variation is likely based on plant community type and overall robustness as well as occurrence of competitive species. For instance, palatable but herbivore-intolerant plant species often cannot withstand heavy grazing and disappear from heavily grazed areas while more tolerant and/or unpalatable plants thrive (Hulme *et al.*, 1999; Jónsdóttir, 1984; Ross *et al.*, 2016). This tilts the scales, with increasing abundance of certain species and paucity of others lowering overall species evenness. Oppositely, grazing of palatable but competitive (and even invasive) species could offer a helping hand to other species in a community by weakening the strongest competition, thus evening the playing-field (and increasing species evenness and diversity in the community) (B. Magnússon *et al.*, 2018; Ross *et al.*, 2016). Changes in species composition are e.g. the result of changes in species cover , with recruitment of new species in heavily grazed areas as well as a loss of other, often palatable species (Allred *et al.*, 2012; Hanke *et al.*, 2014).

Over the past decades, numerous studies have been conducted on sheep grazing in Iceland, and its effects on plant communities and soil health. Many perennial plants rely on root energy reserves from the last season and devote much of their energy and nutrients to building up their root systems in late summer before senescence (A. Arnalds, 1981). Intense grazing during this time can drastically reduce root growth and nutrient allocation, and may result in delayed sprouting the following year (A. Arnalds, 1981; Bai *et al.*, 2015). Intense grazing can decrease overall plant biomass, while in contrast, light grazing can increase growth by stimulating offshoots and leaf formation (A. Arnalds, 1981). With sheep grazing comes trampling of plants, which intensifies with the density of grazing animals (A. Arnalds, 1981; Marteinsdottir *et al.*, 2017). A meta-analysis of Icelandic grazing studies by Marteinsdottir *et al.* (2017) indicated a trend where cover of grasses, bryophytes, and lichens decreases in grazed areas compared to non-grazed areas. The opposite is true for sedges, rushes and forbs, which have more cover in grazed areas (Marteinsdottir *et al.*, 2017). Heavily grazed areas are often rich in herbivory-tolerant plants such as rushes, sedges and small woody shrubs (e.g. *Empetrum nigrum* and *Vaccinium* spp.), while lightly grazed areas are dominated by grasses. Moderately grazed areas however, are often characterised by herbaceous plants and *Salix* species (Ó. Arnalds & Barkarson, 2003).

Rising temperatures due to global warming will affect plant communities

According to the International Panel on Climate Change (IPCC), the global temperature is expected to increase by 1.0-3.7 °C before 2100, and the arctic will warm quicker than other parts of the globe (IPCC, 2014a, 2014b). With this increasing temperature, many plant species may no longer be well adapted to their growing conditions and current habitat. This could have drastic effects on biodiversity and might even lead to species extinction if species cannot adapt to the changes (Bellard *et al.*, 2012).

Plastic changes in phenology (the timing of life cycle events e.g. flowering, fruiting, senescence) are the most commonly observed responses to climate change. This is especially true for many species in the colder climates near the poles, which offer less opportunity for a species' migration to escape the warming and where temperatures are rising at a quicker pace (Bjorkman *et al.*, 2019; Parmesan, 2006; Valdés *et al.*, 2019). Documented plastic changes in phenology have been e.g. earlier greening in the spring, followed by earlier flowering etc. (Bellard *et al.*, 2012; Parmesan, 2006). Studies on geothermally heated areas in Iceland show that phenology can indeed change, with plant phenology advancing with rising temperatures (Valdés *et al.*, 2019).

Community dynamics such as species composition, plant height, species richness, evenness and diversity are also influenced by rising temperatures (Guðmundsdóttir *et al.*, 2014; Walker *et al.*, 2006). Several studies indicate a decrease in species richness, evenness and diversity (Shannon-Wiener) with rising temperatures (Chapin III *et al.*, 1995; Ganjurjav *et al.*, 2016; Klanderud & Totland, 2005; Walker *et al.*, 2006) as well as changes in community composition (Ganjurjav *et al.*, 2016). Plant height will also likely increase with long-term warming effects (Bjorkman *et al.*, 2018; Elmendorf *et al.*, 2012; Ganjurjav *et al.*, 2016; Jonsdottir *et al.*, 2005; Walker *et al.*, 2006). Plant response may, however, differ between plant groups and between species. Studies in the arctic indicate a trend wherein both evergreen and deciduous shrubs, and graminoids are more likely to be positively affected by warming, while lichens and bryophytes will react negatively (Bjorkman *et al.*, 2019; Jonsdottir *et al.*, 2005; Walker *et al.*,

2006). With increasing soil temperature, Icelandic grasslands tend to become species poorer, mostly due to loss of flowering plants (forbs) (Guðmundsdóttir *et al.*, 2014).

Vulnerable ecosystems and sheep in a warming climate

Some studies have been performed on the combined effect of vertebrate (sheep, caribou, etc.) herbivory and warming in high latitudes. Grazing in warmed areas decreases total aboveground community biomass in contrast to protected warmed areas (Kaarlejärvi *et al.*, 2013; Post & Pedersen, 2008). Not all functional groups respond in the same way. Graminoids respond positively to both the combined effects of warming and herbivory and herbivory only, with an increase in both cover and biomass, and grazing seems to mitigate the biomass loss due to warming (i.e. grazed warmed plots fare better than enclosed warmed plots in terms of graminoids). Forbs and deciduous shrubs, on the other hand, prosper in enclosed, warmed plots (Kaarlejärvi *et al.*, 2013; Post & Pedersen, 2008). Species origin also matters; while lowland species are impeded by both warming and grazing, tundra species benefit (Eskelinen *et al.*, 2017). As for plant height, warmed enclosed plots exhibit higher growth than their ambient counterparts (Kaarlejärvi *et al.*, 2013), suggesting a positive effect of warming on plant height. Warming in combination with herbivory can increase species richness in a plant community due to both an increase in species recruitment and a decrease in species loss (Eskelinen *et al.*, 2017; Kaarlejärvi *et al.*, 2017).

Geothermally warmed areas as a proxy for warming climate

Naturally occurring geothermal temperature gradients allow for studying temperature changes in an otherwise unchanging environment without the cost of extensive experimental setups. One advantage of geothermal areas, where the soil has been heated for decades or centuries, is that the plant community has had multiple generations of the higher than ambient soil temperatures (ambient referring to the temperature of unheated soils) and therefore provides insight into the long-term effects of warming (O'Gorman *et al.*, 2014). This provides an advantage over short term artificially heated experiments, wherein the warming is restricted over a short time interval, making it difficult to project the results onto long term effects (O'Gorman *et al.*, 2014). Indeed, in a common garden study by Valdés *et al.* (2019), daughter plants exhibited phenology in relation to the mother's original soil temperature at the Hengill geothermal area.

Naturally warmed ecosystems offer the opportunity to study a combination of decadal warming effects and vast warming gradients at little cost or technical effort. The wide temperature spectrum of naturally heated soils can also offer higher warming levels than many artificial setups, closer to actual predictions for high latitude areas (Leblans, 2016; Sigurdsson *et al.*, 2016). Additionally, as these temperature gradients tend to be steep and occur on a small spatial scale, environmental factors such as precipitation, soil composition, day length, irradiation, altitude etc. are constant (Leblans, 2016; O'Gorman *et al.*, 2014; Sigurdsson *et al.*, 2016). However, environmental factors can co-vary and additional laboratory experiments might be needed in those cases (Leblans, 2016). A possible drawback of such natural experiments is e.g. that the geothermally heated groundwater can affect biological, chemical and physical processes of the plant communities.

Grændalur – a natural warming experiment

Grændalur, a valley in SW Iceland, offers a unique opportunity to study effects of warming on ecosystems as the soil is warmed by geothermal energy. This creates a temperature gradient in the soil, ranging from ambient to +20°C (and higher) without any notable changes of other environmental variables (Sigurdsson *et al.*, 2016). The valley, like most others in Iceland, is home to grazing sheep during the summer months, allowing for a combined study of temperature and grazing effects. Each summer as many as 150-200 sheep can be found roaming the valley (Guðríður Helgadóttir, personal communication). Grændalur is 6.2 km^2 (620 ha), meaning approximately 0.28 sheep/ha (175 sheep/620 ha). This qualifies as low to medium-low grazing intensity (A. Arnalds, 1981; B. Magnússon & Magnússon, 1992). In 2012 and 2013 permanent study plots were established in the area and a year later they were fenced off, making them inaccessible to the sheep in the area. These plots are part of the ForHot research site (www.forhot.is). ForHot is a natural soil warming experiment that has been in place since 2008, where ecosystem responses to +1–20°C soil warming are studied (Forhot research team, 2019; Sigurdsson *et al.*, 2016). In the summer of 2015, a year after the fencing, the vegetation within and outside these fenced areas was compared but no significant difference found, indicating that one year of sheep exclusion did not affect the vegetation structure (Meynzer, 2017).

Objectives

In this study I look at the effects five years of sheep exclusion have had on the plant communities in the ForHot study plots in Grændalur. The aim of this study is to examine if – and then how – sheep grazing affects the plant community's response to a warming climate, using the geothermal temperature gradient as a proxy for rising air temperature. I will also look at the individual effects of rising temperatures and grazing on the plant community. My hypotheses are that (1) species richness, evenness and diversity (Shannon-Wiener and Simpson) will decrease with rising temperature, especially at higher temperatures but (2) that this response will be lessened by grazing, at least at the lower temperatures. Some species in arctic ecosystems may benefit from higher temperature, leading to their dominance lowering biodiversity. Oppositely, grazing can moderate this effect, thus lessening or halting biodiversity loss. I also expect that (3) both grazing and soil temperature will change species composition, e.g. by affecting the abundance of herbivory tolerant and intolerant species as well as variably temperature tolerant species. I predict that (4) vegetation height will increase with rising soil temperatures, but to a lesser extent in grazed plots. For some species, the increased temperatures are beneficial, and induce a higher growing plant, while continuous grazing will stump growth. Lastly, I hypothesise that (5) flowering rates (i.e. number of flowering individuals compared to vegetative) will be significantly lower in grazed plots. Sheep are selective grazers and therefore it can be expected that outside the fence change in vegetation is affected by both the temperature gradient and grazing. For example, if specific plant species that colonise or spread in areas with rising temperatures are continuously grazed, as well as trod on by sheep, this will inevitably hinder these plants in becoming dominant in the ecosystem, possibly allowing for other species, less favoured by sheep to take over. It is possible that the interplay of grazing and temperature imposes an evolutionary conflict of sorts, with the two forces pulling on the plant community from opposite directions.

Methods

Study site

The study was performed in Grændalur, a valley near the town Hveragerði in SW Iceland (N64° 01.631' W21° 11.756', 115-165 m a.s.l., Figure 1). Iceland is a volcanic island in the North Atlantic Ocean. It is situated on an active hotspot (a mantle plume on a mid-oceanic ridge) where two tectonic plates are diverging, causing volcanic activity (Barbier, 2002; Ingólfsson *et al.*, 2008; Saemundsson, 1992; Zakharova & Spichak, 2012). Grændalur is a part of the Hveragerði high-temperature geothermal system (Arnorsson *et al.*, 2008; Saemundsson, 1992; Zakharova & Spichak, 2012). The ground water in Grændalur is warmed by volcanic channels in the underlying bedrock, resulting in hot springs, fumaroles and mud pools, as well as heating the soil that the water percolates through (Gasperikova *et al.*, 2015; Zakharova & Spichak, 2012).
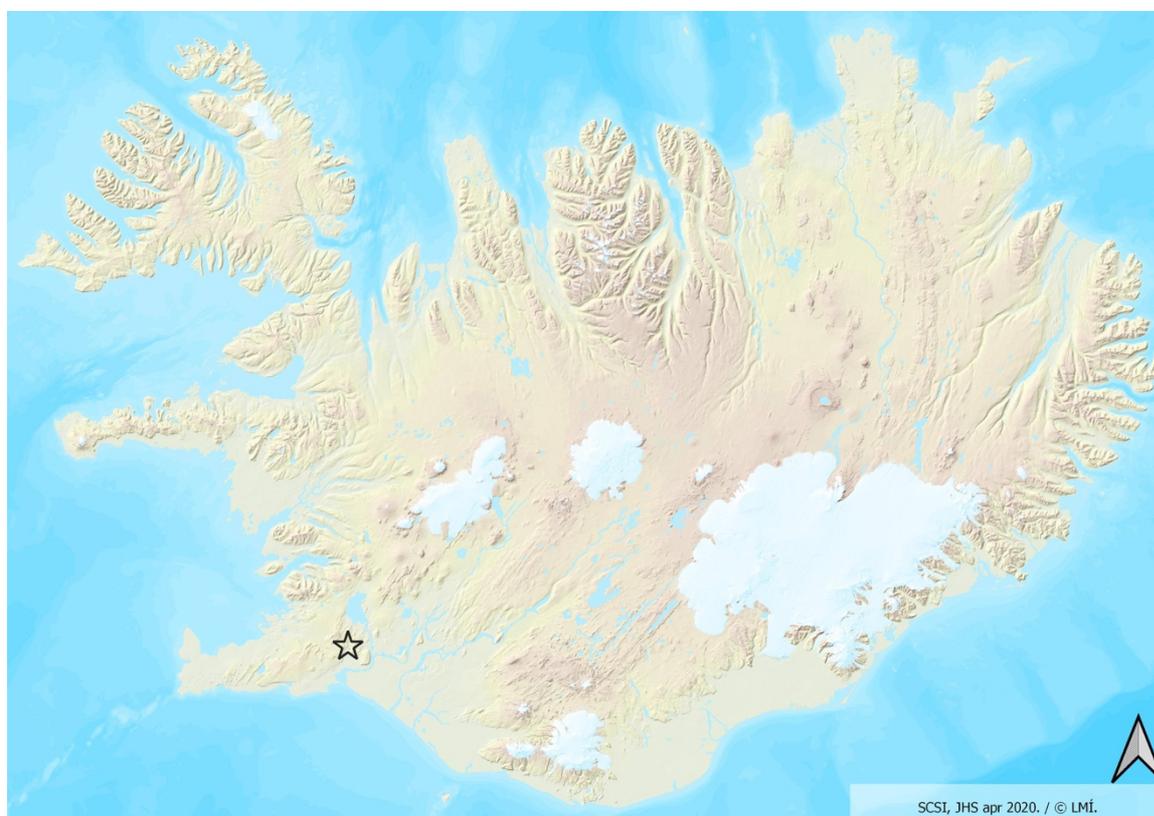
Figure 1. Grændalur (star) is located in SW Iceland near the town of Hveragerði (© Jóhann Helgi Stefánsson).

Icelandic climate is relatively mild considering the islands northerly position; with warm winters and cool summers. This oceanic climate is in part due to the Gulf stream bringing warm ocean water to the shores (Ó. Arnalds, 2015). The growth period for most plants in Iceland ranges from mid-May through late August/early September and most species reach peak growth and flowering in late July (Kristinsson, 2012). The mean annual temperature (MAT) in Grændalur for the years 2006-2016 was 5,18°C (4,4°C for 1958-2016), and MAT for the growing season (May-September) was 10.0°C. Mean annual precipitation for the same period was 1412.94 mm (1398.13 mm for 1958-2016). Weather data comes from the nearest weather station, in Eyrarbakki, a seaside village approximately 17 km south of Grændalur (Icelandic Meterological

Office, 2016). The soil on the site is Andosol, the distinctive soil type of volcanic areas (more specifically Brown Andosol, the soil of vegetated drylands) (Ó. Arnalds, 2008; Sigurdsson *et al.*, 2016). Andosol has a high capacity for accumulation of organic carbon (as much as 25%) as well as low bulk density and high water retention abilities (Ó. Arnalds, 2008, 2015).

The study site is covered by grassland, wherein the three most dominant vascular plants are *Agrostis capillaris, Galium boreale* and *Ranunculus acris* (all favoured by sheep), and bryophytes are abundant in the undergrowth (Sigurdsson *et al.*, 2016). According to the EUNIS habitat classification, the research site falls into three categories; Wavy-hair grasslands (E1.73), Boreo-subalpine *Agrostis* grasslands (E1.7221) and a proposed new category, Icelandic *Empetrum Thymus* grasslands (E1.2617) (Ottósson *et al.*, 2016). Local accounts indicate that the area has been geothermally warmed for centuries. Indeed, the name Grændalur literally means "Green valley", which is accredited to the heated soil keeping the grass green in early spring and long into winter (Sigurdsson *et al.*, 2016).

Research plots

In the autumn of 2012 and spring 2013, 25 plots were set up in Grændalur, as part of the long-term ForHot research project. The plots were located in approximately 50 m transects perpendicular to a temperature gradient from an unheated area (control, +0°C) to c.a. +10°C. Five plots were placed in each transect at five different temperatures (~ +0, +1, +3, +5 and +10°C). Each plot was 2 x 2 m in size. In the spring of 2013, an additional 6th plot was added to each transect at ~ +20°C warming. This plot was only 1 x 1 m in size due to a steeper rise in temperature at that level. In the spring of 2014 these plots were fenced off, making them inaccessible to grazing sheep (Figure 2).

To assess whether sheep grazing affects the ecosystems' response to soil warming, 30 plots were placed outside the fences, following the same method of temperature gradient. Each plot outside the fence corresponded with another inside the fence, i.e. they were paired. Thus, each fenced off transect has a corresponding transect with approximately the same temperature and location, but outside the fence (Figure 3). The soil temperature of the transects fluctuates a little throughout the year but does not interfere with the temperature gradient as such (Leblans, 2016; Meynzer, 2017; Sigurdsson *et al.*, 2016).

Figure 2. Grændalur, SW Iceland, as seen from inside transect 4. Transects 1 and 2 are in the background, as are some of the residential sheep.

In this study I used these plots to examine the effects of both grazing and rising temperatures on plant communities. Prior to gathering the data, all transects were inspected to make sure the heat gradients were still the same. Out of the five transects, two (transects 3 and 5) showed a considerable deviance from the established gradient. Transects 3 and 5 were therefore excluded from this experiment, as it relies on the temperature gradient.
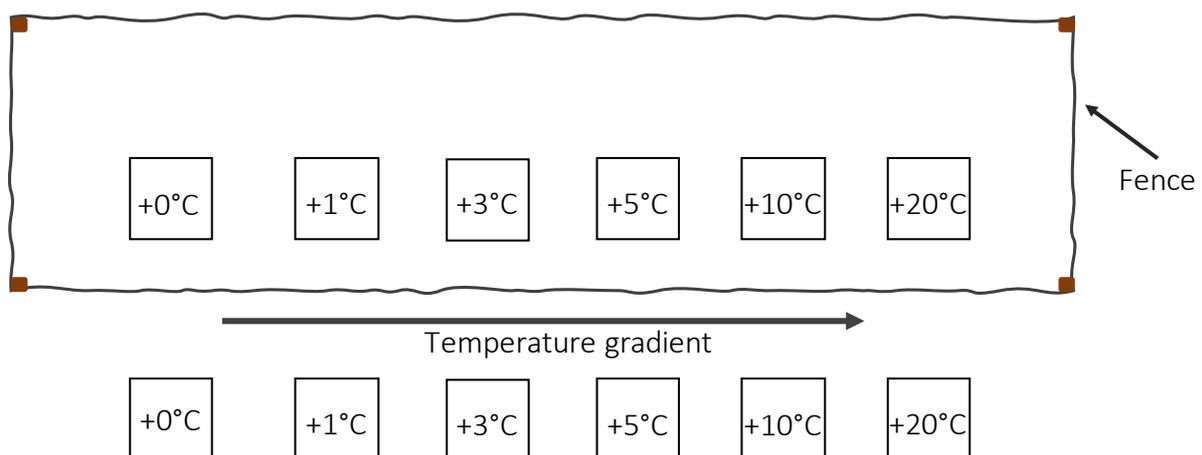
Figure 3. Five transects were established in Grændalur, SW Iceland. Each transect contains six fenced off plots on a temperature gradient from ambient, as well as a paired plot at the same temperature outside the fence. The plots are 2x2 m in size, except for the +20°C plots, which are 1x1 m.

Data collection

Data collection took place at the height of the growing season in late July 2019 (specifically 18th, 19th and 26th July). All field work was conducted by the same two trained and experienced persons, in unison, so as to limit sampling errors.

Within each of the twelve plots per transect all vascular plant species were recorded. Additionally, two 50 x 50 cm subplots were placed at opposite sides of the plot, perpendicular to the temperature gradient (Figure 4). Vegetation height was measured by placing a ruler vertically in each subplot corner and measuring the highest touch, i.e. the highest point where a plant touched the ruler. Average plant height for the plot was then calculated from the eight measurements. Vascular plant species cover – and the cover of lichen, bryophytes and biological crust – was estimated according to an adjusted Braun-Blanquet scale (Table 1)(Braun-Blanquet, 1964). For analysis, average abundance for each score was used. Species nomenclature is according to Kristinsson (2012). All plots were photographed (an overview photograph covering the whole plot) in case any discrepancy or uncertainty came up regarding the data after collection. Photographs could then be referred to later, i.e. double-check species identification.

To study the difference in flowering with and without sheep herbivory, flowering and non-flowering *Ranunculus acris* individuals were counted in each frame. I chose to focus specifically on *R. acris* to study reproductive growth in various soil temperatures and with and without grazing. *R. acris* was chosen since it is abundant in Grændalur (Sigurdsson *et al.*, 2016) and is a favoured fodder plant amongst sheep (Perron, 2017; Þorsteinsson, 1980). A few species were under consideration to be selected based on personal knowledge of the valley: *Cardamine nymanii, Ranunculus acris, Geum rivale, Geranium sylvaticum, Cerastium vulgaris* and *Bistorta vivipara.* Only *R. acris* was selected due to lack of flowering individuals of the other species at the time of collection.

To estimate to what extent species composition in grazed and fenced plots was influenced by species life form or palatability, each species specific for only one plot-type (fenced or grazed) was assigned a Raunkiær's life form according to Stefánsson (1948) and sheep palatability score according to Þorsteinsson (1980). Raunkiær's life form classification system is based on the placement of a plant's buds during winter (e.g. on aboveground shoots or in the soil; Stefánsson, 1948). The palatability scores are: 1 (high palatability), 2 (medium palatability) and 3 (low palatability) (Þorsteinsson, 1980).
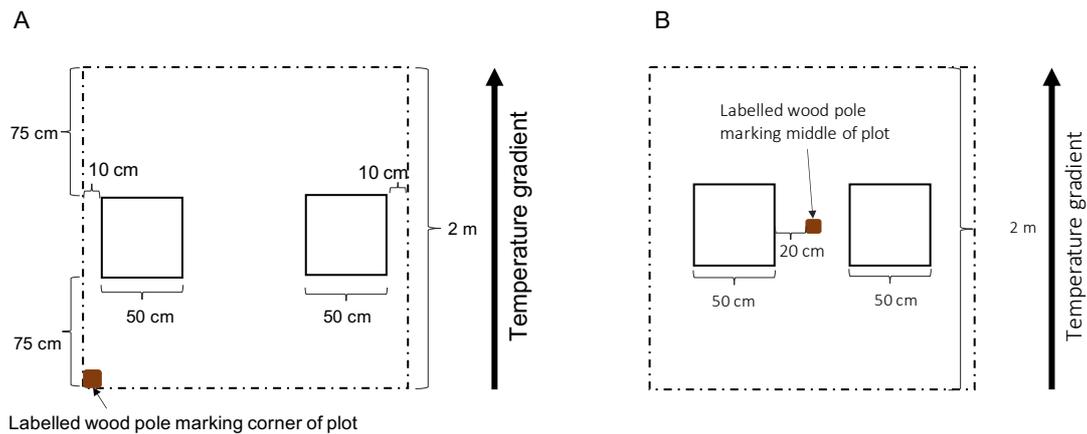
Figure 4. Setup of plots inside (A) and outside (B) the fenced transects in Grændalur, SW Iceland. Each plot is 2x2 m in size, apart from the +20°C plot which is 1x1 m. Two 50x50 cm subplots were placed in each plot, perpendicular to the temperature gradient. The plots inside and outside the fence differ in setup to fit the original experiment done in 2015 *(Meynzer, 2017)*.

Table 1. A modified Braun-Blanquet scale used to estimate vegetation cover (as used by the Soil Conservation Service of Iceland). Each species occurring in a plot is assigned a score (1-8) according to its estimated cover (%). For analysis, the median cover (%) for each score is used.

SCORE	COVER (%)	MEDIAN COVER (%)
1	0-1	0.5
2	1-5	3
3	5-10	7.5
4	10-15	12.5
5	15-25	20
6	25-50	37.5
7	50-75	62.5
8	75-100	87.5

Data analysis

Statistical analysis was conducted in R Studio (Version 1.1.463)(RStudio Team, 2016) using the following packages; Vegan (Oksanen *et al.*, 2019), LmerTest (Kuznetsova *et al.*, 2017), lme4 (Bates *et al.*, 2015) and ggplot2 (Wickham, 2016). For an enhanced visual representation, two R colour palettes were used, RColorBrewer (Neuwirth, 2014) and wesanderson (Ram & Wickham, 2018).

Species richness, species evenness, Shannon-Wiener diversity and Simpson's diversity indices were calculated, as well as community height and % *R. acris* flowering for each plot. All calculations were based on measurements in the two 50x50 cm subplots so as to maximize data collection while minimizing time/effort, but also to lightly follow the methods of Meynzer (2017). The average cover for each plot was calculated as the mean cover from the two subplots. Species richness was determined as the total number of species in subplots per plot. Average community height was calculated from the eight subplot measurements. Before further analysis, all data was checked for normality with the Shapiro-Wilk test in combination with visual inspection. All parameters showed adequate normal distribution.

Linear mixed models

The effects of temperature and grazing on the measured plant community responses (plant height, species richness, Shannon-Wiener diversity and Simpson's diversity) were tested with linear mixed effects models (LMM). Soil temperature, grazing, and their possible interaction were used as fixed explanatory variables. Grazing had two levels; grazing and no grazing, and soil temperature had six levels (+0, +1, +3, +5, 10, +20°C). The aforementioned plant community parameters were used as the response variables. Transect was added as a random effect, as difference between transects (due to transects) was not of interest here. For each parameter the best fitting model was found through model simplification by ANOVA, with each model as separate arguments. Only significant variables (grazing, temperature, interaction, random effect of transect) were included in the final analysis. The best fitting model was selected based on AIC (Akaike information criterion) and BIC (Bayesian information criterion) – for both of which a lower value indicates a better fit – as well as p-values. In all cases the best fitting model excluded an interaction between grazing and soil temperature. Due to singularity (a singular fit) when evenness was tested with the random transect factor, a simpler linear regression model (LM) was used on species evenness, disregarding the random transect factor (Table 3).

NMDS (Non-metric Multidimensional Scaling)

Non-metric multidimensional scaling (NMDS) was used to determine how temperature and grazing affected the plant community composition (Minchin, 1987). The data was transformed into a distance matrix according to the Bray-Curtis dissimilarity method, and then used to create an ordination. In an ordination, the closer together objects are the more similar they are. Environmental factors of interest (grazing, soil temperature) were projected onto the NMDS ordination as vectors. The direction and length of the vectors indicates the degree to which the environmental factor explains the variation. Temperature isoclines were also projected onto the ordination, indicating the placement of plots on the temperature gradient. This was applied to the subplot cover data (Braun-Blanquet cover %). NMDS was also used on presence/absence matrices (subplots and 2 x 2 m plot), and functional groups (in subplots). As these gave very similar results, only sub-plot cover data will be reported in the results chapter and the rest is in appendix (Appendix figure 1 and Appendix table 8). The functional groups were; bryophytes, lichen, equisetum, graminoids, evergreen shrubs, deciduous shrubs and forbs (Appendix table 5 and 7).

Ranunculus acris flowering

The effect of sheep grazing on *R. acris* flowering was tested with a generalised linear model (GLM) with a binomial distribution. The initial model also included effects of soil temperature, but due to scarcity of flowering individuals this proved unfeasible. Transect (random effect) was discarded after model testing based on AIC.

Results

Effects of soil temperature and grazing on species composition and diversity

Plant community composition and diversity

Overall, 41 species were found in the 2 x 2 m plots and of those, 39 species were found within the 50 x 50 cm subplots. Around half the species (20) were found both in grazed and fenced subplots but ten only in grazed subplots and nine in fenced sub-plots (Appendix tables 1 – 4). As for the species found only in one plot type (Table 2), no drastic difference could be discerned when considering palatability. Indeed, four out of nine species that occurred only in grazed plots are considered highly palatable (palatability score 1) and an additional three have medium palatability. As for life forms, all but one species specific for grazed plots were hemicryptophytes, while there was a little more variation in species life-forms in fenced plots (Appendix table 2).

Considering cover, graminoids were the most abundant functional group, followed by forbs, bryophytes and equisetum, and finally evergreen shrubs, ferns and lichen. Graminoids and forbs were recorded in all plots, while other functional groups had lower plot incidence (Table 2, Appendix table 1 and 2). The most common species were amongst others; *Agrostis capillaria*, *Anthoxanthum odoratum*, *Festuca vivipara*, *Potentilla anserina* and *Equisetum arvense* (Appendix table 3 and 4)*.

Table 2. Functional groups in fenced and grazed transects in Grændalur. Plot incidence ratio is calculated as the number of grazed/fenced plots the functional group was recorded in divided by the total number of grazed/fenced plots. Avg. % cover is average cover of each functional group per plot in grazed and fenced transects.

TREATMENT	GRAZED		FENCED	
	incidence in plot	avg.%cover	incidence in plot	avg.% cover
BRYOPHYTES	0.61	33.25	0.67	33.28
LICHEN	0.17	0.36	0	0
GRAMINOID	1	69.17	1	56.31
EQUISETUM	0.67	2.64	0.83	12.21
FERN	0.11	0.06	0.11	0.06
DECIDUOUS.SHRUB	0	0	0	0
EVERGREEN.SHRUB	0.28	1.78	0.06	0.03
FORB	1	21.97	1	35.31

Grazing and soil temperature effects on plant diversity

Grazing did not significantly affect species richness, species evenness, Simpson's diversity and Shannon-Wiener diversity (Figure 5, Table 3) and there was no significant interaction between grazing and soil temperature (Table 3). However, the variance was much greater within the grazed plots (wider confidence intervals) than the fenced plots. Rising temperatures negatively affected Shannon-Wiener (R^2=0.21, t=-3.374, p=0.002) and Simpson diversity (R^2=0.22, t=-3.263, p=0.003) as well as species richness (R^2=0.18, t=-3.128, p=0.004), but temperature did not affect species evenness (R^2=0.03, t=-0.957, p=0.345).
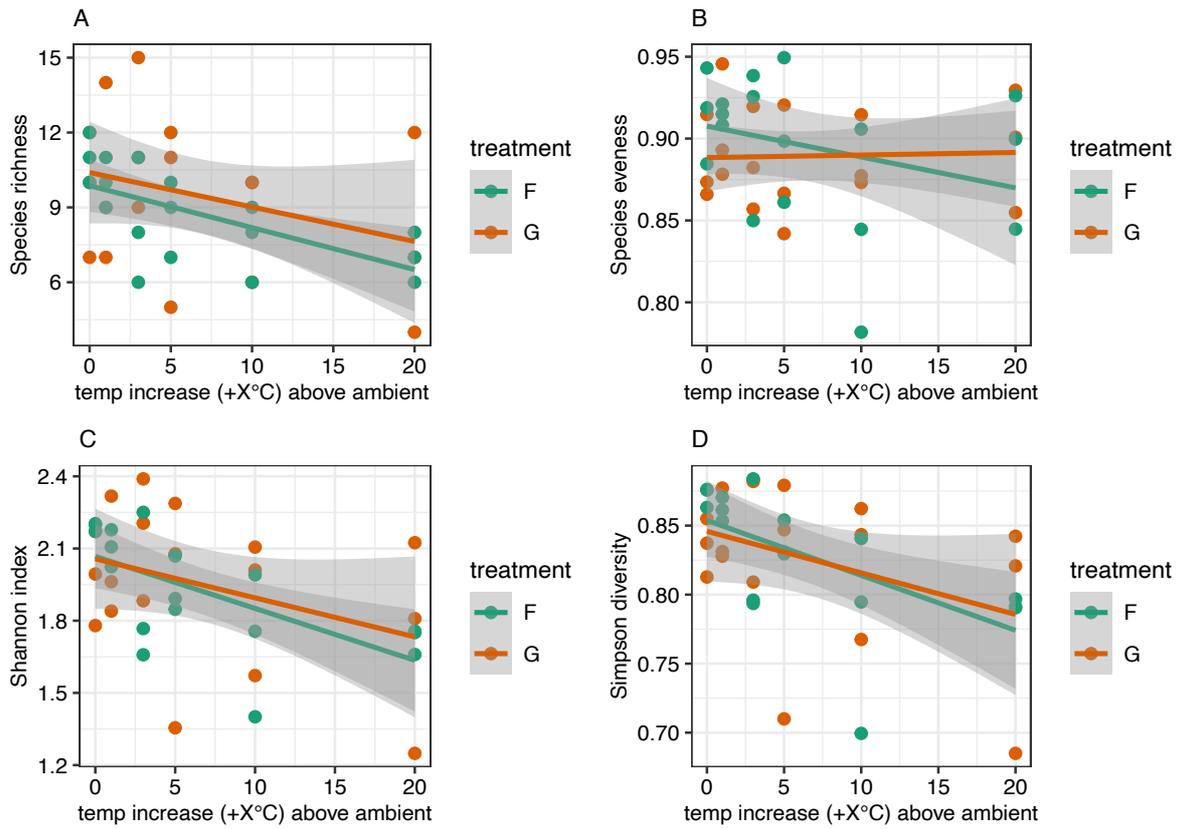
Figure 5. The effect of soil temperature and sheep grazing on species richness (A), species evenness (B), Shannon-Wiener diversity (C) and Simpson's diversity (D) in a geothermal area in Grændalur, SW-Iceland. Fenced plots (F) are green and grazed plots (G) are orange. The grey shade around the fitted lines indicates the 95% confidence interval. The x-axis indicates the plot temperature (°C) in comparison to ambient, i.e. 5 indicates ambient+5°C plots.

Table 3. The effect of sheep grazing and soil temperature on species rishness, diversity, plant height and eveness in Grændalur, SW – Iceland. Results from linear mixed models for species richness, Shannon-Wiener diversity, Simpson diversity and height and linear model for species evenness are shown. The best fitting model was selected for each parameter, following model testing with ANOVA with regards to lowest AIC and BIC values, and p-values. Significant results (P ≤ 0.05) are in **bold**, and marginally significant results (P <0.1) are in *italics*.

Model	R^2 fixed effects	R^2 total	estimate	Std error	t value	Pr(>|t|)
SPECIES RICHNESS						
spec ~ temp + treatment + (1 | transect)	0.18	0.44				**0.002921**
(intercept)			9.77260	0.97246	10.049	**0.00135**
temperature			-0.15305	0.04892	-3.128	**0.00381**
grazing			0.72222	0.67022	1.078	0.28953
Shannon-Wiener diversity						
shan ~ temp + treatment + (1|transect)	0.21	0.37				**0.001442**
(intercept)			2.049488	0.093378	21.948	**1.48e-05**
Temperature			-0.018899	0.005601	-3.374	**0.002**
Grazing			0.025148	0.076733	0.328	0.745
SIMPSON DIVERISTY						
simp ~ temp + treatment + (1|transect)	0.22	0.29				**0.001928**
(intercept)			0.850603	0.014929	56.978	**4.69e-10**
Temperature			-0.003496	0.001071	-3.263	**0.00268**
Grazing			-0.001588	0.014673	-0.108	0.91452
Height						
height ~ temp + treatment +(1|transect)	0.13	0.35				**0.03906**
(intercept)			35.9244	5.1206	7.016	**0.00272**
Temperature			-0.5081	0.2840	-1.790	*0.08331*
Grazing			-7.7847	3.8900	-2.001	*0.05419*
EVENNESS	R^2	Adj. R^2				
even ~ temp + treatment	0.03	-0.025				0.57
(intercept)			0.9009734	0.0105319	85.547	**<2e-16**
Temperature			-0.0008644	0.0009028	-0.957	0.345
Grazing			-0.0059581	0.0123679	-0.482	0.633

Grazing and temperature effects on plant community composition

Grazing did not affect community composition (R^2 = 0.0375, p = 0.54, Appendix table 8) and species composition did not differ between grazed and fenced of plots (Figure 6). Temperature did, however, significantly influence species composition (R^2 = 0.2561, p = 0.005, Appendix table 8), explaining 25% of the observed variance. More thermophilic species such as *Prunella vulgaris* and *Veronica officinalis* (Kristinsson, 2012) replaced others such as *Galium* spp., *Equisetum* spp. and *Rumex acetosa* (Appendix table 1, 3 and 4). The two environmental vectors for grazing (p=0.54, R^2=0.0375) and temperature (p=0.005, R^2=0.2561) lie almost completely opposite each other in the ordination space, indicating a negative correlation between temperature and grazing on community composition. Considering functional types, there was a significant shift in composition, from e.g. *equisetum* in colder plots toward evergreen shrubs (mainly *T. praecox*) in the warmest (R^2=0.45, p=0.001, Appendix figure 1, Appendix table 8).
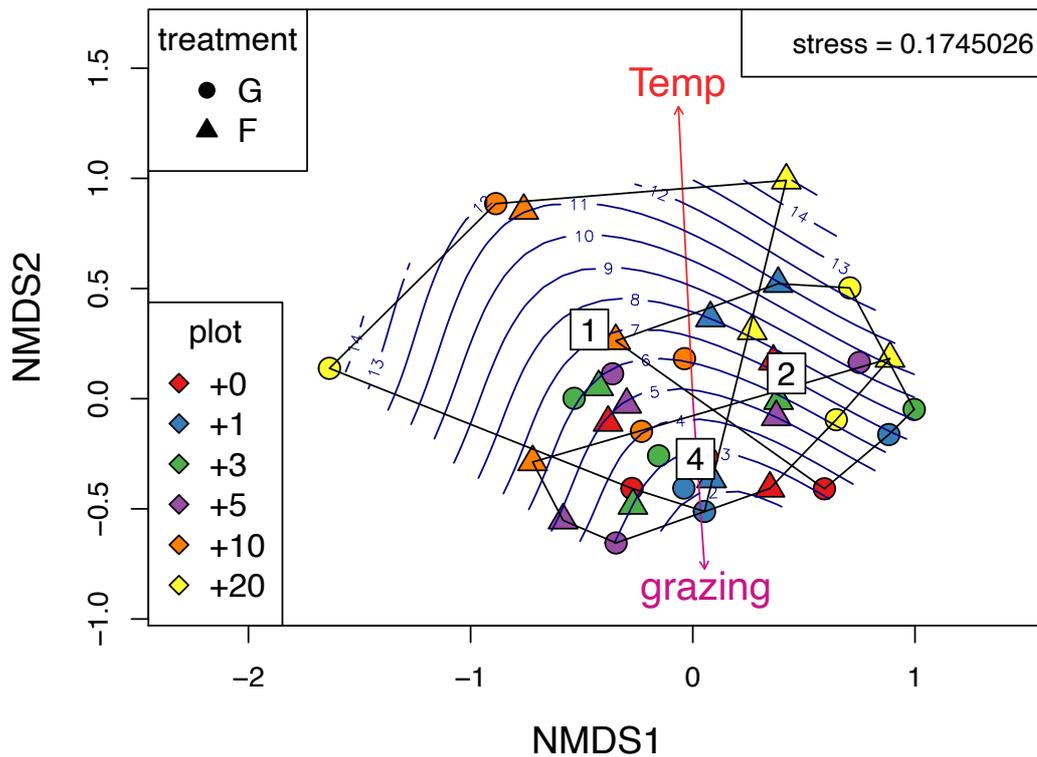
Figure 6. Non-metric multidimensional scaling (NMDS) ordination (Bray-Curtis) illustrating the effect of soil temperature and sheep grazing on community composition in Grændalur, SW- Iceland based on mean Braun-Blanquet values. Circles represent grazed plots, triangles represent fenced plots, and colour indicates plot and consequent soil temperature (+0 to +20°C). The polygon hulls show how the three transects (1, 2, 4) cluster together. The arrows indicate the direction of correlation of environmental factors (grazing, temperature) and the community ordination. The length of the arrows is proportional with the strength of the correlation, i.e. the longer the arrow the stronger the correlation. Appendix table 8 lists the goodness of fit of the two vectors. The contour lines show the lay of the plot points on the temperature gradient. The gradient shows the increase in temperature over ambient (C°), from +0 to +20 °C.

Effects of rising temperature and sheep grazing on plant community height

Plant height was marginally significantly reduced by grazing (p=0.05, t=-2.001, R^2=0.13, Table 3) and temperature (p=0.08, t=-1.790, R^2=0.13), with a drastic decline in plant height at the highest temperature (Figure 7). Leaving out the warmest plots (+20°C) changed the results remarkably, bringing the estimate for temperature from -0.5081 to 1.5904 (std. error=0.4143, p= 0.000749, t= 3.839, R^2=0.4143)(Appendix table 6).
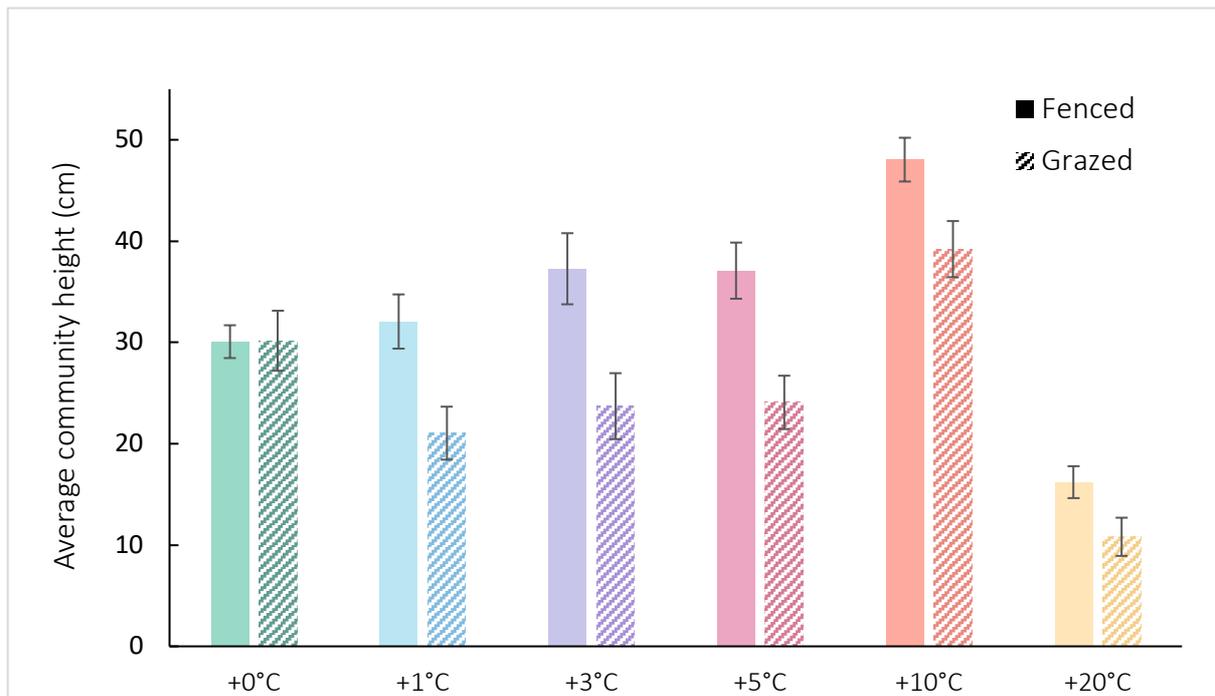
Figure 7. Average plant community height in plots at different soil temperature (degrees above ambient). The filled columns represent fenced plots and the shaded columns represent grazed plots in Grændalur, SW Iceland. Error bars show standard error of the mean (SEM) for each plot.

Sheep grazing reduces *R. acris* flowering

Significantly more *R. acris* flowers were found in fenced plots compared to grazed plots (X^2=13.289, df=5, p=0.02082) and flowering was significantly lower in grazed plots (Estimate = -1,86 +/- 0,67, Z=-2,749, p = 0.006). In grazed plots six of 13 plants flowered and in fenced plots 44 out of 52 plants (Appendix table 9). Most flowers were found within the lower temperature plots (Figure 8).
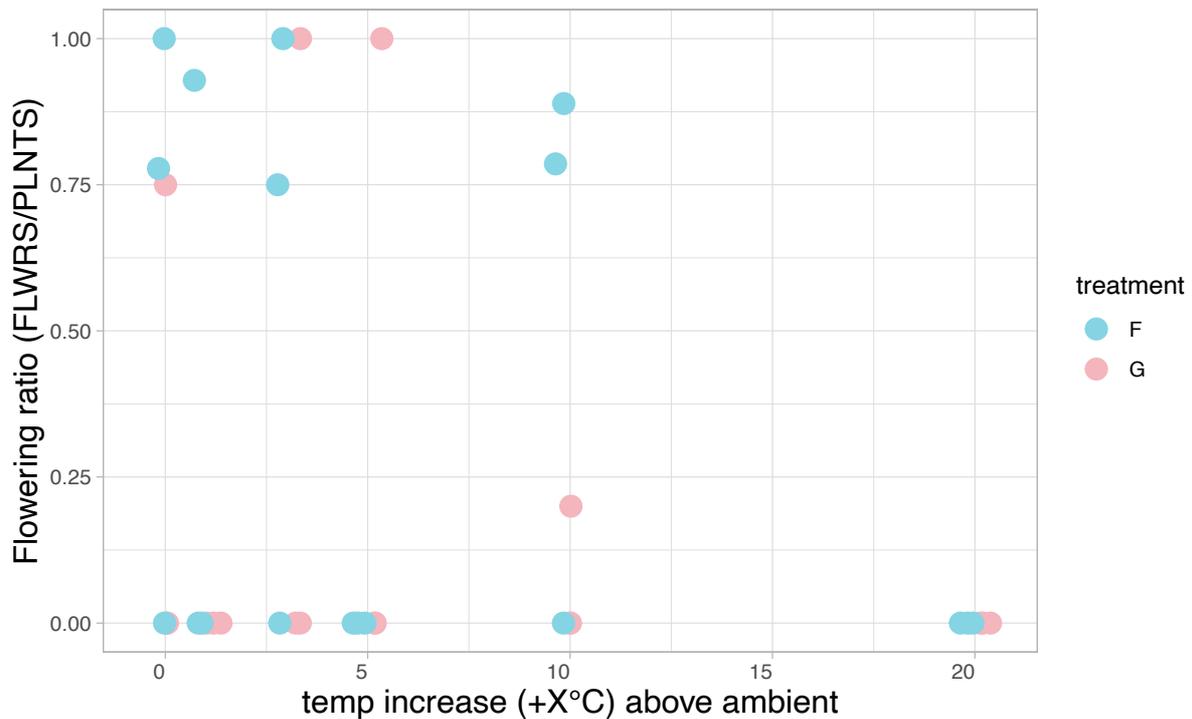
Figure 8. Effects of soil temperature on *R. acris* flowering in Grændalur, displayed as *R. acris* flowering ratio. The ratio was calculated as no. flowers/no. plants per plot. Object size is based on the flowering ratio, fenced plots are blue and grazed plots are pink. The x axis indicates the increase in °C above ambient soil temperature (+0, +1, +3, +5, +10 and +20°C).

Discussion

My results indicate that soil temperature had adverse effects on vascular plant communities, lowering species richness and diversity as well as reducing vegetation height. Five years of grazing exclusion did not affect plant diversity or evenness, but grazing had a negative effect on height. There was little indication that grazing influenced the effect of temperature on plant communities. Additionally, sheep grazing significantly reduced *R. acris* flowering in Grændalur.

Sheep grazing effects on plant community's response to a warming climate

Contrary to my hypothesis, there was no indication that five years of sheep exclusion influenced the plant community's responses to increased soil temperatures. Previous studies in sub-arctic and arctic sites have had mixed results, with some plant community responses to increasing temperatures influenced by grazing and others not. In a low shrub tundra in West Greenland, no community composition differences were found after four years of herbivore exclusion , however, herbivory did influence the plant biomass response to warming (Post and Pedersen (2008). A four year study on the Tibetan plateau, found that grazing influenced plant diversity responses to warming only at some sites (Klein *et al.* (2004). Similarly, after three years of herbivore exclusion and experimental warming in a tundra meadow in Lapland, no interaction was found between grazing and temperature for species richness or tundra species cover, but there was an interactive effect on lowland species cover (Eskelinen *et al.*, 2017). And after three years of reindeer exclusion in Finnmark, Norway, no interaction was found between herbivore exclusion and warming effects on shrubs densities (Bråthen *et al.*, 2017). I cannot rule out that these interactive effects either exist in such a weak capacity as to elude statistical test, or that they will appear after a longer period of sheep exclusion. It is therefore vital to keep monitoring the area and possible changes in the future. This is especially highlighted by the fact that my results indicate that both temperature and grazing affect several aspects of the plant community.

Plant community dynamics with rising temperatures and grazing

No striking difference was found in species presence between grazed and fenced plots. Although not all species were found in both plot types, overall species richness was similar. No indication was found that palatable plant species were fewer in grazed plots. It must however be pointed out that these one plot-type (grazed/fenced) species are mostly rare occurrences and any assumptions should therefore be made with caution (Appendix table 3). Interesting exceptions are *Galium normanii* and *Trifolium repens* which were both quite common in grazed plots (Appendix table 4) although both are preferred by sheep (Þorsteinsson, 1980). There were no flowering *G. normanii* individuals – only vegetative – and although *T. repens* was flowering in grazed plots, the plants were low and cropped in stature. I observed the same short stature and/or lack of flowers in several other flowering species in grazed plots e.g. *Bistorta vivipara, Cerastium fontanum, Galium* spp.*, Potentilla* spp.*, Rumex acetosa* (as well as *R. acris*, see below). These plants were not measured specifically and therefore there is no statistical data to back up these observations. This does however indicate an interesting subject of study for the future, to examine grazing effects on plant's reproductive biomass.

Although grazing did not significantly influence functional group composition, I observed some differences in the data. Overall graminoid cover was higher in grazed plots and overall forb cover in fenced plots. This holds with earlier studies reporting positive relationships between

mammal herbivory and graminoids, including increased graminoid biomass and/or density in grazed plots (Jónsdóttir, 1991; B. Magnússon & Magnússon, 1992; Marteinsdottir *et al.*, 2017; Post & Pedersen, 2008), grassland maintenance by hindering shrub growth (Bråthen *et al.*, 2017) and colonisation and expansion of lowland species (Eskelinen *et al.*, 2017) in warming arctic regions. Managed herbivory could thus be used as a tool to halt the expansion of shrubs and colonising species on warming arctic heath- and grasslands (Eskelinen *et al.*, 2017; Olofsson *et al.*, 2009; Post & Pedersen, 2008). Grazing must however be carefully managed to e.g. avert a transition from heathland to grassland with overgrazing (Ross *et al.*, 2016) and protect degraded areas from additional disturbance, cover losses and soil erosion (Ó. Arnalds & Barkarson, 2003; Marteinsdottir *et al.*, 2017).

Lichen cover tends to lessen with grazing (Marteinsdottir *et al.*, 2017), but this was not the case here; lichen was only found in grazed plots. Vegetation was noticeably denser in fenced plots – which could reduce possible space for lichen growth in the sward – or oppositely, that the grazing provided openings in the vegetation, and thus more possibilities for lichen growth.

Biodiversity

In line with my hypothesis, and concurring with previous studies (Ganjurjav *et al.*, 2016; Robinson *et al.*, 2018; Walker *et al.*, 2006), rising soil temperature decreased species richness and diversity (Simpson and Shannon-Wiener). There was however, as mentioned above, no significant interaction between soil temperature and grazing, and grazing as a single treatment also had no significant effect on biodiversity. This might change with time, and a longer grazing exclusion period is likely to reveal a significant grazing effect (Eskelinen *et al.*, 2017; Kaarlejärvi *et al.*, 2017; Klein *et al.*, 2004). Other studies report opposing results, with increased species richness in fenced plots, but these studies did not include experimental warming (Allred *et al.*, 2012; Deng *et al.*, 2014). As for species evenness, neither grazing nor temperature had a significant effect. This contradicts results of a meta-analysis on Icelandic grazing studies where species evenness was higher in grazed plots compared to non-grazed (Marteinsdottir *et al.*, 2017). This might be explained by the grazing intensity in the valley, which could be light enough not to influence evenness. Another possible explanation is that not enough time has elapsed since the transects were fenced, and that the community needs longer time to reach a new equilibrium.

Species composition

Contrary to my expectations, five years of grazing exclusion did not influence community composition. A likely explanation is that more time is needed for the protected plant community to recover after decades – if not centuries – of grazing and reach a new equilibrium. Five years might thus not be enough time to see the effects reflected in the community composition (Post & Pedersen, 2008). A countrywide study on effects of sheep exclusion on plant communities in Iceland (S. H. Magnússon & Svavarsdóttir, 2007) and another on Texan grasslands (Allred *et al.*, 2012) revealed a significant change in composition after several decades of protection; we could expect to see the same happen in Grændalur. It is therefore important to continue following the trajectory of the plant communities in Grændalur over the long term, both to the transition, as well as the possible final novel community equilibrium. Additionally, the grazing intensity in Grændalur is low to medium-low (A. Arnalds, 1981; B. Magnússon & Magnússon, 1992). Earlier studies have shown little change in plant communities under mild or moderate grazing pressure, but a marked difference in intensely grazed

communities compared to lower grazing pressures (B. Magnússon & Magnússon, 1990). In tundra ecosystems, the opposite can be true, wherein grazing prevents a change in community composition by hindering lowland species from taking over when rising temperatures would otherwise induce their expansion in higher latitudes (Eskelinen *et al.*, 2017; Kaarlejärvi *et al.*, 2013). As for temperature, the species composition did change with rising soil heat, both in grazed and fenced plots (Figure 6). This is in line with earlier work studying warming effects on community composition, where communities change significantly under warming (Ganjurjav *et al.*, 2016; Robinson *et al.*, 2018; Walker *et al.*, 2006; Zhang *et al.*, 2015). The opposite directions of the soil and grazing vectors point towards a negative correlation between the factors. While soil temperature pulls the species composition in one direction, grazing pulls in the opposite direction. However, the grazing vector fit was not significant, so interpretation should be taken with a grain of salt.

Vegetation height is influenced by both warming and grazing

In line with my hypothesis, plants in fenced plots were significantly higher than in grazed plots. Contrary to my expectations, there was a significant reduction in plant height with rising temperature. However, this relationship was driven by the low stature in the warmest plot. Excluding the warmest plots (+20°C) from the analysis revealed a positive relationship between temperature and height (Appendix table 6). These findings concur with earlier studies showing an increase in vegetation height with rising temperatures (Bjorkman *et al.*, 2018; Elmendorf *et al.*, 2012; Ganjurjav *et al.*, 2016; Jonsdottir *et al.*, 2005; Klanderud & Totland, 2005; Walker *et al.*, 2006) and that grazing does reduce plant height (Bråthen *et al.*, 2017; Deng *et al.*, 2014; Kaarlejärvi *et al.*, 2013). The fact of the low stature in the warmest plots might indicate a certain threshold for suitable or viable temperatures for most species in question, which could be interesting to study further.

Grazing reduces *R. acris* flowering

R. acris flowering was, as expected, almost non-existent in grazed plots, despite the occurrence of vegetative plants (Appendix table 9). This is in direct accordance with previous observations that sheep selectively graze *R. acris* (Perron, 2017; Þorsteinsson, 1980) and that mammal herbivory can severely reduce or even negate forb flowering in arctic regions (Kaarlejärvi *et al.*, 2013). Observations of other forbs in the fenced transects but outside the study plots (e.g. *F. ulmaria* and *G. rivale,* as mentioned above) support this result. A more extensive study focusing on reproductive biomass or flowering numbers might be prudent and could add statistical robustness to the human observation that herbivory severely reduces flowering of several forb species. I would suggest species such as *G. rivale, B. vivipara, C. fontanum, G. sylvaticum* and *Gallium* spp. as appropriate candidates for such a study. For example, from my three years of fieldwork in the valley, I have never encountered (neither while gathering data for this study, nor while working on other projects) a single flowering or vegetative *G. rivale* or *G. sylvaticum* individual, except for inside the fenced transects. Previous unpublished studies indicate that grazing severely influences flowering of *C. fontanum* and *Cardamine nymanii* in Grændalur, where they are both grazed and pulled up by sheep (Marteinsdóttir*,* unpublished)

Speculations and prospects

It must be mentioned that all diversity calculations were based on observations from the two 50x50 cm subplots. As most vegetation does not have a constant but rather non-random

distribution, some species might be overcounted while others might be undercounted due to the location of the subplots. It might therefore have been more suitable to base all measurements on the 2 x 2 m plots or more 50 x 50 subplots. However, this would have been too time consuming for a project of this size, or possibly any size. Nevertheless, as was noted in the results, species richness did not change considerably when the 2 x 2 plot was considered (with only two additions in grazed plots). Despite little change in species richness, community composition (abundance of individual species) might have provided a different picture when looking at the whole plot. The same might then be true for species evenness, and the two diversity indices.

Also, due to the clumping or patchy distribution, some species were e.g. observed in abundance within the fenced transect but never occurred within the study plots, neither 2x2 m nor the subplots. This supports the notion that some species might be over or underestimated due to the size of the study plots. Most prominent among these species were *Geum rivale* and *Filipendula ulmaria* which grew in big prominent patches within the fenced transects. Indeed, *F. ulmaria* is a known favourite of sheep, which keep its growth down in grazed areas (Kristinsson & Þórhallsdóttir, 2018). It would therefore have been interesting and possibly informative to include these flowering species in the study – especially including flowering inside and outside the fence – if indeed it could be found in grazed parts of the surrounding valley. Looking back, I would have liked to focus more on e.g. *Galium* spp., *Cerastium fontanum, Bistorta vivipara, Geum rivale* and *F. ulmaria*, focusing on flowering and other physical characteristics such as height and biomass.

For similar studies in Grændalur in future I would suggest looking at aboveground and belowground biomass, with regards to grazing effects on various plant body parts, such as the root system (Allred *et al.*, 2012; A. Arnalds, 1981; Bai *et al.*, 2015; Jónsdóttir, 1991). It would also be interesting to compare various grazing intensities, e.g. to evaluate a possible holding capacity/threshold for sheep numbers in ecosystems such as that found in Grændalur. A longer-term study would also shed light on that, as grazing effects will likely become more prominent as the exclusion period grows longer. Repeated measurements over several years or decades might reveal changes that one year's measurements cannot capture. It would for instance be interesting to follow potential colonisation of woody plants (evergreen or deciduous shrubs) into the study plots, as there are no species of either functional group in the study area yet. As for any flowering studies, it might be prudent to extend data collection over a larger area (e.g. the whole fenced transect), to capture the natural variation in the plant community and produce more robust data.

Conclusions

In this study I showed how both soil temperature and sheep grazing affect various aspects of plant communities in a subarctic grassland. Rising soil temperature – as a proxy for atmospheric warming – reduces species richness and diversity and changes the community composition. Disregarding statistical significance, grazing might have some biological or ecological significance not captured by the test and might become more prominent or robust after a longer time of grazing exclusion. Rising temperatures result in increased plant height, while sheep grazing decreases plant height. As for reproductive biomass, we saw a significant increase in *R. acris* flowering when protected from sheep. These results, although by no means exhaustive, highlight the need for better grazing management in Iceland in the future, in conjunction with more extensive research. It is also clear that rising temperatures will influence and change grassland communities. Plant community dynamics are complex and intricate, and their responses to both grazing and global warming are, and will be, diverse and manifold. Geothermally warmed ecosystems offer a convenient and effective approach to answer many of the questions posed considering impending warming. Still more research is needed to better understand both the individual effects of these factors, as well as their suspected interactions on both whole plant communities and single species in high latitudes.

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Appendix

Appendix table 1. Species list by pot and treatment. Numbers 1, 2 and 4 indicate transects each species occurred in.

PLOT	+0°C		+1°C		+3°C		+5°C		+10°C		+20°C	
TREATMENT	F	G	F	G	F	G	F	G	F	G	F	G
SPECIES												
Bryophytes	2, 4	2, 4	2, 4	2, 4	2	2, 4	1, 2	2	1, 2	2, 4	1, 2, 4	2, 4
lichen		2		2		2						2
Agrostis capillaris	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4	2, 4	1, 4	1, 2, 4	1, 2, 4	1, 2, 4	2, 4	2, 4
Agrostis stolonifera											1	
Agrostis vinealis	4	4	4			1, 2		1, 2		1		
Calamagrostis neglecta												
Anthoxanthum odoratum	1, 2, 4	1, 2, 4	1, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2	1, 2, 4	2, 4	2, 4	2, 4	2, 4
Deschampsia caespitosa	2			1			1		2	1		
Festuca richardsonii	1	1, 4	1	1	1	1, 4	1, 4	1	1, 4	1, 2, 4		1
Festuca vivipara	2, 4	2, 4	1, 2	1, 2	2	1, 2, 4	2	2		2	1, 2, 4	2, 4
Poa pratensis	1, 2	2, 4	4	4	4	1, 4	1, 4	1, 4	1, 2, 4	2, 4	1	1
Juncus arcticus					1							
Luzula multiflora			1, 2	2	2	2		1, 2				2
Carex bigelowii	2		1, 4	1	1, 2	1	1, 2	1, 2	1, 2	1, 2, 4	2	
Equisetum arvense	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2	2, 4	4	2	
Botrychium lunaria	4	1		1			2					
Thymus praecox				2		2		2			4	2, 4
Bistorta vivipara		4	4	2								
Rumex acetosa	1, 2, 4	1	2, 4	4	4	4	4		4	4		
Leontodon autumnalis				2		2						
Taraxacum spp.						2						
Alchemilla filicaulis			2		1	2						
Alchemilla alpina		2										
Potentilla crantzii				2								
Ranunculus acris	1, 2	1, 2	2		1	1		4	2, 4	2		2
Galium verum	1, 2, 4	1	1, 2	1	1	1		1	4			
Galium normanii		2		2		2		2				4
Geranium sylvaticum							4					
Cerastium fontanum												1
Cardamine nymanii	4											
Epilobium sp.												1
Viola palustris	2											
Potentilla anserina	1		1, 2		1	1	1, 2	1	1, 2	1, 2, 4	1, 2	2

PLOT	+0°C		+1°C		+3°C		+5°C		+10°C		+20°C	
TREATMENT	F	G	F	G	F	G	F	G	F	G	F	G
Epilobium palustre							2				1	
Prunella vulgaris												2
Veronica officinalis											4	
Viola canina											4	
Galium boreale	1, 4	1, 4	1, 4	1, 4	1, 2, 4	1, 2, 4	1, 2, 4	1, 2, 4		4	4	4
Trifolium repens				2		2		2		2		2
Equisetum palustre			1									

There was no evident difference in palatability of plants found only on one side of the fence. As for life-forms, all but one species specific for grazed plots are hemicryptophytes, while there is a little more variation in species life-forms in fenced plots (Appendix table 2).

Appendix table 2. Species only occurring on one side of the fence. Plants inside the fence (F) are protected from grazing while plants outside the fence (G) are not. * indicates species that also occur only on one side when the whole 2x2 plot is considered. Palatability rating is as follows: 1 is high palatability, 2 is medium palatability and 3 is low palatability (Þorsteinsson, 1980). Raunkiær's life-forms are; Ph – Phanerophyte, N – Nanophanerophyte, Ch – Chamaephyte, H – Hemicryptophyte, G = Geophyte, HH – Hydrophyte, Helophyte, Th – Therophyte (Stefánsson, 1948).

Outside fence (G)	Palata-bility	Life-form	Inside fence (F)	Palata-bility	Life-form
Lichen	-	-	*Agrostis stolonifera* *	1	H
Leontodon autumnalis *	1	H	*Juncus arcticus* *	3	G
Taraxacum spp. *	1	H	*Geranium sylvaticum* *	1	H
Alchemilla alpine *	3	H	*Cardamine nymanii* *	2	H
Potentilla crantzii *	2	H	*Viola palustris* *	2	H
Galium normanii *	2	H	*Veronica officinalis*	-	Ch
Cerastium fontanum	2	Ch	*Viola canina* *	-	H
Prunella vulgaris *	-	H	*Equisetum palustre* *	2	G
Trifolium repens	1	H	*Epilobium palustre* *		
Epilobium sp. *					
Additions in 2x2 plot					
Luzula spicata	3	H			
Thalictrum alpinum	1	H			

Appendix table 3. Community matrix for **fenced plots** by transect and plot (two subplots, I and II, per plot). Each species is scored 1-8 in cover according to the adjusted Braun-Blanquet scale (Table 1).

transect	1												2												4											
plot	a		b		c		d		e		f		a		b		c		d		e		f		a		b		c		d		e		f	
subplot	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Species																																				
Moss spp.								1	1	1	8	8	8	8	7	8	8	8	7	3		2	8	8	6	7	6	3							8	8
Agrostis capillaris	3	2		2	5	6	4	6	1	1			3	4	2	3	3				6	6		2	3	4	5	4	7	7	6	6	8	8	2	1
Agrostis stolonifera											1	2																								
Agrostis vinealis																									1		1	2								
Anthoxanthum odoratum	5	5	5	5	5	5	4	6					3	5			2	5	6	6	2	3	2	3	5	5	5	4			6		1		2	3
Deschampsia caespitosa							2	3					4								2	2														
Festuca richardsonii	4	2	2	2	5	5	3		1	1																							1	4		
Festuca vivipara			5	3							5	5	4	5	3	5	3	6	6	6			2	5	3	3									6	5
Poa pratensis	3	1					2	1	3	2	3	5	1								2	2							4	6	2	5	5	5		
Juncus arcticus						2																														
Luzula multiflora			1												1		1																			
Carex bigelowii			1	2		2		1	8	8			1	1		1			1	2			3	2			1	1								
Equisetum arvense	6	5	5	3	5	4	6	4					3	2	4	2	1	2	1	2	3	5	1	2	3	2	4	5	6	6	3	4	4	5		
Botrychium lunaria																			1						1	1										
Thymus praecox																																	1			
Bistorta vivipara																											1	1								
Rumex acetosa	2	2											3			2									5	3	1	1	2		3	2		2		
Alchemilla filicaulis					5										5	5																				
Ranunculus acris	5	4			5										1	6	3				5	3											3	2		
Galium verum	1		3	2	2	2							2	2	2	2									2	1								1		
Geranium sylvaticum																															7					
Cardamine nymanii																												2								
Viola palustris													2																							
Potentilla anserina	4	4	3	3	7	5	8	7	5	7	5	5			4					7	8	8	6	4												
Epilobium palustre											2	2							1																	
Veronica officinalis																																	5	4		
Viola canina																																	1	1		
Galium boreale	2	2	1	1	4	5									3	5	4	6							4	4	3	3	2	4	3	2				2
Equisetum palustre			1																																	

Appendix table 4. Community matrix for **grazed plots** by transect and plot (two subplots, I and II, per plot). Each species is scored 1-8 in cover according to the adjusted Braun-Blanquet scale (Table 1).

transect	1												2												4											
plot	a		b		c		d		e		f		a		b		c		d		e		f		a		b		c		d		e		f	
subplot	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Species																																				
Moss spp													8	8	8	8	8	8	8	8	6	5	8	8	7	5	5	5	1	1			2	2	8	7
Lichen spp													2		2	2	2						1													
Agrostis capillaris	8	6	3	2			3		2	2			6	5	4	5	1		2		6	4	2	3	6	6	7	7	6	7	7	8	7	6	5	4
Agrostis vinealis					5	3		5		1					2	2	4	4							2	1										
Anthoxanthum odoratum	5	5	6	6	5	4	7	6					4	3	4	5	5	5	3	4	6	6	1	2	4	5	6	5	6	5	4	5	6	5	5	5
Deschampsia caespitosa				2					2	7																										
Festuca richardsonii	2			1	4	5	3	5	3	2	3	5							2		2						1							1		
Festuca vivipara			3	1	5	5							2	3	4	4	5	5	6	5	2			6	1	1		2							5	5
Poa pratensis					1	1					4	3	2						2	3							2	3	2	1	4	5	4	6	6	
Luzula multiflora							1								1		1	1	2	2			1													
Carex bigelowii			1	1		1	2	2	8	7									2	4	2												1	2		
Equisetum arvense	2	2	1	1	5	3		3					3	2	2	1	2	2	2	2					2	2	1	2	1	2				2		
Botrychium lunaria															1	1																				
Thymus praecox															2	1	2	2		2				3										6		
Bistorta vivipara															2	2									1											
Rumex acetosa														2													3	2		1				1		
Leontodon autumnalis															1			2																		
Taraxacum spp.																		2																		
Alchemilla filicaulis																		2																		
Alchemilla alpina													2	3																						
Potentilla crantzii																1																				
Ranunculus acris	3				1								2								4		1								1					
Galium verum	6	3	4	2	3	3		1																												
Galium normanii													1	1	2	2	1	1	2	1															2	2
Cerastium fontanum									3																											
Epilobium spp.										2																										
Potentilla anserina					5	2	6	7	6	6											6	5		2									4	4		
Prunella vulgaris																							1	3												
Galium boreale	5	4	3	3	2	4	2	2							2	1	1	2							3	3	4	4	2	2	1	2	2	2		2
Trifolium repens															4	3	7	3	2		5	4	5													

Appendix table 5. Functional group occurrence in each plot (presence/absence matrix). If group was present in plot it is marked with 1, while 0 indicates absence.

plot	transect	treatment	bryophytes	lichen	graminoid	equisetum	fern	deciduous Shrub	evergreen Shrub	forb
+0°C	1	Grazed	0	0	1	1	0	0	0	1
+1°C	1	Grazed	0	0	1	1	0	0	0	1
+3°C	1	Grazed	0	0	1	1	0	0	0	1
+5°C	1	Grazed	0	0	1	1	0	0	0	1
+10°C	1	Grazed	0	0	1	0	0	0	0	1
+20°C	1	Grazed	0	0	1	0	0	0	0	1
+0°C	2	Grazed	1	1	1	1	1	0	0	1
+1°C	2	Grazed	1	0	1	1	1	0	1	1
+3°C	2	Grazed	1	1	1	1	0	0	1	1
+5°C	2	Grazed	1	0	1	1	0	0	1	1
+10°C	2	Grazed	1	0	1	0	0	0	0	1
+20°C	2	Grazed	1	1	1	0	0	0	1	1
+0°C	4	Grazed	1	0	1	1	0	0	0	1
+1°C	4	Grazed	1	0	1	1	0	0	0	1
+3°C	4	Grazed	1	0	1	1	0	0	0	1
+5°C	4	Grazed	0	0	1	0	0	0	0	1
+10°C	4	Grazed	1	0	1	1	0	0	0	1
+20°C	4	Grazed	1	0	1	0	0	0	1	1
+0°C	1	Fenced	0	0	1	1	0	0	0	1
+1°C	1	Fenced	0	0	1	1	0	0	0	1
+3°C	1	Fenced	0	0	1	1	0	0	0	1
+5°C	1	Fenced	1	0	1	1	0	0	0	1
+10°C	1	Fenced	1	0	1	0	0	0	0	1
+20°C	1	Fenced	1	0	1	0	0	0	0	1
+0°C	2	Fenced	1	0	1	1	0	0	0	1
+1°C	2	Fenced	1	0	1	1	0	0	0	1
+3°C	2	Fenced	1	0	1	1	0	0	0	1
+5°C	2	Fenced	1	0	1	1	1	0	0	1
+10°C	2	Fenced	1	0	1	1	0	0	0	1
+20°C	2	Fenced	1	0	1	1	0	0	0	1
+0°C	4	Fenced	1	0	1	1	1	0	0	1
+1°C	4	Fenced	1	0	1	1	0	0	0	1
+3°C	4	Fenced	0	0	1	1	0	0	0	1
+5°C	4	Fenced	0	0	1	1	0	0	0	1
+10°C	4	Fenced	0	0	1	1	0	0	0	1
+20°C	4	Fenced	1	0	1	0	0	0	1	1

Appendix table 6. Results from linear mixed model for plant height excluding the warmest plot (+20°C). Significant results (P ≤ 0.05) are in **bold**.

| Model	R^2 fixed effects	R^2 total	estimate	Std error	t value	Pr(>|t|)
Height						
height ~ temp + treatment +(1|transect)	0.27	0.66				
(intercept)			13.2942	7.9699	1.668	0.126731
Temperature			1.5904	0.4143	3.839	**0.000749**
Grazing			-7.5468	2.9532	-2.555	**0.017068**

Appendix table 7. All occurring species sorted by functional group.

Functional group	Species	Functional group	Species
Graminoid	*Agrostis capillaris*	Forb	*Cerastium fontanum*
Graminoid	*Agrostis stolonifera*	Forb	*Epilobium palustre*
Graminoid	*Agrostis vinealis*	Forb	*Epilobium sp.*
Graminoid	*Anthoxanthum odoratum*	Forb	*Equisetum palustre*
Graminoid	*Carex bigelowii*	Forb	*Galium boreale*
Graminoid	*Deschampsia caespitosa*	Forb	*Galium normanii*
Graminoid	*Festuca richardsonii*	Forb	*Galium verum*
Graminoid	*Festuca vivipara*	Forb	*Geranium sylvaticum*
Graminoid	*Juncus arcticus*	Forb	*Leontodon autumnalis*
Graminoid	*Luzula multiflora*	Forb	*Potentilla anserina*
Graminoid	*Poa pratensis*	Forb	*Potentilla crantzii*
Equisetum	*Equisetum arvense*	Forb	*Prunella vulgaris*
Fern	*Botrychium lunaria*	Forb	*Ranunculus acris*
Evergreen shrub	*Thymus praecox*	Forb	*Rumex acetosa*
Forb	*Alchemilla alpina*	Forb	*Taraxacum spp.*
Forb	*Alchemilla filicaulis*	Forb	*Trifolium repens*
Forb	*Bistorta vivipara*	Forb	*Veronica officinalis*
Forb	*Cardamine nymanii*	Forb	*Viola canina*
		Forb	*Viola palustris*

Appendix table 8. Two environmental vectors were fitted onto the ordinations; temperature and grazing. The temperature vector fits significantly onto each of the four ordination variations. The grazing vector is not significant. Significant values are in **bold**.

	NMDS1	NMDS2	R^2	p-value
Temperature				
Species cover (BB)	0.050407	0.998730	0.2561	**0.005**
Presence/absence	-0.0078534	0.9999700	0.2	**0.024**
Functional type	0.38755	0.92185	0.4493	**0.001**
2x2 plot	-0.13974	0.99019	0.3229	**0.003**
Grazing				
Species cover (BB)	0.064485	-0.997920	0.0375	0.54
Presence/absence	-0.088487	-0.996080	0.0183	0.747
Functional type	0.44699	0.89454	0.0414	0.488
2x2 plot	0.27103	0.96257	0.0048	0.924

NMDS was also performed for subplot presence absence data, whole 2x2 plots, and subplot functional type presence absence data (Appendix figure 1). These show more or less the same result – there is no clear clustering between grazed and fenced plots – i.e. there is no clear difference in species composition between treatments. As for environmental vectors, temperature fits significantly onto the ordination space in all cases, but grazing is not significant (Appendix table 8). Looking at functional types, increased temperature pulls the community towards a more evergreen dominant community (here *Thymus praecox*). Here, temperature accounts for almost half of the variation ($R^2 = 0.4493$, p = 0.001).
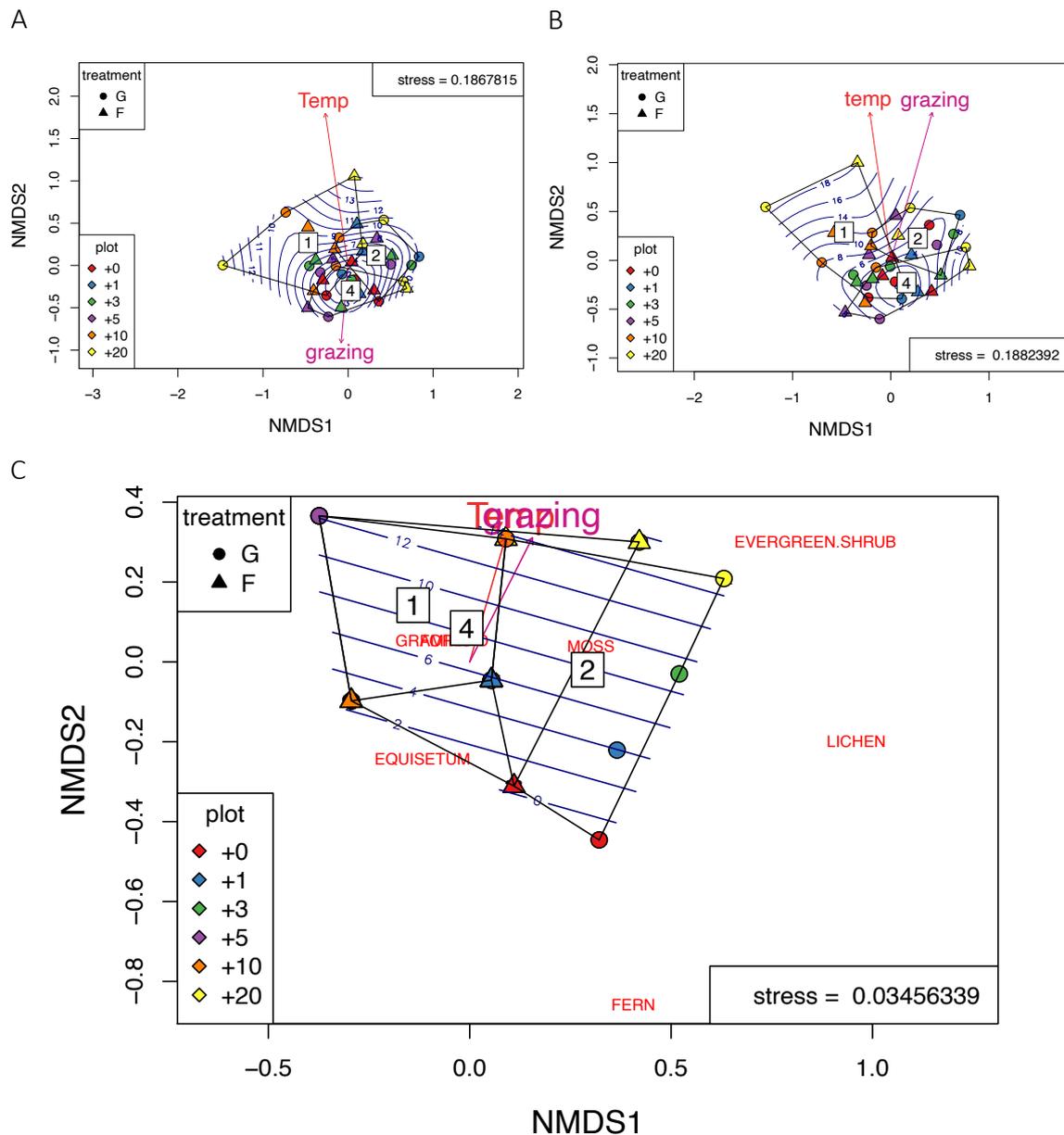
Appendix figure 1. NMDS ordination illustrating the effects of grazing and soil temperature on community composition based on (A) presence/absence data from the subplots and (B) presence absence data from the 2x2 m plots, and functional groups (C). Circles represent grazed plots, triangles represent fenced plots, and colour indicates plot and consequent soil temperature (+0 – +20°C). The polygon hulls show how the three transects (1, 2, 4) cluster together. The arrows indicate the direction of correlation of environmental factors (grazing, temperature) and the community ordination. The length of the arrows is proportional with the strength of the correlation, i.e. the longer the arrow the stronger the correlation. Appendix table 8 lists the goodness of it of the two vectors. The contour lines show the lay of the plot points on the temperature gradient. The gradient shows the increase in temperature over ambient (C°), from +0 to +20 °C.

Appendix table 9. *R. acris* flowering by plot. #FLWRS indicates number of flowering *R. acris* plants in plots, #PLNTS indicates total *R. acris* plants in plot.

plot	Transect	Treatment	#FLWRS	#PLNTS	ratio
+0°C	1	Grazed	3	4	0.75
+1°C	1	Grazed	0	0	0
+3°C	1	Grazed	1	1	1
+5°C	1	Grazed	0	0	0
+10°C	1	Grazed	0	0	0
+20°C	1	Grazed	0	0	0
+0°C	2	Grazed	0	1	0
+1°C	2	Grazed	0	0	0
+3°C	2	Grazed	0	0	0
+5°C	2	Grazed	0	0	0
+10°C	2	Grazed	1	5	0.2
+20°C	2	Grazed	0	1	0
+0°C	4	Grazed	0	0	0
+1°C	4	Grazed	0	0	0
+3°C	4	Grazed	0	0	0
+5°C	4	Grazed	1	1	1
+10°C	4	Grazed	0	0	0
+20°C	4	Grazed	0	0	0
+0°C	1	Fenced	7	9	0.78
+1°C	1	Fenced	0	0	0
+3°C	1	Fenced	3	4	0.75
+5°C	1	Fenced	0	0	0
+10°C	1	Fenced	0	0	0
+20°C	1	Fenced	0	0	0
+0°C	2	Fenced	1	1	1
+1°C	2	Fenced	13	14	0.93
+3°C	2	Fenced	0	0	0
+5°C	2	Fenced	0	0	0
+10°C	2	Fenced	11	14	0.79
+20°C	2	Fenced	0	0	0
+0°C	4	Fenced	0	0	0
+1°C	4	Fenced	0	0	0
+3°C	4	Fenced	1	1	1
+5°C	4	Fenced	0	0	0
+10°C	4	Fenced	8	9	0.89
+20°C	4	Fenced	0	0	0

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Takk! Tack! Thanks!
Rán Finnsdóttir