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Short communications

Estimating the effects of grazing exclusion on the seed bank in Icelandic rangelands

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INTRODUCTION

Soil seed banks are an essential resource for vegetation regeneration (Ma et al. 2018, Huang et al. 2022), as viable seeds can help maintain plant populations and increase the resilience of vegetation to disturbances (Kiss et al. 2018). Despite the potential relevance of seed banks for natural recovery of degraded rangelands, very little research has been conducted on this topic in Iceland (Magnússon 1994, Marteinsdóttir et al. 2010). Land degradation and soil erosion are main environmental issues in Iceland, and extensive grazing has been pointed out as one of the key drivers of degradation (Arnalds et al. 1987). In other degraded rangelands, grazing exclusion has been suggested as a potential strategy to strengthen soil seed banks (Huang et al. 2022). In Iceland, the lack of seed sources has been proposed as one of the reasons for the slow natural revegetation of eroded areas (Arnalds et al. 1987), but the effects of grazing exclusion on vegetation recovery from soil seed banks have not been extensively studied.

Here, we assess the potential for natural recovery of degraded rangelands in the Icelandic highlands, by germinating seeds in the soil and comparing above- and belowground species composition under different management and ecosystem conditions. Seedling emergence methods are well established for estimating the number of viable seeds in the soil (Gross 1990). The degree of similarity between soil seed banks and aboveground vegetation has been suggested as an indicator of the role of seed banks in plant community regeneration (Huang et al. 2022), with high similarity interpreted as a strong contribution of soil seed banks to vegetation recovery. We collected soil samples and measured vegetation in an ongoing field experiment. We excluded sheep grazing at two sites in two habitats, a moderately-degraded heathland and a heavily-degraded, gravelly desert (Mulloy et al. 2019). Given that the vegetation in the highlands is dominated by perennial species, we expected little effect of grazing exclusion on soil seed banks (Huang et al. 2022). In the heavily-degraded, gravelly desert, where soil seed banks could contribute more to vegetation regeneration, plant species represented in soil seed banks should be more similar to those present in aboveground vegetation (Huang et al. 2022).

MATERIALS AND METHODS

The study was conducted at two highland sites, Auðkúluheiði (65°13'N, 19°42'W, 470 m a.s.l.) and Þeistareykir (65°52'N, 17°02'W, 380 m a.s.l.), which are traditionally used for extensive sheep grazing from June to mid-September. At both sites, a mosaic of low-statured shrub vegetation (heath) and gravelly deserts (Icelandic: melur) dominated the landscape. In the heath, vegetation covered about 90% and included small shrubs (mainly *Betula nana*), bryophytes and lichens; in the melur, vegetation covered less than 10% and was dominated by graminoids and forbs (Mulloy et al. 2021). Soils are well-drained andosols in the heath and vitrisols in the gravelly desert, but Þeistareykir is inside the active volcanic zone, with younger soils and more prominent volcanic features. In 2016 a field experiment was set up at both sites, on adjacent heath and melur patches. In each habitat, six pairs of experimental plots (12 x 12 m) were established. Pairs of plots were separated by more than 100 m, and plots within a pair were 4 m apart. Experimental treatments were assigned randomly to the plots in each pair and consisted of a grazing exclosure (fence) and open control plots (hereafter referred to as non-grazed and grazed plots). Fences were 1.2 m high and prevented access by sheep. Although avian herbivores were not excluded, their use of the experimental plots was minimal (Mulloy et al. 2019).

Soil samples were collected at the beginning of the growing season (16-17 June 2022) to target persistent soil seed banks (i.e. seeds that persist in the soil for over one year). Within each plot a composite soil sample was collected by taking five subsamples of the first 10 cm of soil using a 2 cm diameter soil corer, following a 3-m linear transect from the edge of the plot inwards, for a total of 48 composite samples (24 from each site). Samples were air dried at room temperature for 48 hours and sieved (2 mm) to remove stones, roots and other large plant fragments. Soil samples were mixed and standardised by volume (125 cm^3 per sample, equivalent to a sampled soil surface of 12.5 cm^2). Layers 0.5-1 cm thick were spread on germination trays (23 x 17 x 6 cm), pre-filled to half their volume with commercial soil for structural support. A thin semi-permeable cloth separated the commercial soil from the soil samples to prevent germination of seeds from the commercial soil. On 20 June 2022, trays were placed in two germination chambers (Bioevopeak ICB-450L, programmed to 20° C and a 16:8 day/night cycle. Information on the origin and experimental treatment of the samples was blinded to the researchers. Trays were assigned randomly to each chamber, where they were watered daily. The position of the trays within the chambers was changed every week. Germination trials were run for twelve weeks (until 20 September 2022). The number of germinated seedlings and their identity were recorded daily. Once identified, seedlings were removed from the germination trays. The focus of the study was on seeds, so plants emerging from plant fragments or non-seed structures (Table 1) were not further considered in the analyses, although they can also be important for revegetation. For comparison to other studies, seed densities estimated with the seedling emergence method were calculated as the estimated number of seeds per m^2 of sampled soil.

Plant community composition of aboveground vegetation was assessed in all plots in summer 2021 using the point intercept method. In four permanent subplots (50 x 50 cm) all intercepts were recorded in 25 regularly distributed points. The number of intercepts by vascular plant species or bare ground was recorded in each point, for a total of 100 points per plot (**Supplementary materials**).

To evaluate the effects of site, habitat and grazing exclosure on the number of seedlings that emerged from soil seed banks, we used Generalized Linear Mixed Effects Models (GLMM) with a Poisson distribution. The number of emerged seedlings in each plot was included as response variable, plot pair as a

Table 1. Emerged species in germination trays and number of seedlings emerged, total and separately for each site (Auðkúluheiði and Þeistareykir), habitat (heath and gravelly desert) and experimental treatment (grazed and non-grazed) combination. The total number of species found belowground (without species emerging from fragments or non-seed structures) and aboveground is also indicated. Asterisks indicate plants emerging from fragments or non-seed structures, which were not further considered in the analyses.

		Auðkúluheiði				Þeistareykir			
		heath		gravelly desert		heath		gravelly desert	
species	total	grazed	non-grazed	grazed	non-grazed	grazed	non-grazed	grazed	non-grazed
Empetrum nigrum	14	1	2	0	0	9	2	0	0
Arenaria norvegica	8	0	1	0	0	2	1	4	0
Festuca spp.	7	2	1	0	0	3	0	1	0
**Bistorta vivipara*	3	0	2	0	0	1	0	0	0
Rumex acetosella	3	0	0	2	1	0	0	0	0
Anthoxanthum odoratum	2	0	0	0	0	1	0	1	0
Kobresia myosuroides	2	0	0	0	0	0	0	2	0
Poa alpina	2	0	0	2	0	0	0	0	0
Thymus praecox	2	1	0	0	0	1	0	0	0
Armeria maritima	1	1	0	0	0	0	0	0	0
**Equisentum variegatum*	1	0	0	0	0	1	0	0	0
Galium normanii	1	0	0	0	1	0	0	0	0
Rumex acetosa	1	0	0	0	1	0	0	0	0
**Salix herbacea*	1	0	0	0	0	0	1	0	0
Thalictrum alpinum	1	0	0	0	0	1	0	0	0
unidentified seedling	1	0	0	0	0	0	0	0	1
Nr species belowground	13	4	3	2	3	6	2	4	1
Nr species aboveground	100	32	31	24	19	42	36	19	20

random variable, and the three-way interaction between site, habitat and grazing exclosure as a predictor variable. The initial model was subsequently simplified by dropping non-significant interactions. Model assumptions, including overdispersion, were checked by visual inspection of model residuals.

Similarity in above and belowground species composition was calculated for plots where seedlings emerged using the Sørensen index (Legendre and Legendre, 2012), which is based on the presence of species and does not take into account species missing from both samples. Due to the limited sample size, it was not possible to compute statistical models to assess the differences in similarity between sites, habitats and experimental treatments. All analyses were conducted in R version 4.1.2 (R Development Core Team 2022). All datasets and R code used are openly accessible at https://github.com/icbarrio/SeedlingEmergence.git

RESULTS

By the end of the study, 45 seedlings had emerged (Table 1) from 20 of the 48 plots. Seed densities based on seedling emergence ranged from 0-7 per germination tray or 0-5,600 seeds m^{-2}. The most abundant seedlings were *Empetrum nigrum* (14 seedlings), *Arenaria norvegica* (8 seedlings) and *Festuca* spp. (either *F. vivipara* or *F. richardsonii*; 9 seedlings). Grazing exclusion affected the total number of seedlings differently

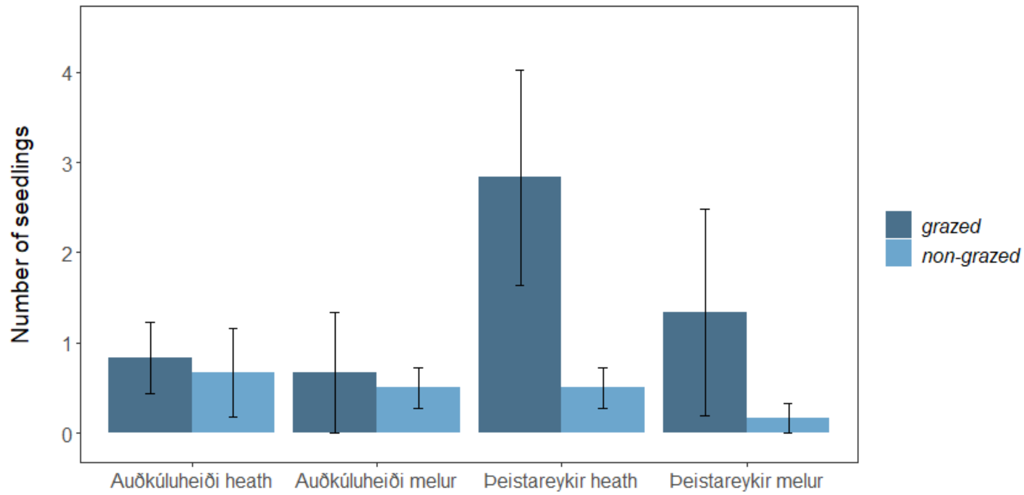

Figure 1. Number of emerged seedlings at two sites (Auðkúluheiði and Þeistareykir) in different habitats (heath and melur) and in grazed versus non-grazed fenced plots. Means and SE are shown (n=6 for each treatment combination).

at the two study sites (GLMM; interaction between grazing exclosure and site, z=-2.14, p=0.032; Figure 1). In Þeistareykir grazing exclusion significantly reduced the number of seedlings (GLMM; z=-3.40, p<0.001), whereas in Auðkúluheiði it had no effect (GLMM; z=-0.5, p=0.62). Habitat did not significantly affect the number of emerged seedlings (GLMM; z=-1.4, p=0.16). The number of species found in aboveground vegetation was higher than in the soil samples (Table 1). Similarity between aboveground and belowground for plots where

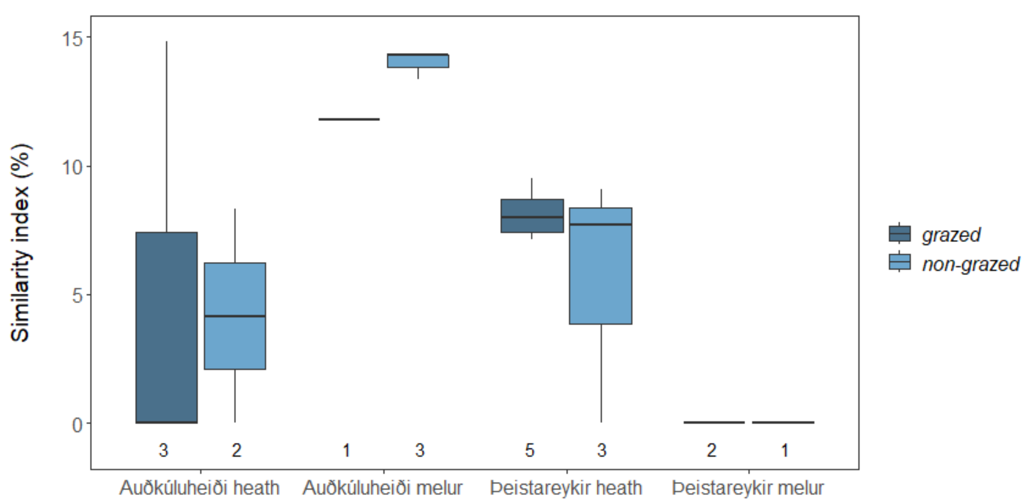

Figure 2. Similarity in species composition of aboveground vegetation and the corresponding seed bank sample, as indicated by Sørensen's similarity index (%) at two sites (Auðkúluheiði and Þeistareykir) in different habitats (heath and melur) and in grazed versus non-grazed plots, for plots where at least one seedling emerged (number of plots out of 6 for each site, habitat and treatment combinations are indicated below the boxplots).

at least one seedling emerged was on average 6.72% (SE=1.24%). The maximum value of similarity was 14.8% in a non-fenced heath plot in Auðkúluheiði (Figure 2).

DISCUSSION

Our study investigated the potential role of persistent soil seed banks in the recovery of degraded rangelands in Iceland. The number of seedlings that emerged from soil seed banks and the number of species found were low (45 seedlings from 14 species), but seed densities estimated by the seedling emergence method were comparable to seed banks from high arctic communities (Cooper et al. 2004). Seedling emergence methods are known to underestimate seed numbers, as not all viable seeds may germinate (Gross 1990). Seeds of many arctic and alpine plants require specific conditions to break dormancy (McGraw & Vavrek 1989), so our single germination trials provide only a partial picture. Future studies including stratification of soil samples and multiple exposures to germination conditions, as well as more extensive sampling, will provide a more complete assessment of seed banks of Icelandic rangelands.

Nevertheless, we found indications that six years of grazing exclusion reduced the number of seeds germinating from the soil seed banks at one of the sites, while it had no effect at the other site. This result is consistent with findings from other studies in systems dominated by perennial species, where grazing exclusion had no effect or even reduced persistent soil seed banks (Huang et al. 2022). Given the low abundance of seeds found in rangeland soils and the low seedling establishment rates found by other field studies (Marteinsdóttir et al. 2010), our results suggest that the role of soil seed banks in the regeneration of rangeland vegetation in Iceland may be limited. This conclusion is also supported by the low similarity in species composition between below and aboveground communities, which is typical of systems dominated by perennial species (Ma et al. 2018) and can indicate that the seed bank is contributing little to vegetation recovery (Huang et al. 2022). Our results suggest that grazing exclusion may not be an efficient short-term strategy to strengthen soil seed banks in rangelands that have been grazed for centuries and that restoration of degraded rangelands may require additional active measures.

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