GRÓ Land Restoration Training Programme
Árleynir 22, 112 Reykjavik, Iceland

Final project 2022

IDENTIFICATION OF LAND POTENTIAL BY SEED BANKS UNDER SHEEP GRAZING IN THE ICELANDIC HIGHLANDS

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ABSTRACT

The soil seed bank is an essential source for the natural restoration of degraded rangelands. This study assessed seed density and species composition of soil seed banks in plots where grazing had been excluded by fencing for six years and in control plots in Auðkúluheiði and Þeistareykir in the highland rangelands of Iceland. Soil samples were collected from 48 experimental plots at 0-10 cm depth. Emerged species from the soil seed bank (belowground) were compared with existing vegetation (aboveground). Only 48 seedlings from 15 species emerged from the soil samples. The results showed a negligible correlation between species richness in the aboveground vegetation and the number of seedlings that emerged from soil seed banks. The number of emerged seedlings did not significantly differ between fenced and control plots. However, the species richness of the soil seed banks in the non-fenced plots was higher than in fenced plots, and this was mirrored by higher species richness in non-fenced plots in the aboveground vegetation. The results of this study indicate that six years of grazing exclusion in the Icelandic highlands might not be long enough to drive differences in the soil seed banks, suggesting that grazing exclusion may not be an efficient short-term strategy to strengthen soil seed banks in rangelands that have been grazed for centuries.

Keywords: soil seed bank, grazing exclusion, degradation, germination, highlands

This paper should be cited as:

Kushbokov A (2022) Identification of land potential by seed banks under sheep grazing in the Icelandic highlands. GRÓ Land Restoration Training Programme [Final project] https://www.grocentre.is/static/gro/publication/840/document/kushbokov2022.pdf

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1. INTRODUCTION

1.1 Background and problem statements

Livestock grazing is an extensive land use around the world. More than 80% of agricultural land, or 3.4 billion hectares worldwide, is used for livestock grazing (FAO 2015). Grazing affects rangeland productivity, vegetation dynamics, and soil structure of rangeland ecosystems worldwide (Chen et al. 2017).

Rangeland conservation is an essential task today since rangelands are in decline globally. Rangelands contribute significantly to biodiversity by harbouring various plants and animals at varying spatial scales and therefore have excellent conservation value (Donath et al. 2007; Reitalu et al. 2014). Vast rangeland ecosystems worldwide are used for extensive grazing by domestic animals. For example, sheep grazing is a significant agricultural practice globally (Johnson & Matchett 2001). However, the interactions between animal husbandry production, biodiversity and other ecosystem provisioning services have not been thoroughly evaluated (Petz et al. 2014).

Several anthropogenic and environmental factors, such as the overutilization of natural resources and climate change, are the main drivers of ecosystem collapse (Rajabov 2022). Usually, Nordic rangelands are very sensitive to disturbances, including heavy grazing, cold weather, and short vegetation periods with a lack of sunlight during half of the year; these are the main obstacles to plant regeneration (Ross et al. 2016). For instance, in Iceland, overgrazing, harsh climate, and volcanic activity were as early as in the 1960s identified as critical environmental issues that have led to degradation and soil erosion (Thorarinsson 1961; Sigbjarnarsson 1969). The Icelandic highlands have been traditionally used for grazing activities (the grazing season is from June to September), leading to extensive soil erosion in some cases. The Icelandic highlands (rangelands) are dominated by low-lying tundra vegetation, including heathlands dominated by short-statured shrubs, semi-shrubs, and vascular plant species, and volcanic deserts with low vegetation cover, dominated by some forb species (Thórhallsdóttir 1997). The main rangelands are situated in the highlands. Research in the highlands is needed to help achieve revegetation, restoration and increase aboveground plant biomass (Mulloy et al. 2021).

In Iceland, heavy utilisation of natural resources has lead to desertification, with sparsely vegetated areas covering around 42% of the country's total area (Marteinsdóttir et al. 2020). Livestock was introduced to Iceland by the first human settlers in the 9th century (Streeter et al. 2015). In the 20th century, the number of sheep heads rapidly increased from 300,000 to more than 600,000, reaching a peak of about 960,000 heads in the 1970s (Arnalds & Barkarson 2003). Following the introduction of a livestock quota in the 1980s, the number of sheep was reduced to about 460,000 heads and remained relatively constant after that. Despite the reduction of livestock, overgrazing has been highlighted as one of the main reasons for vegetation loss and soil erosion in Iceland (Sierro Miguel 2017).

Similarly, grazing is an important land use in Uzbekistan, where rangelands occupy roughly 57% of the country's total area or approximately 255,000 km^2 (Gintzburger et al. 2003). About 78% of those rangelands are related to arid and semi-arid plains. These areas have been used for local animal husbandry for many years. Unsustainable grazing throughout the year around settlement areas has caused trampling and overgrazing, leading to rangeland degradation and biodiversity loss (Gintzburger et al. 2003). Roughly 70% of total degradation disturbances are related to livestock overgrazing and uprooting essential shrubs for firewood, which account for 44% and 25% of the disturbances, respectively (Yusupov 2003). Other disturbances include abiotic disturbances such as drought, wind, and water erosion. As in Iceland, the number of livestock has increased rapidly in Uzbekistan, but this increase is more recent and continues today, putting significant pressure on rangelands. For example, until the 1990s in Uzbekistan, around 10 million head of sheep and 5 million head of cattle were kept at all types of farms throughout the Republic. By 2017, this figure increased sharply, reaching about 20 and 12 million heads, respectively (UZSTAT 2018). At the same time, the extent of rangeland areas has decreased due to constant exploitation (Rajabov 2022). According to Ruzmetov (2021), the sharp increase in the number of livestock, overgrazing and lack of science-based management of the grazing system has led to the degradation of 50-70% of rangelands in Uzbekistan, and the rangeland areal decreased by 90,000 km^2 between 1959 and 2010. Recently, the government and scientists have initiated studies and reclamation activities to monitor the restoration of degraded areas.

1.2 Importance of soil seed banks

One aspect of rangeland restoration that has received little attention in Iceland and Uzbekistan is the role of soil seed banks in ecosystem dynamics. Soil seed banks represent the reservoir of viable, persistent seeds stored in the soil to provide natural regeneration and restoration of degraded areas (Roberts 1981; Christoffoleti & Caetano 1998). Persistent soil seed banks represent seeds that can persist in the soil and include an accumulation of seeds from many years (Thompson & Grime 1979). By providing primary sources for ecosystem succession, persistent seeds in the soil are responsible for maintaining the regeneration capacity of annual species after natural death and when perennial species face various diseases and disturbances (Baker 1989). Therefore, increasing the amount and diversity of persistent seeds in the soil is essential to promote ecosystem resilience. The availability of viable seeds in the soil is an essential attribute of ecosystem restoration because seeds can be the main mechanism allowing a change from degraded ecosystems to well-vegetated land through ecosystem succession (Marteinsdóttir et al. 2010; Tessema et al. 2012; Ma et al. 2021). In addition, the soil seed bank is an effective way to stabilise mechanisms and maintain rangeland productivity and species richness, including grazing management efforts in degraded rangelands (Sternberg 2003).

Management approaches based on natural regeneration are more cost-effective to the government and scientific organisations than active restoration interventions such as transplanting or seeding (Valkó et al. 2016). Understanding the importance of seed resources in the soil is vital to improving rangeland regeneration and reaching sustainable rangeland management. Assessing the soil seed bank's potential for degraded areas is critical to understanding the condition of the rangeland, as it allows for determining the resilience of rangeland ecosystems to various disturbances (Gross 1990; Ma et al. 2018; Zhao et al. 2021).

In degraded rangelands, various disturbances influence ecosystems. For instance, high stocking rates and unsustainable land use are the main reasons for declines in seed bank density in the soil and plant communities (Solomon et al. 2006). Usually, grazing by livestock negatively affects rangeland vegetation and the persistent seed bank by trampling. Moreover, increasing grazing pressure can lead to irreversible shifts in plant community composition (Rietkerk & van de Koppel 1997) and reductions in vegetation cover, the amount of seeds in the soil, and their viability. During grazing, livestock can reduce the plants' photosynthetic capacity by consuming and removing reproductive organs, i.e. seeds and flowers (Sternberg 2003). If overgrazing continues, there might be some limitations to the persistence of edible plant species in the plant community (O'Connor & Pickett 1992). The recovery of locally extinct species can be facilitated by seed resources in the soil (Baker 1989; de Villiers et al. 2003).

Despite the relevance of soil seed banks and their potential for the natural restoration of rangelands, very little work has been conducted in Iceland or Uzbekistan on this topic. Icelandic rangelands are grazed seasonally by sheep, which is known to influence biodiversity, ecosystem function, the amount and quality of plant biomass, and soil stability (Ross et al. 2016; Marteinsdóttir et al. 2017). In Iceland, few studies have assessed the responses of seed resources to grazing activities (Table 1), and further research is needed on this topic.

Table 1. Examples of studies assessing seed resources in Iceland.

Reference	Topic	Main findings
Arnalds et al. (1987)	Restoration of denuded areas	One of the main reasons for the slow restoration of degraded areas is the soil´s lack of seed resources.
Marteinsdóttir et al. (2010)	Primary succession	Soil seed banks are essential to plant colonisation and primary succession processes.
Jargalsaikhan (2014)	Aboveground and belowground relationships under grazing pressures	Significant differences in species content within current vegetation and seed banks under different grazing regimes.
Sierro Miguel (2017)	Seed rain	Short-term grazing exclusion influenced neither seed rain nor aeolian deposition.

1.3 Study goal and research questions

The aim of this study was to learn about the importance of seed bank resources in the soil in the Icelandic highlands and their interactions with the regeneration of aboveground plant communities following management interventions geared towards rangeland restoration (i.e. grazing exclusion). The main goal of the study was to assess rangeland potential by assessing seed density and species composition of soil seed banks. Soil samples were collected to explore soil seed banks in an ongoing field experiment excluding sheep grazing in habitats with contrasting vegetation cover at two sites in the Icelandic highlands to address the following research questions:

1) Does long-term (6-year) grazing exclusion affect the number of seeds in soil seed banks?
2) Does the response of soil seed banks to grazing exclusion differ between habitats and sites?
3) What is the relationship between soil seed banks and aboveground plant species richness?

The expectations of the study were based on several hypotheses related to seed banks in degraded areas. They were the following:

1) The soil seed bank and species richness will be higher in plots where grazing has been excluded for six years than in grazed control plots because overgrazing reduces seed density in the soil and aboveground species richness (Loydi 2019).
2) The sites will be similar in terms of species composition, but differences will be found between habitats and experimental plots in terms of soil seed banks (Erkkilä 1998).
3) There will be a positive correlation between the number of germinating seeds and aboveground species richness because areas with higher aboveground species richness tend to have higher seed densities in the soil (Zhao et al. 2011).

2. METHODS

2.1 Study sites

This study was conducted at two sites in the Icelandic highlands (Figure 1). Auðkúluheiði (65.13'30"N, 19.42'43"W) is located in the north-western central highlands at 480 m above sea level, outside the active volcanic zone. Þeistareykir (65.52'26" N, 17.02'52" W) is located in the north-east part of Iceland at 300 m above sea level, within the active volcanic zone. These areas have been traditionally used for grazing by free-roaming sheep during the summer months (June to mid-September). In these areas, it has been suggested that overgrazing has reduced vegetation cover and thus increased the amount of exposed bare ground (Marteinsdóttir et al. 2017), and that rangeland degradation has become a concern (Arnalds 2015). Both study sites are currently in a similar stage of ecosystem degradation, and the number of sheep using the areas is similar (Sierro Miguel 2017).

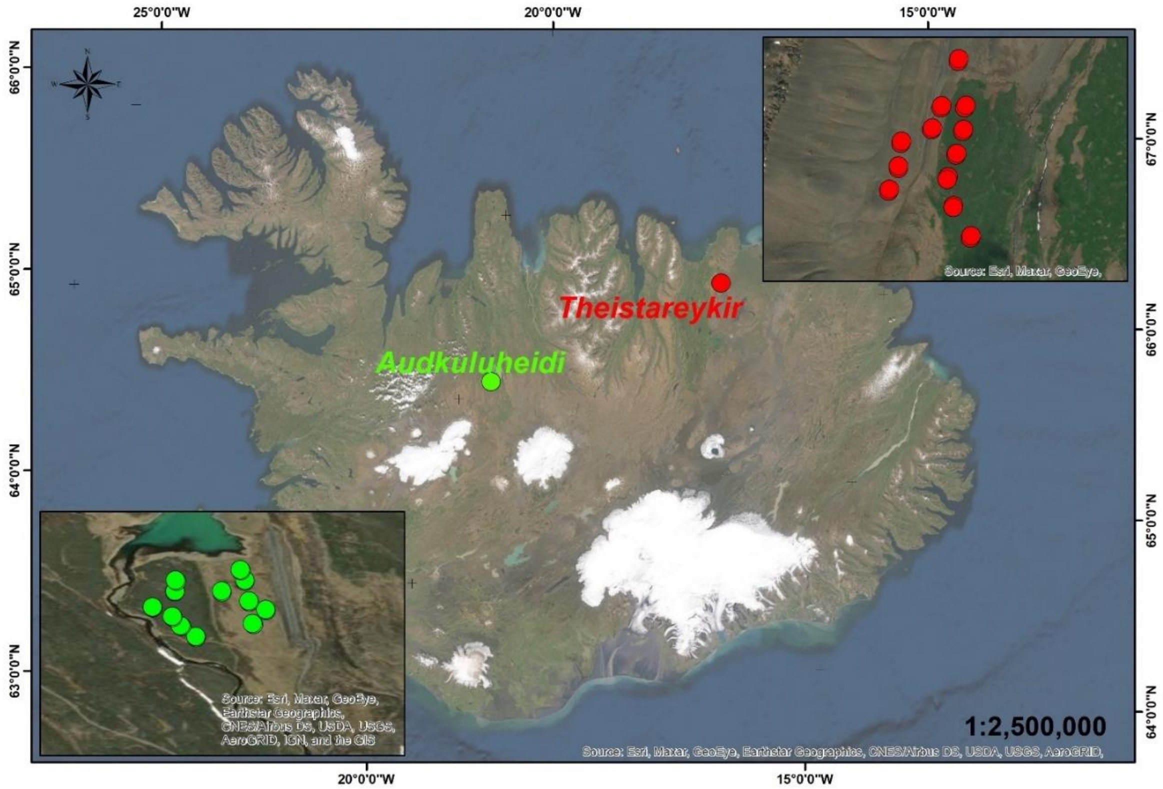

Figure 1. The study areas are in the highlands of Iceland. Auðkúluheiði is located outside the active volcanic zone, and Þeistareykir is inside the active volcanic zone.

Climatic conditions are similar at both sites, but there are some differences as shown by climate data between 2012 and 2022 from nearby weather stations in Auðkúluheiði and Þeistareykir (Table 2).

Table 2. Climate data for the last decade (Icelandic Meteorological Office 2022).

Study sites	Mean annual temperature	Average summer temperature	Average wind speed	Maximum three second wind gust speed	Average relative humidity	Average annual precipitation*
Auðkúluheiði	0.9°C	8.0°C	7.57 m/s	43.8 m/s	83.90%	707 mm
Þeistareykir	2.0°C	8.7°C	6.35 m/s	41.7 m/s	79.70%	657 mm

*Precipitation data refer to the period 1996-2003 when data for weather stations at both sites were available.

At both sites, landscapes comprise a mosaic of low-statured shrub vegetation (heath) and gravelly deserts (“melur” in Icelandic). Plant communities in the heath, where vegetation covers about 90%, include semi-shrubs dominated by *Betula nana* with numerous species of bryophytes and lichens (Jónsdóttir et al. 2005). In Þeistareykir, plant communities in the heath are similar, but some species are distinct, such as *Calluna vulgaris* and *Loiseleuria procumbens* (Sierro Miguel 2017, Mulloy et al. 2021). In contrast, in the melur, where vegetation cover is less than 10%, plant communities are dominated by forbs (*Silene uniflora*, *Cerastium alpinum*, *Armeria maritima*, *Arabidopsis petraea*) and graminoids (*Festuca richardsonii*, *Juncus trifidus*).

The soils of Þeistareykir are similar to the soils of Auðkúluheiði, with well-drained basaltic andosols; however, the pH value is higher than in other parts of northeast Iceland (Arnalds 2015). The soils in Auðkúluheiði are well-drained brown andosols with a high amount of carbon and pH in the neutral range, which is suitable to plant growth (Arnalds 2015, Jonsdottir et al. 2005). In addition, the distinctive characteristics of andosols are a high cation exchange capacity and water-holding capacity (Arnalds 2004).

2.2 Experimental design and data collection

In 2016, a field experiment was set up at both study sites. The current research project complements other research conducted at the sites, for instance, investigating the responses of rangeland ecosystems to grazing exclusion (soil properties; Akello 2019); decomposition rates (Bjornsdottir 2018; Olupot 2022); seed rain (Sierro Miguel 2017); aboveground biomass and bare ground cover (Mulloy et al. 2019); and plant community composition (Mulloy et al. 2021).

At each site, 24 plots were set up in two contrasting habitat types: heath and melur. Adjacent habitat patches were selected so that they would be exposed to the same environmental conditions but differ in their level of degradation, with the heath representing a less degraded ecosystem and the melur representing a highly degraded, collapsed ecosystem. In each habitat, six pairs of experimental plots were established (Figure 2), separated at least 100 m from each other. Experimental plots are 12 x 12 m in size, and plots within a pair are 4 m apart. Experimental treatments (fenced and control) were allocated randomly to each plot within a pair. Fences are 1.2 m high and prevent access by sheep. Geese and ptarmigan also occur in the area but infrequently visit the plots.

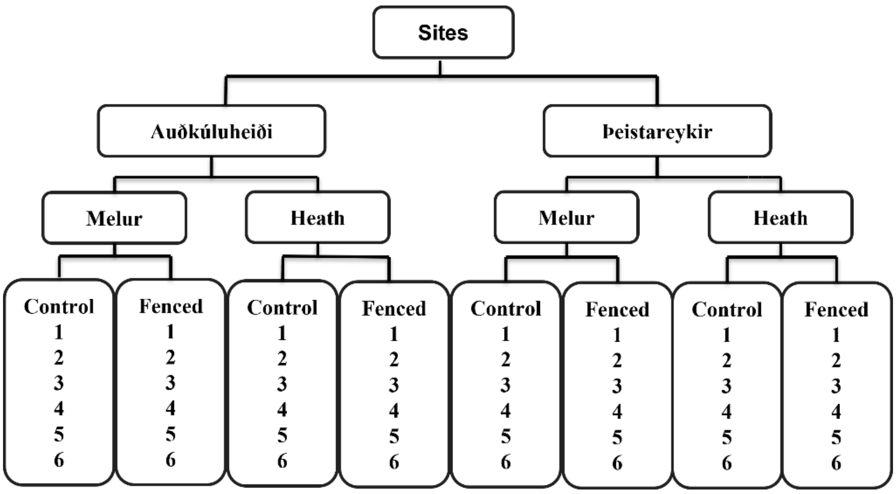

Figure 2. General view of the hierarchical experimental design.

2.2.1 Soil sampling

Soil samples were collected from the field sites on June 16-17, 2022, at the beginning of the vegetation growing period. At each plot, five soil samples 0-10 cm deep were collected with a soil corer (2 cm diameter) and pooled per plot to account for potential heterogeneity in soil seed banks at a local scale, for example, due to microtopography or the presence of vegetation patches acting as seed traps. Samples were collected following a linear transect from the edge of the plot inwards with a distance between samples of ca. 50 cm (Fig. 3). Samples were collected into paper bags labelled with a unique plot identifier, indicating the sample's location and treatment. In total, 48 composite samples were collected, actually 24 from Auðkúluheiði and 24 from Þeistareykir.

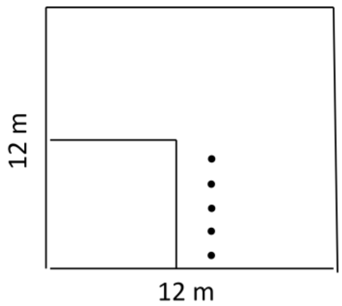

Figure 3. Diagram of experimental plot and places where soil samples are taken

2.2.2 The germination method

The soil samples were transported to the greenhouse facilities at the Reykjavik campus of the Agricultural University of Iceland on June 18. Due to the high moisture in the sampled soils, the samples were first air-dried for 48 hours in the lab at room temperature. The germination trials were set up on June 20. The soil samples were sieved through a 2 mm sieve to remove stones, roots, and larger plant fragments that could regenerate and be confused with new seedlings that emerged from seeds. Since the amount of soil collected in the field for each sample was slightly different, the soil samples used in the germination trials were standardised by volume (125 cm^3 per sample). The soil samples were placed on germination trays (23 x 17 x 6 cm) pre-filled with commercial soil to half their volume and a thin cloth used for separating the commercial soil from the soil samples collected from the field (Fig. 4). The cloth prevents the germination of undesired seeds in the commercial soil and helps retain moisture. The soil samples were spread on the trays in a 0.5-1 cm thick layer.

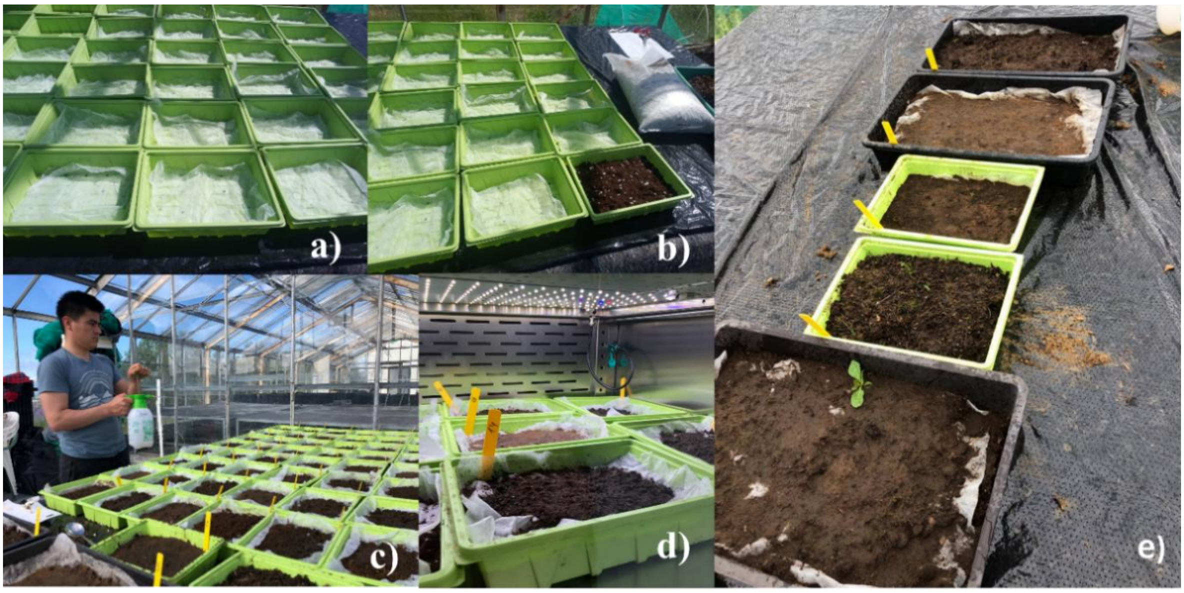

Figure 4. Set up of the germination trays for the germination trials: a) placing the cloths under commercial soil, b) placing the commercial soil on the cloth, c) watering the soil samples after placing them on the germination trays, d) putting them in the germination chamber, e) remaining soils after taking a standardised volume, combined by habitat and site.

All germination trays were placed into two germination chambers (Bioevopeak ICB-450L) programmed to 20°C and 16 hours of light / 8 hours of darkness. The trays were watered daily (once or twice a day, depending on the soil's moisture). To avoid being aware of the origin of the samples or the experimental treatments, the samples were randomised and given a non-descriptive sample identity number between 1 and 48. Samples 1-24 were placed in one germination chamber, and samples 25-48 in the second. The germination trials were run for six weeks (until August 5), a period recommended by earlier studies (Sierro Miguel 2017; Jargalsaikhan 2014).

The remaining soil samples, after taking the volume required for the germination trials, were pooled by habitat and site (i.e., Auðkúluheiði – melur / heath and Þeistareykir - melur / heath) (Fig. 4). These pooled samples were placed in a greenhouse to germinate and to identify existing plant species in the soil of the research area that may have been missed in the studied samples. In addition, all the remaining material after sieving (material >2 mm) was placed on separate germination trays to assess if some seeds or particular species were missed after the sieving process. In the greenhouse, the trays were illuminated by natural light (a longer light period than in the germination chamber). The temperature in the greenhouse could not be controlled accurately but was around 15-35°C.

The experiment continued for six weeks after setting up the germination trays. The number of germinated seedlings and their identity were recorded daily during the investigation. In order to assess the weekly germination rate of the seedlings (i.e. how many seedlings germinated per week) over time, the number of germinated seedlings was summed for each week. After identification of the species of seedlings, seedlings were removed from the germination trays and pressed for validation of identification.

2.2.3 The point intercept method

Aboveground vegetation was assessed in 2021 by other research team members using the point intercept method, which quantifies the abundance of plant species or the amount of bare ground area in a study site. This method uses sampling pins to assess plant canopy and cover. This study used four permanently marked plots (50 x 50 cm) with 25 regularly placed pins. The number of "hits" by each plant species or the bare ground was recorded at each pin. Based on the point intercept data, I calculated the species richness of each plot.

Although I did not conduct the point intercept assessments myself for the present study, I learned the technique by collecting data using this method in a trial example.

2.2.4 Statistical analysis

To evaluate the effect of locations and habitats on the effect of grazing exclosure on the number of seeds in the soil seed banks, I used Generalized Linear Mixed Effects Models (GLMM) with a Poisson distribution (Zuur et al. 2009), which is particularly well suited for analysing count data. All analyses were conducted using R version 4.1.2 and RStudio software. To assess the differences between grazed and non-grazed plots, I used a paired t-test. In the GLMMs, the number of germinated seeds in each plot was included as the response variable, and the identity of the pair of plots was included as a random effect variable. As predictor variables, I included the three-way interaction between treatment (grazing exclosure), habitat and site. The interaction term allows testing if the number of germinated seeds in grazed and non-grazed plots differs between habitats and sites. The initial model was built with the three-way interaction, and models were subsequently simplified by dropping non-significant interactions. Finally, I used Pearson's product-moment correlation test to assess the relationship between the number of seedlings (belowground) and aboveground species richness.

3. RESULTS

3.1 Seedling emergence

Six weeks after the germination trial was set up in the germination chamber, 48 seedlings had emerged from all germination trays. The seedlings belonged to 15 species (Table 3). The most abundant seedlings were *Empetrum nigrum* (11 seedlings), *Arenaria norvegica* (8 seedlings), and an unidentified "*thin grass"* (6 seedlings). Some species were only found in soil samples from Auðkúluheiði, such as *Festuca vivipara, Rumex acetosa, Armeria maritima* and *Galium normanii*. In contrast, others were present only in soil samples of Þeistareykir, like *Salix herbacea, Kobresia myosuroides*, *Poa pratensis* and *Equisetum variegatum.* In this study, the species emerging from the soil seed bank represented 20% of all plant species of the aboveground vegetation in Auðkúluheiði and 17.9% in Þeistareykir (Fig. 9; Table 3).

In addition, 42 seedlings emerged from the additional trays containing the remaining soils after standardisation and the remaining samples after sieving that were located in the greenhouse. In those extra trays, I found additional species that were not found in the germination trays in the germination chamber, like *Betula nana* (dwarf shrub) and *Luzula spicata* (graminoid).

Table 3. Emerged species in germination trays and the number of seedlings.

	Total number of emerged seedlings	Plant life forms	Species (number of seedlings)
Auðkúluheiði	18	Dwarf shrubs	*Empetrum nigrum (3)*
			Thymus praecox (1)
		Graminoids	*Festuca vivipara (1)*
			Thin grass (2)
			Poa alpina (2)
		Forbs	*Arenaria norvegica (1)*
			Bistorta vivpara (2)
			Galium normanii (1)
			Rumex acetosa (1)
			Rumex acetosella (2)
			Thalictrum alpinum (1)
			Armeria maritima (1)
Þeistareykir	30	Dwarf shrubs	*Empetrum nigrum (8)*
			Salix herbacea (1)
			Thymus praecox (1)
		Graminoids	*Thin grass (4)*
			Kobresia myosuroides (2)
			Poa pratensis (2)
			Poa alpina (1)
		Forbs	*Arenaria norvegica (7)*
			Bistorta vivpara (1)
			Rumex acetosella (1)
			Thalictrum alpinum (1)
			Equisetum variegatum (1)

The germination rates of the seedlings increased in the first two weeks of the germination trials, but emergence rates experienced a downward trend in the last four weeks of the experiment. The highest number of seedlings was counted in the second week, while the lowest number of seedlings emerged in the last week of the experiment (Fig. 5). The accumulated number of seedlings increased towards the end of the experiment, from three to 48 seedlings by the end of the experiment. Unfortunately, some seedlings died during the germination trials.

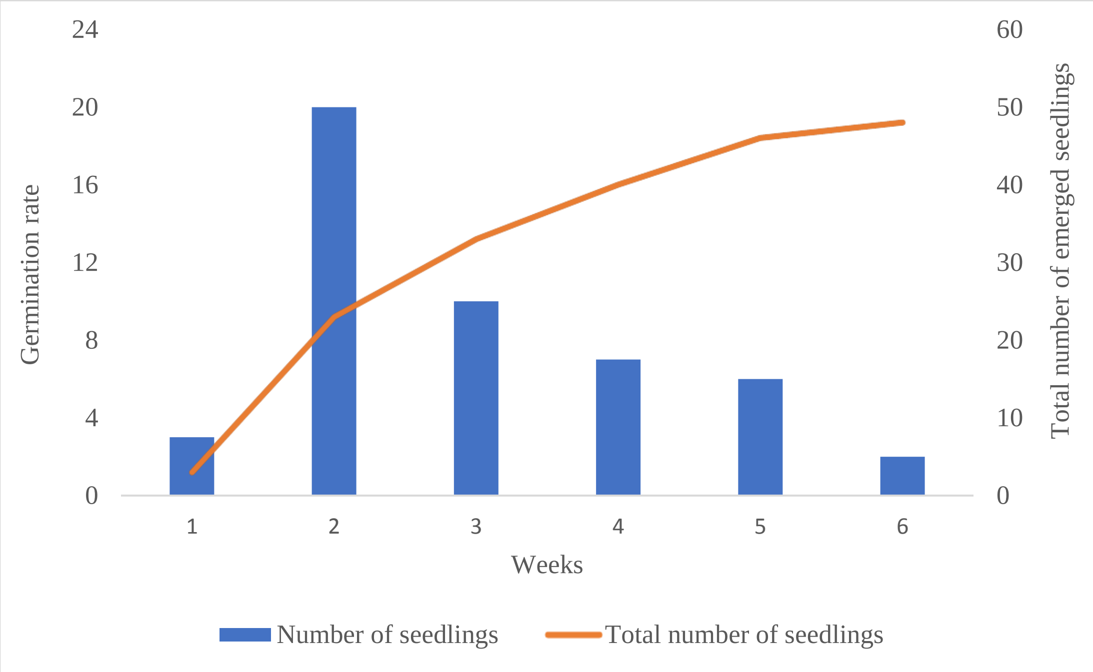

Figure 5. Germination rate (number of emerged seedlings per week) for the duration of the germination trials. The accumulated number of seedlings is also shown (orange curve).

3.2 Comparison between grazed and non-grazed plots

Overall, the number of emerged seedlings did not differ when comparing fenced and non-fenced plots within pairs of experimental plots (paired t-test; $t = 1.76$; $df = 23$; $p = 0.09$). Although there were no significant differences, more seedlings tended to emerge from control than from fenced plots (Fig. 6).

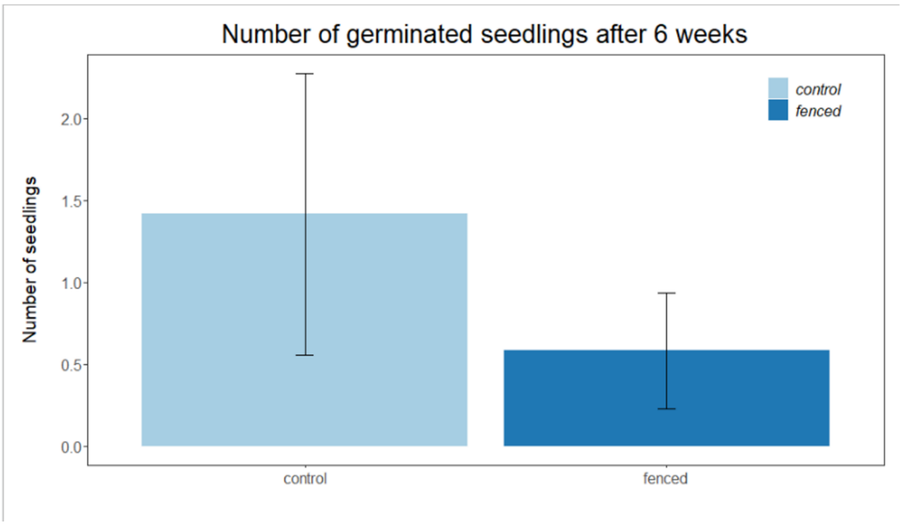

Figure 6. Number of germinated seedlings after six weeks in two different treatments.

3.3 Comparison between habitats and sites

The results of the GLMM models showed that the effect of grazing exclusion on soil seed bank did not depend on the location or the habitat. The three-way interaction between treatment, habitat and site was not significant (TTM*HAB*SITE, $p = 0.321$), and none of the two-way interactions had a significant effect (TTM*SITE, $p = 0.05$; TTM*HAB $p = 0.55$). After simplifying the model and removing non-significant interactions, the model showed that neither site nor habitat had an effect on the number of emerged seedlings (Fig. 7; Table 4).

Table 4. Factors affecting the number of germinated seeds after six weeks resulting from the GLMM model.

Fixed effects	Value	Std. Error	DF	t-value	p-value
(Intercept)	1.542	0.464	23	3.319	0.003
Treatment fenced	-0.833	0.464	23	-1.794	0.086
Habitat melur	-0.8	0.464	21	-1.615	0.121
Location Theistareykir	0.5	0.464	21	1.076	0.294

Nine seedlings were found in fenced plots and nine in control plots in Auðkúluheiði, while 25 seedlings were counted in the Þeistareykir control, and only five seedlings in the Þeistareykir fenced experimental plots. In total, 34 seedlings were found in control and 14 in fenced plots in both study sites.

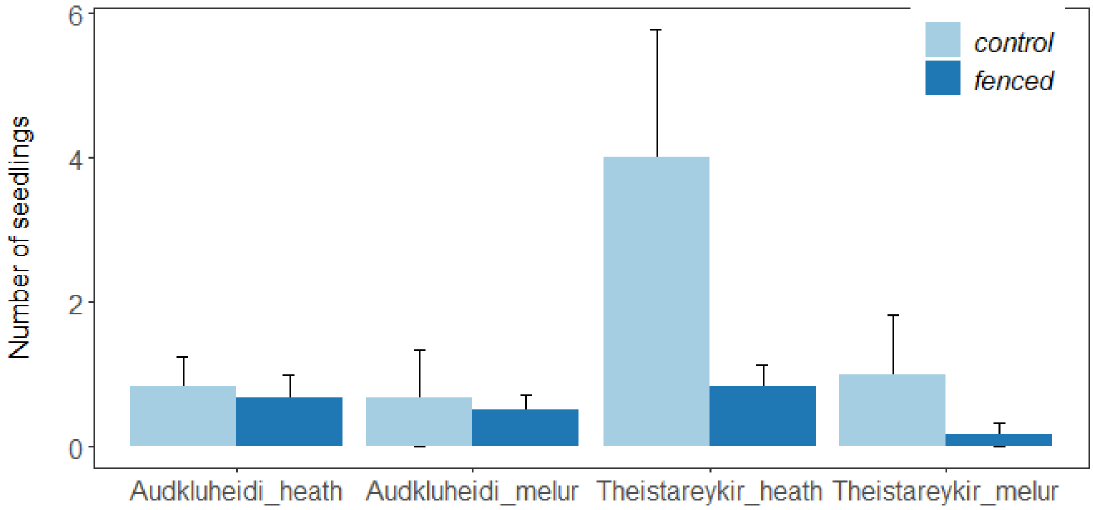

Figure 7. Number of germinated seedlings after six weeks in different habitats and treatments.

In the heath in Þeistareykir, eight emerged plant species were found in control plots (THC) and three in fenced plots (THF), while only one species was found in the melur fenced plots in Þeistareykir (TMF) and two species in the melur control plots (TMC; Fig. 8). In Auðkúluheiði heath, five emerged plant species were found in control plots (AHC) and four in fenced plots (AHF). However, the number of emerged plant species in Auðkúluheiði melur was three for both control (AMC) and fenced plots (AMF).

A total of 11 species were found from Þeistareykir heath while nine species were found in Auðkúluheiði heath. In Þeistareykir melur, three species were found, and three species were found from Auðkúluheiði melur habitat types. Finally, 14 species were found from Þeistareykir, and 15 from Auðkúluheiði, while 18 species were found from control and 11 species from fenced plots in both study sites and habitats (some species repeated in both sites and habitats) (Fig. 8).

3.4 Aboveground vs belowground

Of the emerged seedlings, forb and graminoid species dominated in both study sites. A total of 60 species were identified from aboveground vegetation in Auðkúluheiði (36 in heath and 24 in melur), while 67 species were found in Þeistareykir (44 in heath and 23 in melur). In contrast, only 12 species emerged from soil samples taken from Auðkúluheiði, of which there were eight species from Auðkúluheiði heath and four from Auðkúluheiði melur. In Þeistareykir, the number of totals emerged species from the soil seed bank was 12, nine from Þeistareykir heath and three from Þeistareykir melur (Fig. 9).

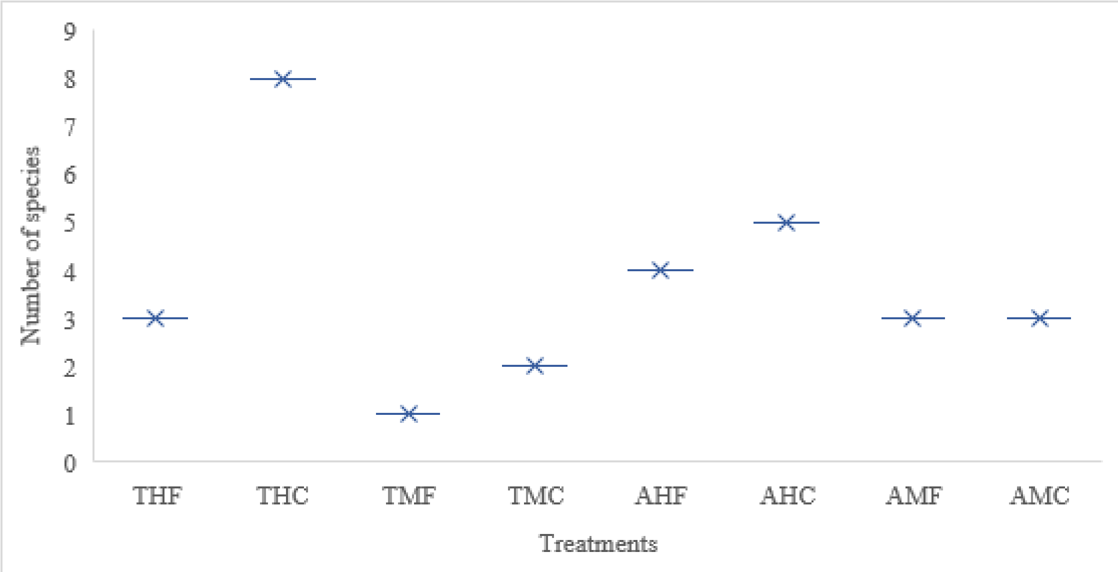

Figure 8. The number of germinated species within treatments. THF – Þeistareykir heath fenced, THC – Þeistareykir heath control, TMF - Þeistareykir melur fenced, TMC - Þeistareykir melur control, AHF - Auðkúluheiði heath fenced, AHC - Auðkúluheiði heath control, AMF – Auðkúluheiði melur fenced, AMC - Auðkúluheiði melur control.

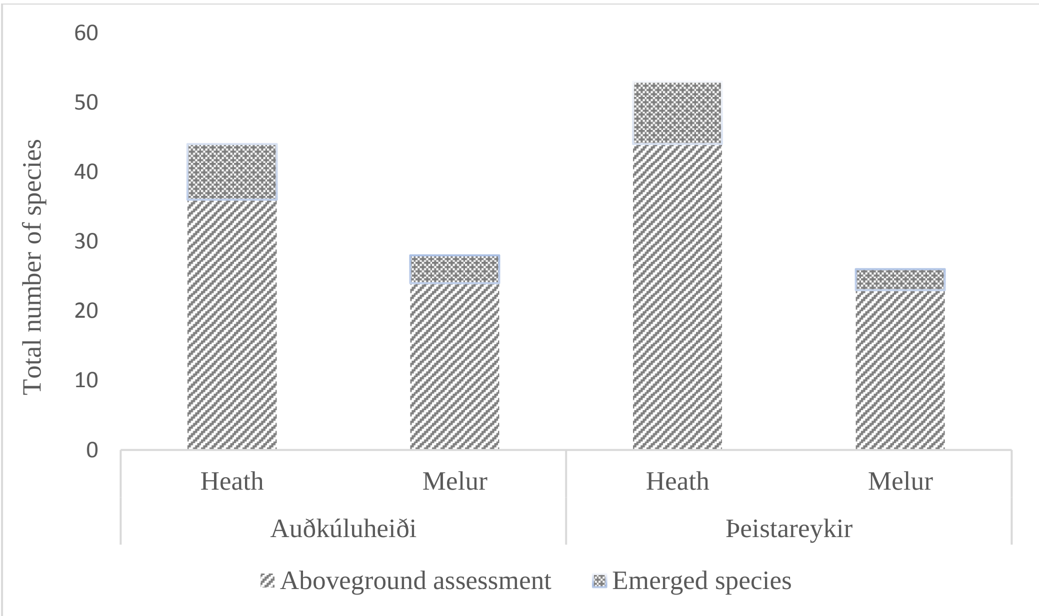

Figure 9. A total number of species in aboveground vegetation and soil seed bank in the two habitats (heath and melur) at each study site.

As assessed using Pearson's product-moment correlation test, the correlation between the number of seedlings after six weeks and aboveground species richness indicated a weak, non-significant correlation between seed banks and aboveground vegetation ($t = 1.58$, $df = 45$, $p = 0.12$; Fig. 10).

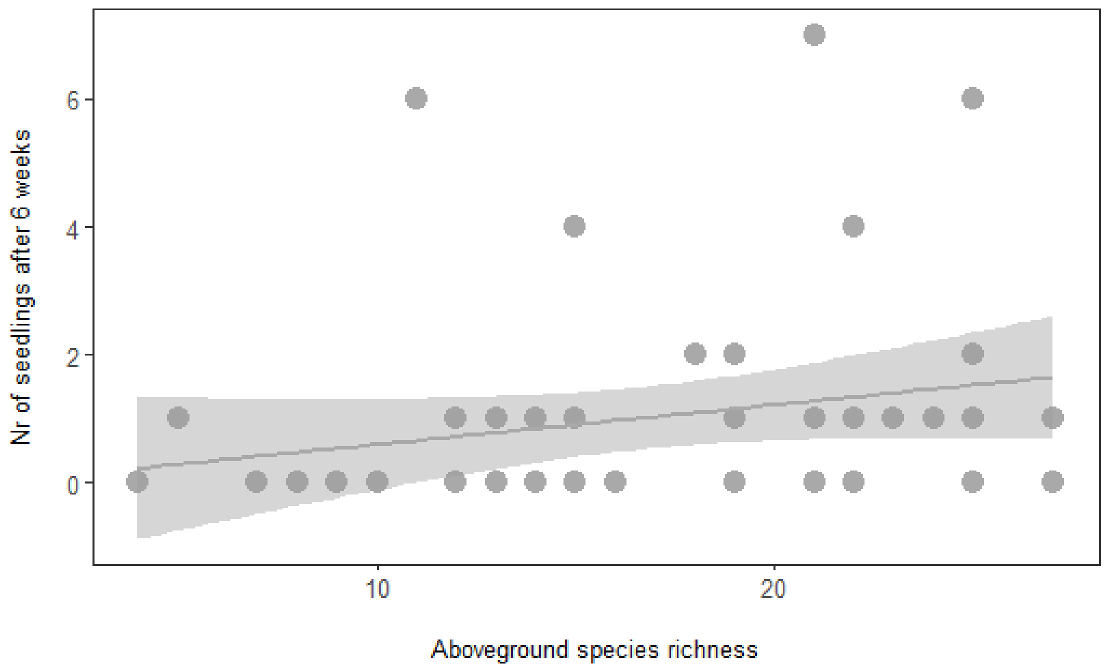

Figure 10. Correlation between number of germinated seedlings and aboveground species richness.

4. DISCUSSION

This project investigated the potential for rangeland recovery in the Icelandic highlands based on soil seed banks, following management interventions aimed at rangeland restoration. A total of 48 seedlings from 16 species emerged from soil seed banks collected from rangelands, but six years of grazing exclusion did not influence the number of seeds germinating from the soil seed banks at any of the sites or in the different habitats.

The number of seedlings that emerged from soil seed banks in the present study was relatively low compared to other studies. For example, Jargalsaikhan (2014) found 68 species in soil seed banks in other Icelandic rangelands. One explanation for the reduced number of seedlings could be the sampling timing (the soil samples were collected in mid-June). Most studies investigating soil seed banks collect soil samples at the end of the growing season (Sternberg et al. 2003; Tessema et al. 2012) or in early spring (Aboling et al. 2008; Dreber 2011; Valko et al. 2014; Erfanzadeh et al. 2015; Mndela et al. 2020). I collected soil seed banks in mid-June, which is often considered to be shortly after snowmelt (Mulloy et al. 2019). However, this may mean that some seedlings might have germinated already and were thus not detectable in this study. Therefore, the timing might be the reason for getting lower numbers of seedlings from the soil samples.

Although grazing exclusion did not affect the number of germinated seeds, there was a trend towards more seeds germinating from soil seed banks from plots open to grazing (control plots) compared to fenced plots. Previous studies have shown that the responses of plant cover and species diversity of the soil seed bank to grazing exclusion are not always the same. Aboveground vegetation cover and species diversity of soil seed banks differ depending on exclusion periods and the condition of the rangelands (Huang et al. 2022). For example, some studies have shown greater species richness in both the aboveground and belowground parts of rangelands, while vegetation cover in the aboveground parts was higher in the grazing-excluded areas (Osem et al. 2006; Klaus et al. 2018). According to other studies, grazing exclusion can be a helpful tool to increase soil seed bank density and aboveground species richness by giving the rangeland ecosystem a rest from grazing (Larson et al. 2016; Sun et al. 2020). However, other studies have indicated that soil seed banks included fewer seeds after long-term grazing exclusion periods (Saatkamp et al. 2018).

On the other hand, grazing exclusion can cause a decrease in species diversity and seed bank density by colonising dominant plant species (Tessema et al. 2012). This hypothesis was consistent with my results, where I found fewer species emerging from fenced plots than from control plots open to grazing. Some studies have hypothesised that the seed bank density in the soil increases for up to five years of grazing exclusion, and then seed density and species diversity begin to decrease (Huang et al. 2022), while other studies have found that even 25 years of grazing exclusion help to significantly increase soil seed bank density and species richness of the grazing excluded areas (Zhao et al. 2011). In addition, elevation can influence the effect of grazing exclusion on the amount of seedlings from the soil seed bank, with sites at elevations higher than 4,500 m having limited seedbanks (Lee et al. 2013; Sharma et al. 2014). However, the study sites in the present study were located in the highlands of Iceland (300-480 m.a.s.l), so elevation is likely not the main reason why my study found a lower number of seedlings than in previous studies.

This study and former studies have found differences between aboveground species composition and species present in the soil seed banks (Valkó et al. 2014; Erfanzadeh et al. 2015). Lower species richness was found in grazing excluded plots. However, there was no correlation between species richness and the number of emerged seedlings. For instance, some frequent species in the aboveground vegetation, like *Betula nana,* were absent from the sampled soil seed banks, and *Salix herbacea* was unique within the germinated seedlings in the soil seed bank and not detected in the aboveground vegetation measurements. Grazing exclusion can lead to increased plant-plant interactions (competition), facilitate colonisation by dominant plant species and thereby reduce species richness in the plots (Tessema et al. 2012; Erfanzadeh et al. 2015). However, overgrazing and overstocking rates can be a reason for the reduction of annual and perennial species in the soil seed bank (Tessema et al. 2012). In addition, overgrazing, destruction of reproductive organs of plants and trampling effects in the open rangelands might be a reason for the decrease in the ability of plants to produce seeds (Paruelo et al. 2008).

The present study focused on the soil seed banks of Icelandic rangelands. I propose that similar analyses could be conducted in Uzbek rangelands in the future. Several studies have been conducted in Uzbekistan to assess and improve rangeland ecosystems and their productivity. Studies have, for instance, assessed the ecological changes of vegetation in semi-arid rangelands using NDVI analysis (Rajabov 2009), increased stakeholder engagement in rangeland restoration and applied large-scale seeding activities in degraded areas (Christmann et al. 2015), improved soil conditions and vegetation cover by minimum soil tillage and seeding phytoameliorants in degraded rangelands (Mirzaev et al. 2019), studied the ecophysiological indicators of desert plants among the different grazing gradients (Kushbokov 2021), and evaluated the ecological and phytocenotic transformation of plant cover in semi-desert rangelands (Rajabov 2022). Although soil seed bank experiments or related studies on soil seed banks have not been conducted in Uzbekistan, the current study will hopefully be the foundation for further investigations on restoring and improving the rangeland ecosystem's productivity and resilience to various disturbances in Uzbekistan.

5. CONCLUSIONS

To summarise, the present study analysed soil seed banks and aboveground vegetation by comparing two treatments (fenced and control experimental plots) and habitats in two study sites, Auðkúluheiði and Þeistareykir. The main conclusions are:

- Even though there are no significant differences in seedling emergence between grazed and non-grazed experimental plots, more seedlings tended to emerge from grazed areas than grazing-excluded plots.
- The effect of grazing exclusion on soil seed banks does not depend on habitat or location. In other words, there are no significant interactions between site or habitat on the number of emerged seedlings.
- No significant correlations existed between the number of seedlings in the soil seed bank and aboveground species richness in control and fenced plots. However, grazing exclusion seems to have led to a decrease in the species richness within experimental plots.

Despite the lack of effect of grazing exclosure on soil seed banks in this study, more species were found in the soil seed banks of control plots than from grazing-excluded plots. On the one hand, this suggests that grazed areas still have the potential for revegetation through their existing seed bank resources in the soil. On the other hand, six years of grazing exclusion might not be long enough to enhance soil seed banks and aboveground species richness.

ACKNOWLEDGEMENTS

I want to express my utmost appreciation to all the Agricultural University of Iceland staff and the Soil Conservation Service who taught and shared knowledge and experience on land restoration. I also am grateful to the Icelandic government and UNESCO for their generous support in organising the GRÓ LRT Program and for giving us an excellent opportunity to enhance our knowledge and experience in Iceland. Special gratitude is addressed to the GRÓ LRT staff. Thank you so much Sjöfn Vilhelmsdóttir, Berglind Orradóttir, Brita Berglund and Halldóra Traustadóttir, for your always kindly attitude to the fellows, friendly atmosphere, well-structured courses and all other support. I am also thankful to Sumjidmaa Sainnemekh for watering the seedlings during my absences on campus, Kristín Svavarsdóttir and Ingibjörg Svala Jónsdóttir for help with the identification of seedlings and Isaac Olupot for assistance with fieldwork in Auðkúluheiði and Þeistareykir. I am also grateful to Alejandro Salazar Villegas for his assistance in running the germination chamber. Above all, I wish to thank my supervisor Isabel C Barrio for her professional, scientific support and constructive guidance during completion of this report. I believe that her meaningful comments and excellent scientific writing skills helped me write the current paper and will be extremely helpful for future scientific papers. I am thankful that I was a student under her supervision. I would like to express my sincere appreciation to Toshpulot Rajabov for his valuable advice and recommendations as my teacher at Samarkand state university. I also appreciate my GRÓ LRT fellows' generous support, great friendly environment, and unforgettable experience together. Additionally, I would like to express my gratitude to Erdentuya Boldbaatar for her spending time with me to learn ArcGIS and to Bayartulga Altankhuyag for his kind support in improving my English language skills. I am deeply grateful for the understanding and enduring support of my parents and family, Mukhayyo, when I lived far from my home during these six months of training.

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