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Response of plant functional groups to grazing exclusion and fertilization in the Icelandic highlands

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Yfirlýsing

Hér með lýsi ég því yfir að verkefni þetta er byggt á mínum eigin athugunum, er samið af mér og að það hefur hvorki að hluta né í heild verið lagt fram áður til hærri prófgráðu.

Hanna Laufey Jónasdóttir

Nafn nemanda

Abstract

From the time of settlement the Icelandic highlands have undergone a drastic ecological change. This is partly due to climate and geological factors, but the introduction of large herbivores at the end of the 9th century had a strong influence on the ecosystems, especially those in the highlands. Nowadays, grazing practices in Iceland rely on extensive sheep grazing in summer rangelands, mainly located in the highlands, from June and until the autumn. Centuries of high grazing pressures in these ecosystems have driven some of them to a degraded state, with little chance of recovery unless active restoration measures are implemented.

In this study, I use plant community data from a field experiment to examine the effects of two management practices, grazing exclusion and fertilization, on the cover of different plant functional groups after four years of treatment. Plant functional groups are groups of plants that share similar characteristics and functions in an ecosystem. In this study I categorized plants into three groups: facilitating, neutral and retarding, depending on their effects on ecosystem processes.

Following my expectations, the facilitating group showed a positive response to the fertilizing experimental treatments and increased their cover in response to fertilization. The neutral plant functional group did not respond to the treatments, and the retarding group reduced its cover in favor of the facilitating group. Grazing exclusion did not show a strong effect on the cover of the different plant functional groups, but this was to be expected given the relatively short duration of the experiment (4 years). Grazing exclusion generally needs more time to have an effect on ecosystems than fertilization.

Keywords: Plant functional groups (PFGs), fertilization, grazing, grazing exclusion, rangelands, rangeland degradation, Icelandic highlands.

Ágrip

Frá tímum landnáms hefur íslenska hálendið gengið í gegnum miklar vistfræðilegar breytingar. Þær hafa að hluta til orðið vegna breytinga á loftslagi og einnig vegna jarðfræðilegra þátta, en það má með sanni segja að innflutningur beitardýra til landsins í lok níundu aldar hafi haft gríðarleg áhrif á vistkerfi Íslands, einkum þau á hálendinu. Enn þann dag í dag liggur góð afkoma húsdýra, sérstaklega fjár, á beitarlöndum hálendisins, þar sem féið gengur frá júní og fram á haust. Hár beitarþrýstingur á þessi vistkerfi hefur rýrt framleiðslugetu og stöðugleika þeirra svo mikið að ólíklegt er að þau nái fyrri stöðugleika sjálf og án inngrips er hætta á að mörg þeirra rýrni enn frekar.

Í þessari rannsókn nota ég gögn um plöntusamfélög til að skoða áhrif tveggja aðferða, áburðargjafar og útilokun beitar, á þekju virknihópa planta eftir fjögurra ára meðferðartímabil. Virknihópar eru hópar plantna sem hafa álíka virkni og hlutverk í vistkerfi. Í þessari rannsókn flokkaði ég plöntutegundir í þrjá hópa: virkar, hlutlausar og hindrandi, eftir áhrifum þeirra á vistkerfisferli.

Líkt og við var búist sýndi hópur virku platnanna jákvæð viðbrögð við áburðargjöf og jók þekju sina. Hlutlausi hópurinn sýndi lítil sem engin viðbrögð við aðferðunum. Hindrandi hópurinn dróg úr þekju sinni og þær virku komu þar inn í staðinn. Það að útiloka beit hafði ekki marktæk áhrif á neinn af virknihópunum, en það kom ekki á óvart þar sem að tilraunin hafði ekki verið í gangi nema í fjögur ár þegar gögnunum var safnað. Það að útiloka beit eða draga úr henni hefur ekki eins snör áhrif á vistkerfi og áburðargjöf.

Lykilorð: Virknihópar plantna, áburðargjöf, beit, stöðvun beitar, beitarlönd, gróðurhnignun beitarlanda, hálendið.

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1. Introduction

1.1 Rangeland degradation

Rangelands are an integral part of animal husbandry in many places around the world and play a key role in food security worldwide. Rangelands are a source of income for many local communities, especially in developing countries (Reid, Fernández-Giménez and Galvin, 2014), and are important for maintaining biodiversity and providing diverse ecosystem services (Alkemade, Reid, van den Berg, de Leeuw, and Jeuken, 2013). For example, rangelands are a source timber, medicinal herbs and other important products, and they also provide recreational opportunities. For all these reasons, we need to see to their continued health and make sure they are used sustainably (Lund, 2007, Archer and Stokes, 2000).

However, in many parts of the world, rangeland degradation has become a serious concern. Stocking (1996) estimated that up to 73% of rangelands in drylands worldwide are degraded, mainly in Asia, Africa and South America. In contrast, other estimates of rangeland degradation worldwide go as low as 20% (Lund, 2007). Those varying numbers are to be expected since definitions of degradation are not set in stone. For instance, the IPCC report from 2019 (Olsson *et al*. 2019) found that there are no reliable estimates about how much land in the world has been degraded or to what extent. Gibbs and Salmon (2015) estimated the amount of land degradation worldwide to be somewhere between <6-40%. In all, it is very challenging to assess the extent of land degradation because of conflicting definitions of what a degraded land is. A common definition of degraded land is land “characterized by reduction in productivity of the land or soil” (Archer and Stokes, 2000). If we go by that, what looks like a perfectly healthy land can be in a state of degradation, because by only looking at an area we are not always able to assess its productivity and stability.

1.2 Rangeland degradation in Iceland

Land degradation is also a main environmental concern in Iceland (Arnalds, 1987). Icelandic ecosystems have changed dramatically since human settlement ~1100 years ago. It has been suggested that the total loss of cover of birch forests since settlement has been around 50% and up to 90% in some parts of the country (Ólafsdóttir, Schlyter, and Haraldsson, 2001). At present, it is estimated that 42% of the land in Iceland has minimally degraded vegetation cover, and 3.8% is covered in moss (Arnalds, 2011). The rest of Iceland’s 103.000 km^2 are in a declining or vulnerable ecological state, with some areas completely devoid of vegetation (Arnalds, 2011).

Before human settlement, the ecosystems in Iceland were in a climate driven decline (Ólafsdóttir, Schlyter, and Haraldsson, 2001) or perhaps in somewhat of a transitional state where the ecosystems moved from one threshold to another without human interference (Arnalds, 2015). The total vegetation cover declined steadily from a maximum extent around 3500 BP until the settlement of Iceland (Ólafsdóttir, Schlyter, and Haraldsson, 2001). This decline was accelerated by the arrival of the first humans and large herbivores in Iceland (Dugmore *et al*. 2005). The import of domestic animals and need for wood were some of the factors that pushed the ecosystems in an already compromised state over the brink (Arnalds, 2015, Rannveig Ólafsdóttir, Schlyter, and Haraldsson, 2001). The severe climatic conditions of the so called "little ice-age", starting in the 11th century and persisting into the late 19th century did not help the matter (Miller *et al*. 2012). The lack of knowledge of the first settlers about the climate and ecosystems in this new land, which was deceptively similar to other North-Atlantic agricultural areas, was another unexpected problem. Soon many areas in Iceland became degraded and are still recovering to this day (Arnalds, 2015, McGovern *et al*., 2007).

But what is so different in Iceland? The new settlers were farmers that had successfully farmed the neighbouring countries for a long time and even had laws in place to prevent the overuse of land (Karlsson, Sveinsson og Árnason. 1992). One of the main differences between Iceland and its neighbouring countries lies in the soil composition of the island and the introduction of large herbivores into an environment where they had not been before.

Andosols, the main soil type in Iceland, originate from volcanic parent materials and are one of the rarest soil types in the world (Arnalds, 2015). Andosols lack phyllosilicates which provide cohesion. They are also able to hold great amounts of water and seem dry until a disturbance happens, which can result in water erosion and landslides. This innate lack of cohesion combined with a lack of coarse parent material makes them extremely susceptible to wind erosion once the vegetation cover has been removed (Arnalds, 2015). The high susceptibility of andosols to wind and water erosion makes them highly unstable and renders land use very challenging.

In addition, the first settlers introduced large mammalian herbivores to the ecosystems in Iceland. Nowadays, sheep and lambs are gathered up in early summer and moved to the grazing commons, most of them located in the highlands (>400 m above sea level). The size of the commons ranges from 400 km^2 and up to >1000 km^2. The sheep spend up to 4 months in the highlands and are then rounded up and moved to lowland pastures (Arnalds, 2015, Arnalds and Barkarson, 2003, Ross *et al*., 2016). The sustainability of grazing practices in Iceland has been repeatedly questioned and the condition of the grazing commons has been severely compromised, with 40% of them currently considered in poor condition (Marteinsdóttir *et al*., 2020). Similar patterns of rangeland degradation are also seen in other areas in the North-Atlantic region, such as Norway, Scotland, Faroe Islands and Greenland, where extensive summer grazing by sheep is a common practice (Ross *et al*., 2016). The condition of the commons in Iceland varies across the country. The most degraded areas are located near or inside the active volcanic zone, while areas outside the active volcanic zone can be in good condition (Arnalds, 2015, Marteinsdóttir *et al*., 2020).

The management of the commons is in the hands of local government or counsels of farmers, who decide the length of the grazing period and stocking rates (Arnalds and Barkarson, 2003). Subsidies from the government aim at encouraging more sustainable management practices and in recent years, a warmer climate coupled with lighter grazing pressures have had positive outcomes, especially outside the active volcanic zone (Ross *et al*., 2016). However, some areas within the active volcanic zone are still in very poor condition and some would require total exclusion of grazing for a long period of time to prevent further degradation (Arnalds, 2015, Ross *et al*., 2016).

1.3 Processes and recovery of rangelands.

Grazing at moderate intensities can increase the presence of graminoids (Pakeman and Nolan, 2009). In some tundra ecosystems, grazing can cause a shift towards grass-dominated states (van der Wal, 2006). Graminoids are more capable of sustaining grazing than other types of plants, such as dwarf shrubs and mosses, and therefore become dominant (van der Wal *et al*., 2003). However, if the stocking rates increase further, palatable species like grasses decrease in abundance, with a parallel increase in the relative abundance of unpalatable plants (Bråthen *et al*., 2007). In the highlands of Iceland, heavy grazing has a negative impact on palatable species. As well, mosses and lichens decline in grazed areas even though they are not grazed by sheep because they are sensitive to trampling (Jónsdóttir, 1984).

Natural recovery of ecosystems can be a very long process. In the last 100 years or so, there has been increased interest from private groups and the public sector to recover ecosystems in Iceland, among them highland areas which are or have been grazed in the past. Restoration efforts have shown great progress, with new forests being planted and areas becoming more vegetated (Aradóttir and Halldórsson, 2011). Grazing exclusion and fertilization are good ways to improve ground cover and biomass. Grazing reduces plant cover and biomass and excluding it has positive effects, although these effects may take time to show (Mulloy, Barrio, Björnsdóttir, Jónsdóttir and Hik, 2019). In the long-term grazing exclusion increases biomass, above- and below ground, and cover (Cheng, Jing, Wei and Jing, 2016). Changes in species composition also occur as a response to grazing exclusion. Often, there is a decrease in species diversity following grazing exclusion when more dominant species, such as graminoids, are able to grow without interference from grazers. This leads to those dominant plants to monopolize resources, reducing the likelihood of new, subordinate species to gain ground in an ungrazed system (Hill, Evans and Bell, 1992). Van der Wal (2006) showed that moss and lichens will give way to graminoids and other species in grazed systems, leading to increased plant diversity. In turn, fertilization can drive rapid changes in species composition by providing opportunities for certain species, such as graminoids, to thrive, while reducing the abundance of mosses and lichens in a system (van der Wal *et al*., 2006). This can have cascading impacts on an ecosystem leading to a great change in a short time.

1.4 Plant Functional Groups

Plant functional groups (PFGs) are groups of plants that have similar roles in ecosystem processes and respond similarly to stress, disturbance and other environmental factors. There are several ways to group species together in PFGs based on the different characteristics chosen for grouping the species. The ecosystem and environment, as well as the aim of the particular study, play a main role in the choice of these characteristics and groupings (Lavorel, McIntyre, Landsberg and Forbes, 1997).

Individual plant species can tell us much about the general state of a particular ecosystem, but the responses might be difficult to generalize to ecosystems with different species composition. Therefore, it may be more informative to identify groups of plants based on their traits. As such, PFGs can be used as more general indicators of ecosystem processes. PFGs can be used as indicators of change in vegetation, whether they are caused by environmental changes or by management practices, for example in rangelands. Such changes can give an idea about how the ecosystem responds to changes in management practices and give indications of which management practices should be implemented (Días, Briske, and McIntyre, 2002). It is therefore important to link together PFGs and ecosystem functions to further assess land use and uphold ecosystem sustainability (Días, Briske, and McIntyre, 2002).

The dominance of a particular PFG can give an idea of the state of an ecosystem. Grime (1998) suggested that the group with the most biomass in an environment would be driving the functioning of the ecosystem. This theory was however refuted by McLaren and Turkington (2010) who found that the identity of these groups (graminoids, legumes and non-legume forbs) was more important. They found that graminoids had the greatest ability to compensate for lost biomass, compared to other groups. Graminoids also had the most impact on light interception, soil moisture and nutrients. These characteristics make the graminoids fall into a facilitating PFG, as they are productive, palatable and resistant to grazing, being able to quickly regrow after disturbances like grazing (Coughenour, 1985).

The neutral PFGs, as the name suggests, play a lesser role in ecosystem processes. Thus, increases or decreases in the relative abundance of this group in a community have little to no impact on ecosystem processes (Bråthen *et al*. 2007). Neutral PFGs can be removed from an area completely and that will have less impact on an ecosystem than the removal of graminoids (McLaren and Turkington, 2010). This group usually includes forbs and shrubs.

Finally, retarding PFGs are generally species such as lichens and mosses or evergreen shrubs. Retarding PFGs can colonize barren areas and once established, can maintain their presence for a long time. They however make an otherwise inhospitable landscape more hospitable overtime for other PFGs (Cutler, Belyea and Dugmore, 2008). The dominance of retarding PFGs in grazed systems may increase because those species are generally unpalatable to grazers (Bråthen *et al*. 2007). Another fact is that retarding species keep the soils unproductive and cold, slow down nutrient cycling, and many are able to secrete secondary metabolites that decrease the productivity of the soil and prevent the growth of other plants (van der Wal, 2006).

1.5 Aim of the study

In this thesis I aim at understanding how a degraded rangeland ecosystem changes in response to two common management practices: addition of fertilizer and grazing exclusion. To address this goal, I assess how the plant community as a whole responds to those factors, by looking at the changes in the cover of different plant functional groups in response to four years of grazing exclusion and fertilization in two locations in the Icelandic highlands. I hypothesized that the effects of the treatments on the PFGs would be as follows:

1) facilitating PFGs will respond positively to both fertilization and grazing protection treatments and increase in cover,
2) neutral PFGs will not be affected by the experimental treatments, and

3) retarding PFGs will respond negatively to all the treatments and reduce in cover.

These hypotheses are in line with previous studies that have shown that certain plant groups respond differently to grazing exclusion (Bråthen *et al.*, 2007, Jónsdóttir, 1984, Lavorel *et al.*, 1997, Medina-Roldán, Paz-Ferreiro and Bardgett, 2012) and fertilization (McLaren and Turkington, 2010, van der Wal *et al.*, 2003).

2. Methods

For this thesis I used data collected by others from an ongoing field experiment. In the following sections (2.1 and 2.2) I describe the study sites, the experimental design and the data collection as reported by the researchers collecting the data, to provide the context for the study. In sections 2.3 and 2.4, I describe how I classified plant species into functional groups and the data analyses that I conducted using this dataset.

2.1 Study sites

The field experiment was established in 2016, in two locations in the highlands of Iceland, Audkuluheidi and Theistareykir (Mulloy *et al.,* 2019). Audkuluheidi (65°13’N, 19°42’W; 470 m above sea level) is situated in the county of Austur-Hunavatnssysla in NW Iceland on basaltic bedrock covered by glacial deposits from the last glaciation (Arnalds, 2015). The climate is described as oceanic-subarctic-alpine (Björnsdóttir, 2018), and the average annual temperature is around 1.02°C and average precipitation is 311.3 mm (2006-2016) (Mulloy *et al.*, 2019).

Theistareykir (65°52’N, 17°03’W; 380 m a.s.l.) is located within the active volcanic zone in the county of Þingeyjarsveit, in NE Iceland. The study area is situated on a <7,000 year old post glacial lava shield; 2,400 years ago there was a volcanic event which deposited what is now known as Theistareykjahraun (lava field) (Ísor, jarðfræðikort-kortavefsjá). Data from the weather station Stadarholl, approximately 20 km away from the study site, show a mean annual temperature of 1.74 °C and an average precipitation of 576.9 mm (Mulloy *et al.,* 2019).

Both areas have been used as summer ranges for extensive sheep grazing for centuries and are still being used today for summer grazing. Vegetation is dominated by dwarf shrub heathlands interspersed with eroded gravelly deserts. The field experiment targeted adjacent patches of these two habitats at each site (Mulloy *et al*., 2019).

In Audkuluheidi the dwarf shrub heath had >90% vegetation cover, dominated by dwarf shrubs, forbs, graminoids and other vascular plants and mosses. The main vascular plant species found in the area alongside the dominating *Betula nana*, are *Empetrum nigrum, Vaccinium uliginosum* and *Silene acaulis*. The gravelly desert in Audkuluheidi is sparsely vegetated with <10% cover of, mostly, graminoids and forbs. The main species found are *Armeria maritima, Cerastium alpinum, Arabidopsis petraea* and *Juncus trifidus* (Miguel, 2017, Mulloy *et al*., 2019). The dominating cryptogams in Audkuluheidi are *Racomitrium lanuginosum* and *Cetraria islandica* (Jónsdóttir *et al.*, 2005)

The site in Theistareykir has many similarities to Auðkúluheiði but there are some differences in species composition of the vegetation. The dwarf shrub heath, like in Auðkúluheiði, is dominated by *B. nana* and *E. nigrum,* but *Calluna vulgaris* and *Loiseleuria procumbens* are also common. The gravelly desert has less than 10% cover and the main species found are *A. maritima*, *C. alpinum*, *A. petraea* and *J. trifidus* (Miguel, 2017). Mosses are more abundant in Theistareykir compared to Audkuluheidi, with *R. lanuginosum* being most common (Björnsdóttir, 2018).

The different soil properties of the heath and gravel desert contribute to the difference in vegetation cover. Soils in the gravelly desert habitat are classified as Vitrisols, while soils in the heath have a higher carbon content, falling into the category of Brown-Andosol (Arnalds, 2015).

2.2 Experimental design

At each of the study sites and in each of the habitats, six pairs of plots were set up in late spring 2016. Each plot was 12x12 meters in size, and plots within a pair were separated 4 m. Pairs of plots were at least 100 meters apart, and two pairs of plots constituted a block (Figure 2-1). In each pair, one of the plots was randomly allocated to a grazing exclusion treatment, while the other was left unfenced and served as a control. The fenced plots were closed off by fences that were 1.2 m tall. The mesh size was 20 x 10 cm and intended to exclude the larger herbivores in the area (sheep). Fences were not meant to exclude smaller herbivores such as geese and ptarmigan, but their activity within the plots was minimal (Mulloy *et al*., 2019).

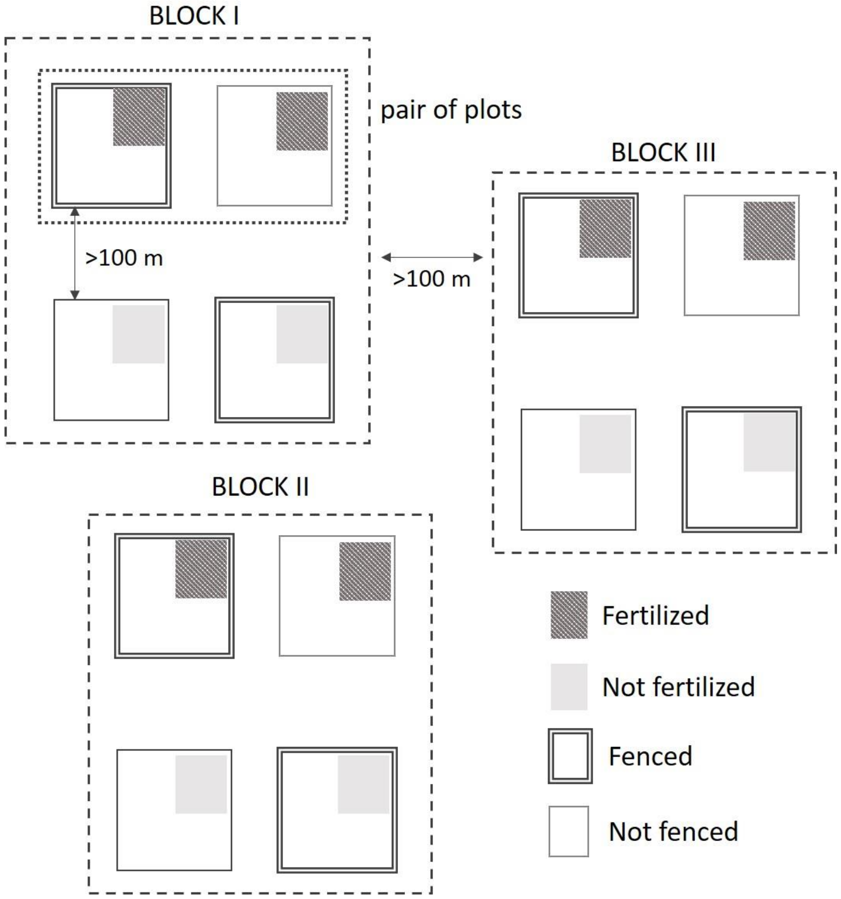

Figure 2-1 – The experimental plots were arranged in pairs, where one plot was fenced and the other left open to grazing. Two pairs formed a block; there were three blocks in each habitat and each site. One pair of plots within each block received fertilizer (NPK) or remained as a control.

One of the pairs within each block was treated with fertilizers (NPK) and the other left untreated, as a control. Within each plot a smaller 5x5 m experimental plot was established for the fertilizer treatment. Half of the plots were assigned to fertilization treatments while the other half remained as non-fertilized controls. Plots were fertilized with nitrogen (10 g/m^2), phosphorus (10 g/m^2), and potassium (10 g/m^2) every year in early summer between 2016 and 2019. The first year of the experiment micronutrients were added alongside the standard fertilizer (Table 2-1), following the protocols of the Nutrient Network (Borer *et al*., 2014).

Each block included one plot of each kind: control, control fenced, NPK and NPK fenced (Figure 2-1). In total there were 12 blocks in the experiment (3 blocks per habitat in each of two sites).

Table 2-1 – Micronutrients (amounts in g/m^2) were added together with the fertilizers in 2016.

Added micronutrients (g/m^2)								
Fe	S	Ca	Mg	Mn	Cu	Zn	B	Mo
17	12	6	3	2.5	1	1	0.1	0.1

In 2016 local farmers accidentally fertilized and seeded (*Festuca rubra*) three pairs of plots (one fertilized pair and two control pairs) in the gravelly desert in Theistareykir, adding 5 g/m^2 of nitrogen and 0.4 g/m^2 of phosphorus to these plots.

2.2.1 Data collection

The data was collected in summer 2019 by Isabel C Barrio, Tara Mulloy and Ingibjörg Svala Jónsdóttir, by visually estimating the percent cover of each species of vascular plants and cryptogams. Cover was estimated in a permanently marked plot (1x1 m) within each of the experimental plots.

2.3 Classification of plant species into plant functional groups

Classification into plant functional groups is a common approach in plant ecology that allows generalizing the ecological responses of different plants irrespective from their species identity (Lavorel *et al*. 1997). These classifications can differ depending on the objectives of the study and the traits chosen to represent each group (Fry, Power and Manning, 2014). I used the classification proposed by Bråthen *et al*. (2007) as a base for my classification, with some modifications. Bråthen *et al.* (2007) based their classification on palatability of the plants along with the facilitating and retarding traits in ecosystem processes, classifying them into facilitating and neutral species, slightly retarding and, finally, retarding. Here, I classified all species into facilitating, neutral and retarding PFGs based on the classification of Bråthen *et al*. (2007) with some modifications (Appendix 7-1). For example, they classified *V. uliginosum* as slightly retarding but here I classified this species as a neutral PFG because it sheds its leaves in the autumn unlike evergreens such as *E. nigrum*, that is more clearly in the retarding PFGs. Other difference between the classification in this study and Bråthen *et al.* (2007) is that I included mosses and lichens along with the vascular plants. The facilitating group was thus mostly composed of graminoids, sedges and *Salix* species while the retarding group was made up of mosses, lichens and evergreen shrubs (Appendix 7-1). I calculated the cover of each PFG as the sum of the cover of all species within that PFG. Therefore, the total cover of PFGs could exceed 100%.

2.4 Data analysis

To describe the baseline conditions at each site and habitat, I analyzed the data from non-fenced and non-fertilized plots (control; n=3 plots per habitat and site) and compared the cover of facilitating, neutral or retarding PFGs in control plots using linear models (LM). The percent cover of each plant functional type was included as response variable and the combination of habitat and site was included as predictor variable.

To assess the effects of the experimental treatments on the cover of each PFGs in both habitats at the two study sites, I used Linear Mixed Effects Models (LMM). Block identity was included as a random effect in the models to take into account the hierarchical structure of the study design, as each block was comprised of four plots. The response variables included in the three models were the cover of facilitating, neutral and retarding PFGs. As predictor variables, I included experimental treatment, habitat, site and their three-way interaction. Experimental treatment was a categorical variable with four levels, corresponding to the experimental manipulations possible within a block: non-fenced and non-fertilized plots, non-fenced fertilized plots, fenced non-fertilized plots and fenced fertilized plots. From the models with the three-way interaction, I simplified the model structure when interactions were not significant, so that the final models contained only significant interactions and main independent terms. The significance of the interactions or the main terms was assessed by comparing models with and without the corresponding term and are reported here as Log-Likelihood Ratio Tests (LRT).

I ran all analyses with and without the gravelly desert plots in Theistareykir that had been accidentally fertilized in 2016. Since excluding these plots did not affect the results, I report here the outcome for the analyses when all plots were included. All statistical analyses were performed in R 4.0.1 (R Core Team 2020), using the library *nlme* to build LMMs (Pinheiro, Bates, DebRoy and Sarkar, 2020).

3. Results

3.1 Differences in percent cover of PFGs between habitats and sites

The cover of facilitating PFGs did not differ significantly between habitats and sites (LM; F=0.662, p=0.62; Figure 3-1), and was consistently low (<8%). However, the cover of neutral PFGs (LM; F=10.68, p=0.004) and retarding PFGs (LM; F=16.56, p=0.001) differed significantly between the sites and habitats. The cover of neutral PFGs was highest in the heath in Theistareykir, while retarding PFGs had the highest percent cover in the heath in Audkuluheidi. In the gravelly desert habitat the percent cover of the three PFGs was more similar and was generally low.

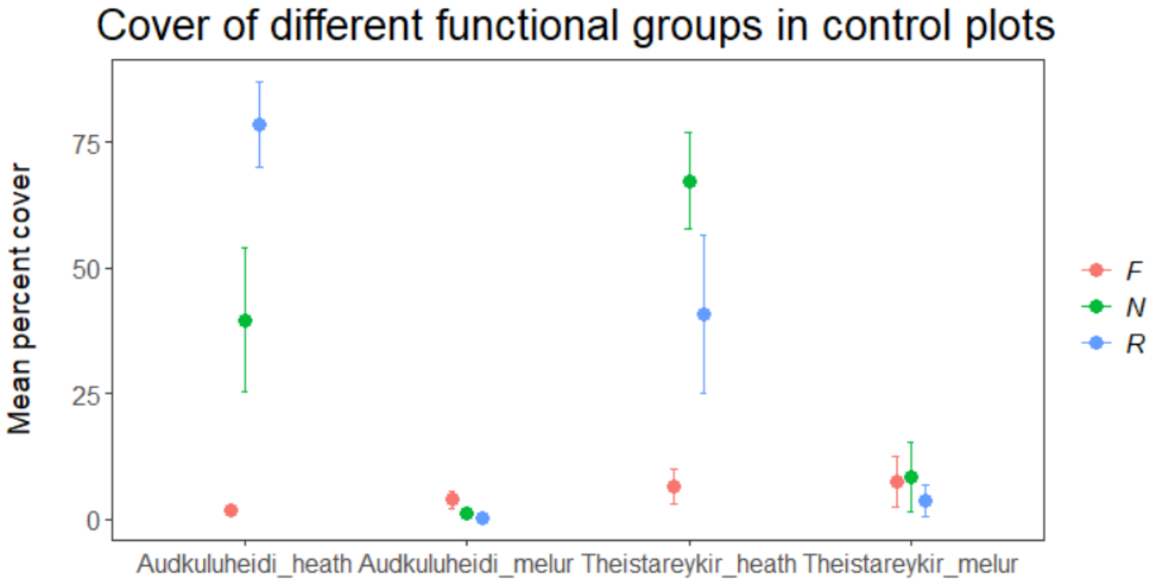

Figure 3-1- Mean percent cover of PFGs: facilitating (F), neutral (N) or retarding (R), in the control plots of the experiment separated by site and habitat.

3.2 Effects of the experimental treatments on the percent cover of PFGs

The cover of PFGs was affected differently by the experimental manipulations, and in some cases depended on the sites and the habitats. The final models are shown in Table 3-1. The difference between the cover of the different PFGs in the habitats, sites and treatments are detailed in Appendix 7-2.

Table 3-1- Linear Mixed Effects Models (LMM) for the effects of habitat, site and treatment on facilitating, neutral and retarding PFGs. Block identity was included as random effect to take into account the experimental design.

Variable	**Final model**
Facilitating PFGs	cover ~ habitat + treatment*site
Neutral PFGs	cover ~ treatment + habitat*site
Retarding PFGs	cover ~ habitat*treatment + habitat*site

3.2.1 Facilitating PFGs

The cover of facilitating PFGs did not significantly differ between the habitats (LMM; LRT=2.688, p=0.10), but there was a significant interaction between treatment and site (LMM; LRT= 15.48, p=0.002), indicating that the responses to the experimental treatments differed between two locations. In Audkuluheidi, the cover of facilitating PFGs in the habitats increased from an average of 3% (sd= 2.2) in the non-fenced and fenced unfertilized plots to 50% (sd=22.2) and 88% (sd=29.1) in the non-fenced and fenced plots with the added fertilizer (Figure 3-2). This represents a 16-fold increase in the cover of facilitating PFGs in the non-fenced fertilized plots, and a 29-fold increase in the fenced and fertilized plots relative to the control. Fenced plots with added fertilizer had a significantly higher cover of facilitating PFGs compared to fertilized plots open to grazing (LMM; t=3.56, p=0.003).

In Theistareykir the increase was more moderate. The cover of facilitating PFGs in the control plots (non-fenced, non-fertilized) was 7% (sd=6.7), slightly higher than in Audkuluheidi. The cover of facilitating PFGs increased significantly in the non-fenced fertilized plots and fenced fertilized plots (Figure 3-2). In non-fenced plots where fertilizer was added there was a four-fold increase in the cover of facilitating PFGs, from 7% to 30%. In the fenced fertilized plots there was an increase from 7% to 50%, or seven times more than in the control plot. As in Audkuluheidi, in Theistareykir fenced plots with added fertilizer had a significantly higher cover of facilitating PFGs compared to fertilized plots open to grazing (LMM; t=2.44, p=0.023).

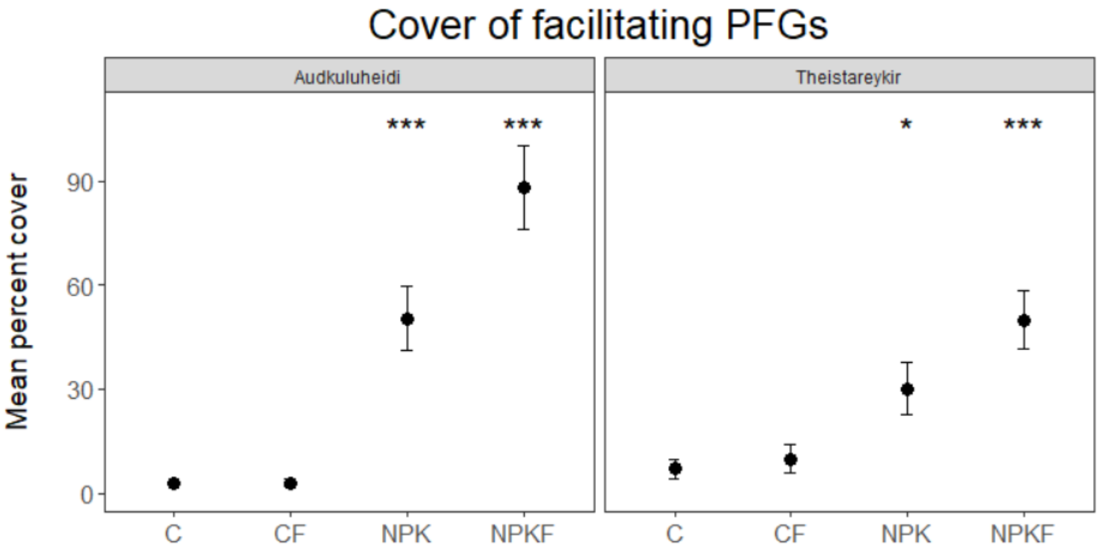

Figure 3-2 – Mean percent cover of facilitating PFGs in the two study sites, Audkuluheidi and Theistareykir, in the experimental treatments: control (C), control fenced (CF), fertilized (NPK) and fertilized fenced (NPKF) plots. Asterisks indicate significant differences relative to the control (p<0.05; *** p<0.001)*

3.2.2 Neutral PFGs

Experimental treatments did not have a significant effect on the cover of neutral PFGs (LMM; LRT=1.84, p=0.61). However, there was a significant interaction between habitat and site (LMM; LRT= 6.91, p=0.009). This indicates that the cover of neutral PFGs differs between habitats in each site. At both sites the mean cover of neutral PFGs was higher in the heath, but this difference was more pronounced in Theistareykir, where the cover of neutral PFGs in the heath (57.3%, sd = 17.7) was 5.8 times greater than in the gravel desert (9.9%, sd= 9.7). In Audkuluheidi, the cover of neutral PFGs (30.3%, sd= 20.0) was 7.4 times higher in the heath than in the gravel desert (4.1%, sd= 2.3; Figure 3-2).

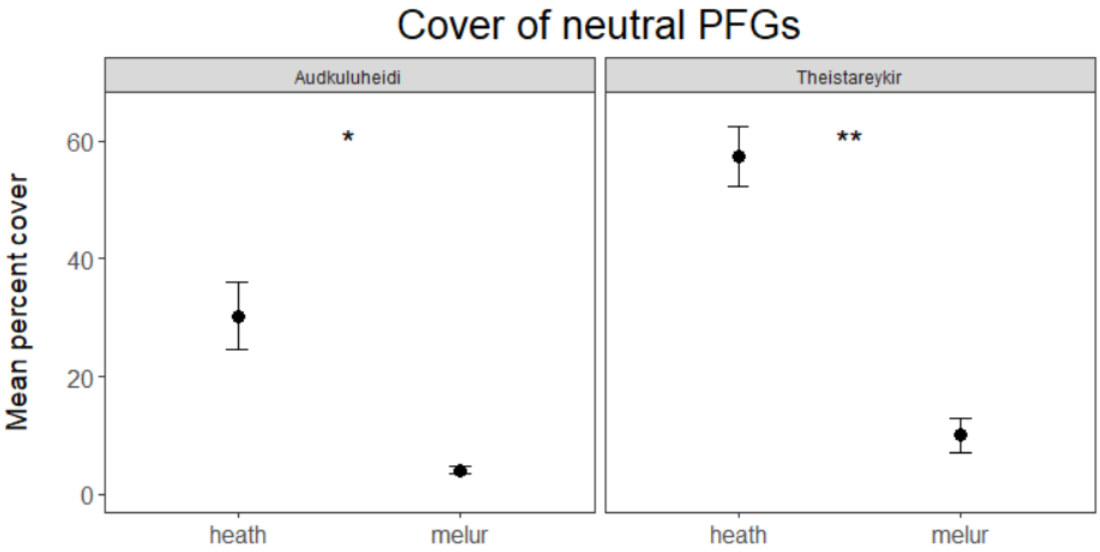

*Figure 3-3 – Mean percent cover of neutral PFGs in the two study sites, Audkuluheidi and Theistareykir, in the two habitats. Asterisks indicate significant difference between the two habitats (*p<0.005, **p<0.001).*

3.2.3 Retarding PFGs

The cover of retarding PFGs responded differently to the treatments depending on the habitat, as indicated by a significant interaction between treatment and habitat (LMM; LRT= 40.82, $p<0.001$). As well, there was a significant interaction between habitat and site (LMM; LRT= 7.87, $p=0.005$), indicating that differences in cover of retarding PFTs between the habitats were different between the sites.

When looking at the heath, there was a sharp drop in the cover of retarding PFGs when fertilizer was added (Figure 3-3a). The control plots showed more cover than the non-fenced fertilized plot and more cover than the fenced and fertilized plots, where the cover of retarding PFGs was virtually zero. However, there were no significant differences in the cover of retarding PFGs between the fertilized fenced and non-fenced plots (LMM; $t=-1.17$, $p=0.26$). These patterns were not observed in the gravelly desert habitat, where there were no significant differences between treatments in comparison with the control (Figure 3-3a) and the cover of retarding PFGs was consistently low.

Similar to the cover of neutral PFGs, the differences in cover of retarding PFGs between the two habitats differed between the two sites (Figure 3-3b). In both cases the cover of retarding PFGs was higher in the heath, but this difference was more pronounced in Audkuluheidi where the mean cover in the gravel desert was only 0.3% while it was 40% in the heath (LMM; LRT=

34.6 p < .0001). In contrast, in Theistareykir the cover of retarding PFGs in the heath was only 3.3. times more than in the gravelly desert (LMM; LRT= 15.2, p= 0.002).

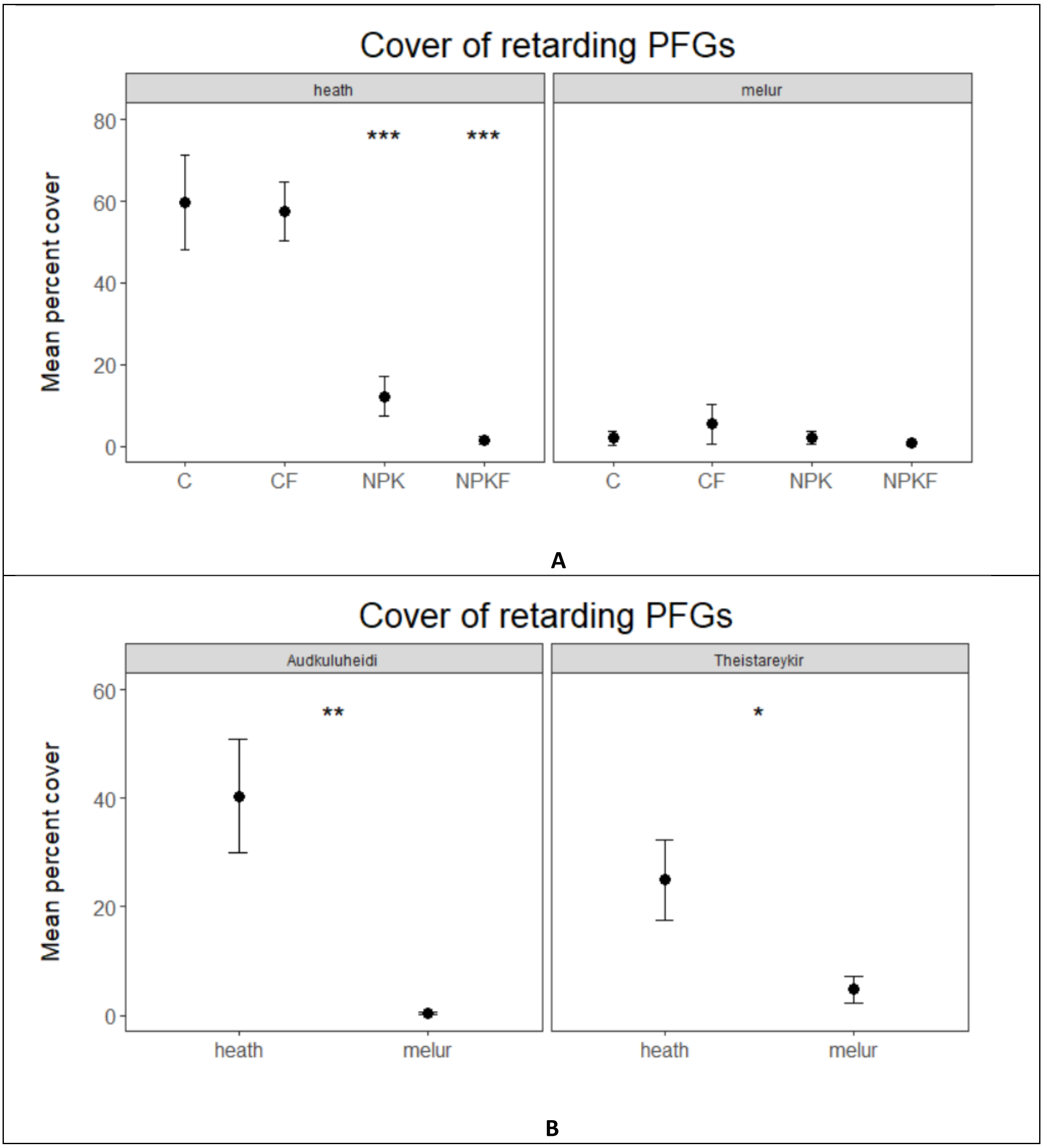

Figure 3-4 – The cover of retarding PFGs responded differently to the experimental treatments in the two habitats (A). The differences between habitats were stronger in Audkuluheidi than in Theistareykir (B). Asterisks indicate significant differences relative to the control (p<0.05; ** p<0.01; *** p<0.001)*

4. Discussion

Overall, the cover of facilitating and retarding PFGs responded differently to the treatments, while neutral PFGs did not respond to the experimental treatments. The facilitating PFGs were positively affected by fertilization and grazing exclusion and showed an increase in cover at both sites. The cover of retarding PFGs decreased significantly when fertilizer was added, irrespective of the plots being fenced or not. The only differences in the cover of neutral PFGs were found between the sites and habitats indicating that factors not related to the experimental treatments were responsible for the differences in cover of neutral PFGs.

The results show that different PFGs respond differently to the experimental treatments, combining fertilization and grazing exclusion. The facilitating and retarding PFGs had a strong response to the treatments in the relatively short time (4 years) during which the treatments were applied. As expected, the facilitating PFG increased in cover and the retarding PFG reduced in cover, only in response to fertilizer applications.

Other studies assessing changes in PFGs mainly report responses of biomass, especially above ground biomass, while the present study reports changes in cover. However, the responses of cover and biomass are strongly correlated (Jiang *et al*., 2017, Röttgermann, Steinlein, Beyschlag and Dietz, 2000). In arctic and subarctic ecosystems, the biomass of facilitating PFGs, like grasses and herbs, generally increases following the addition of fertilizers, while retarding PFGs, like mosses, often decrease (Jiang *et al*. 2017). In the short term, facilitating graminoids and other herbaceous species allocate most of the extra nitrogen available into above ground growth, while other plants like shrubs allocate it to increases below ground growth (Röttgermann *et al*. 2000). In the long term, herbaceous species and deciduous shrubs can gain a competitive advantage relative to mosses and retarding shrubs in response to fertilization (Sorensen, Michelsen and Jonasson, 2008, Graglia *et al.*, 2001). Graglia *et al.* (2001) found similar changes over a 10 year period, where graminoids and herbaceous plants along with deciduous shrubs and forbs increased steadily in response to fertilization, while mosses, lichens and evergreens decreased. Such changes were more pronounced in the longer term (10 years) than in the short term (3 years). Interestingly, this change was not as strong in plots that were experimentally warmed, indicating a slower response to fertilization under a warmer climate (Graglia *et al*., 2001). These changes however, also indicate that experimental treatments as short as 3-10 years can push a system into a new equilibrium, promoting stable changes that persist even after treatments have been discontinued (Graglia *et al*., 2001., Liu, Michelsen and Rinnan, 2020). Such persistent changes can have direct application to management practices in higher altitude systems or under sub-arctic and arctic conditions. In this sense, fertilization treatments may not need to be applied continuously to retain a certain ecological state, as treatments over a few years may be enough.

A recent study at the same sites assessed the impact of fertilization and fencing on above ground biomass (Mulloy *et al*., 2019). After two years, they found that fertilized plots were more attractive to sheep, compared to areas that had not been fertilized, indicating that fertilizer could be used as a tool to distribute grazing pressures in rangelands. Further, they found that bare ground did not increase in grazed fertilized plots, where grazing intensity increased, which may give an opportunity for facilitating species to close those open spots with added fertilizer.

The present study shows that the increase in cover of facilitating PFGs was stronger in the fertilized plots that were fenced, compared to those that were open to grazing. In the case of retarding PFGs in the heath, fertilizers reduced their cover, but there were no differences between fenced and non-fenced fertilized plots, indicating a slight difference in the impact of the fences on the different PFGs. This was similarly observed by Jónsdóttir *et al.* (2005) where grazing exclusion of four years yielded negligible results.

5. Conclusion

Management interventions, like fertilization and grazing exclusion, affected the relative cover of different PFGs on ecosystems in the Icelandic highlands. These effects were diverse and depended on the site and the habitat considered but were detected already in a relatively short period of time. After four years the relative cover of PFGs in the fertilized plots in the heath showed the largest changes. There, retarding PFGs were steadily giving way to the more productive species belonging to the facilitating PFGs. This shows that a relatively stable system dominated by retarding PFGs does not need a long time of fertilizer application to shift into a different state and potentially reach a new equilibrium with more productive species dominating the area.

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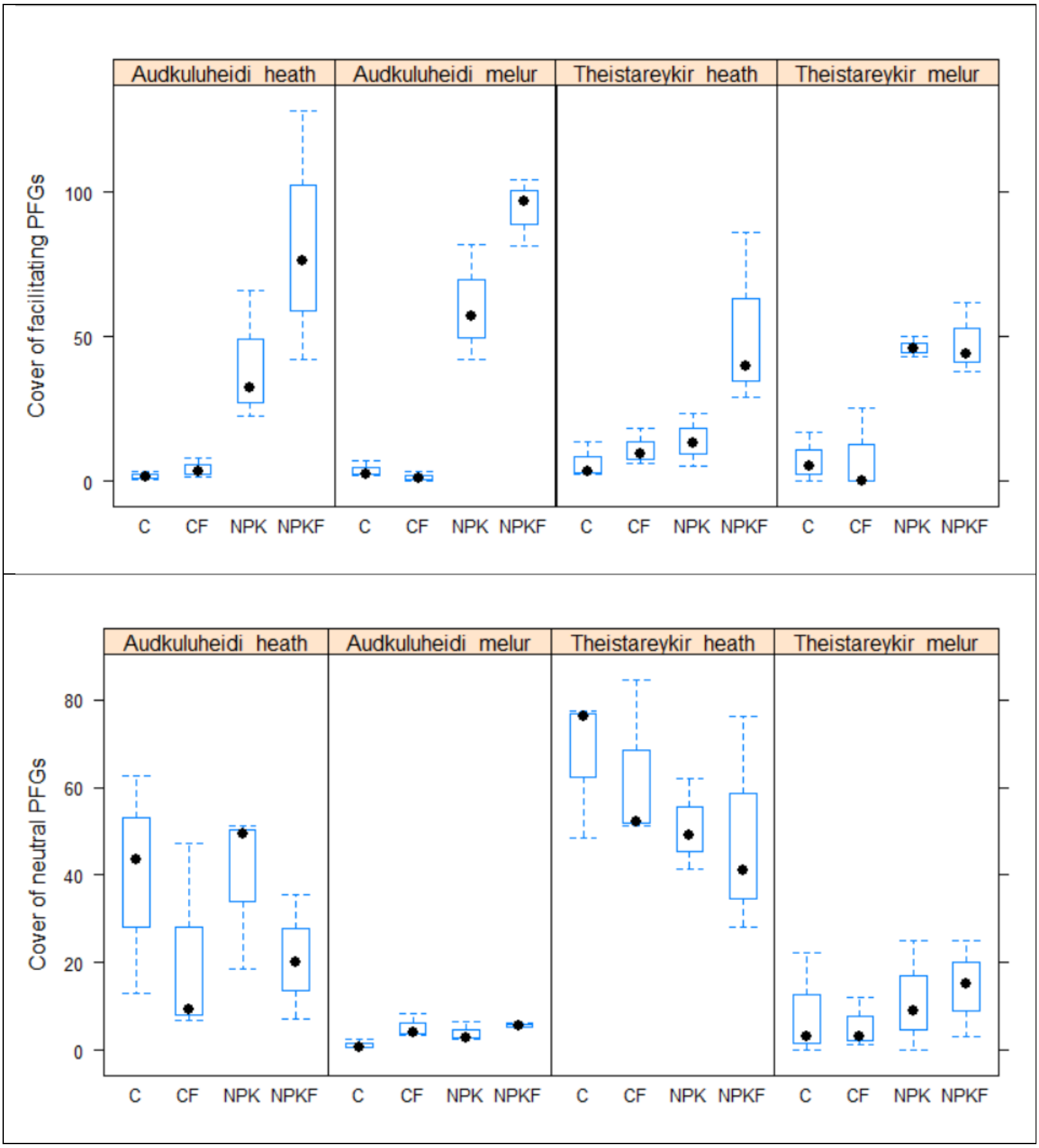
7. Appendix

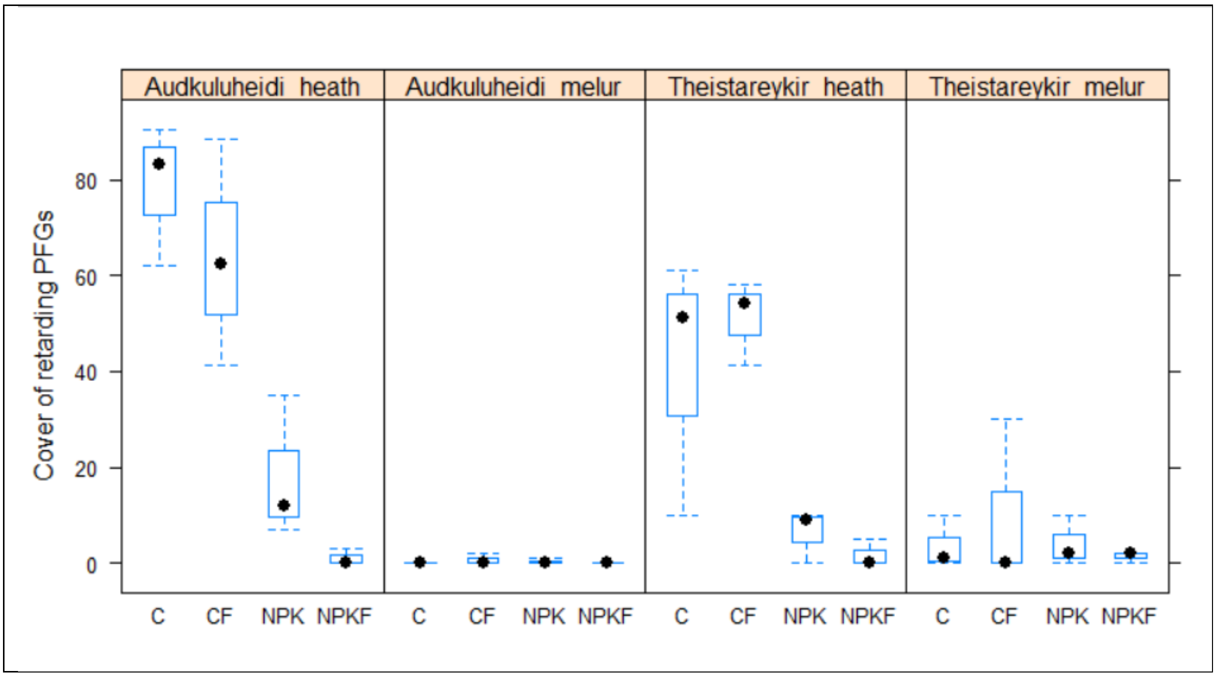
Appendix 7-1. List of species found in 2019, including their scientific name and the common name in Icelandic. PFG indicates the classification used in this study: F: facilitating, N: neutral, and R: retarding. In addition the classification proposed in Bråthen *et al.* (2007), is shown (KAB), where 1 indicates facilitating or neutral, 2 slightly retarding, and 3 retarding PFGs.

PFG	Scientific name	Icelandic common name	KAB
F	*Agrostis stolonifera*	Skriðlíngresi	1
F	*Agrostis vinealis*	Týtulíngresi	1
F	*Anthoxanthum odoratum*	Ilmreyr	1
F	*Bartsia alpina*	Smjörgras	1
F	*Carex bigelowii*	Stinnastör	1
F	*Carex capillaris*	Hárleggjastör	1
F	*Carex rupestris*	Móastör	1
F	*Carex vaginata*	Slíðrastör	1
F	*Coeloglossum viride*	Barnarót	1
F	*Deschampsia alpina*	Fjallapuntur	1
F	*Deschampsia cespitosa*	Snarrótarpuntur	1
F	*Deschampsia flexuosa*	Bugðupuntur	1
F	*Equisetum arvense*	Klóelfting	1
F	*Festuca richardsonii*	Túnvingull	1
F	*Festuca rubra*	Rauðvingull	1
F	*Festuca vivipara*	Blávingull	1
F	*Poa alpina*	Fjallasveifgras	1
F	*Poa glauca*	Blásveifgras	1
F	*Poa pratensis*	Vallarsveifgras	1
F	*Polygonum viviparum*	Kornsúra	1
F	*Rumex acetosa*	Túnsúra	1
F	*Rumex acetosella*	Hundasúra	1
F	*Salix arctica*	Fjallavíðir	1
F	*Salix herbacea*	Grasvíðir	1
F	*Salix lanata*	Loðvíðir	1
F	*Salix phylicifolia*	Gulvíðir	1
F	*Saxifraga caespitosa*	Þúfusteinbrjótur	1
F	*Thalictrum alpinum*	Brjóstagras	1
F	*Trisetum spicatum*	Fjallalógresi	1
N	*Alchemilla alpina*	Ljónslappi	1
N	*Arabidopsis petraea*	Melablóm	1
N	*Arenaria norvegica*	Skeggsandi	1
N	*Armeria maritima*	Geldingahnappur	1
N	*Betula nana*	Fjalldrapi	2
N	*Calluna vulgaris*	Beitilyng	2
N	*Carex capitata*	Hnappstör	1
N	*Cerastium alpinum*	Músareyra	1

N	*Draba norvegica*	Hagavorblóm	1
N	*Dryas octopetala*	Holtasóley	2
N	*Equisetum variegatum*	Beitieski	1
N	*Euphrasia frigida*	Augnfró	1
N	*Galium normanii*	Hvítmaðra	1
N	*Galium verum*	Gulmaðra	1
N	*Juncus trifidus*	Móasef	2
N	*Kobresia myosuroides*	Þursaskegg	2
N	*Luzula spicata*	Axhæra	2
N	*Minuartia rubella*	Melanóra	1
N	*Minuartia stricta*	Móanóra	1
N	*Parnassia palustris*	Mýrasóley	1
N	*Pinguicula vulgaris*	Lyfjagras	2
N	*Platanthera hyperborea*	Friggjargras	1
N	*Silene acaulis*	Lambagras	1
N	*Silene uniflora*	Holurt	1
N	*Thymus praecox*	Blóðberg	2
N	*Tofieldia pusilla*	Sýkigras	2
N	*Vaccinium myrtillus*	Aðalbláberjalyng	1
N	*Vaccinium uliginosum*	Bláberjalyng	2
N	*Viola palustris*	Mýrfjóla	1
N	*Viscaria alpina*	Ljósberi	1
R	*Alectoria species*	NA	3
R	*Cetraria islandica*	Fjallagrös	3
R	*Cetraria muralis*	Maríugrös	3
R	*Cetraria nivalis*	Maríugrös	3
R	*Cladonia arbuscula*	Hreindýrakrókar	3
R	*Empetrum nigrum*	Krækiberjalyng	3
R	*Loiseleuria procumbens*	Sauðamergur	3
R	*Peltigera species*	NA	3
R	*Racomitrium lanuginosum*	Hraungambri	3
R	*Stereocaulon alpinum*	Grábreyskja	3
R	*Thamnolia vermicularis*	Ormagrös	3
R	Unidentified moss	NA	3

Appendix 7-2. The figure shows the cover of the PFGs in the different treatments: control (C), control fenced (CF), fertilized (NPK) and fertilized fenced (NPKF), in the two sites (Audkuluheidi and Theistareykir) and habitats (heath and gravel dessert (melur)).




Audkuluheidi heath
Audkuluheidi melur
Theistareykir heath
Theistareykir melur
Cover of retarding PFGs
0
20
40
60
80
C
CF
NPK
NPKF