Effects of nutrient transfer by great skuas (*Stercorarius skua*) and arctic skuas (*Stercorarius parasiticus*) on vegetation and soil at Breiðamerkurjökull, SE-Iceland

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ABSTRACT
Seabirds can play a vital role in primary succession by transferring nutrients from sea to land. Here, we examine the effects of sparse seabird colonies on primary succession at the Breiðamerkurjökull glacial fore-field in SE-Iceland. The area is generally characterized by low vegetation cover, where mosses are dominant, with scattered, grassy vegetation "islands" (bird hummocks) formed through point-centered influence of seabirds. The aim of this study was to assess the influence of bird presence on vegetation and soil properties. This was done by examining how vegetation and soil properties changed with the distance from bird hummocks and the influence of time on that relationship. Total vegetation cover and grass and forb cover were found to be significantly affected by the birds' presence, as well as the concentration of soil organic matter and pH_{H2O}. These results demonstrate the importance of seabirds as natural fertilizers in primary succession and early soil formation processes.

INTRODUCTION
As primary succession allows new ecosystems to develop after a significant ecological disturbance, understanding its processes is of great importance to the fields of soil science and ecology, among others. However, as such large disturbances are relatively uncommon globally, opportunities to study primary succession *in situ* are rare. The eruption at Surtsey in 1963, in which new land was created, provided an excellent natural laboratory in which primary succession could be studied *in situ* (Ólafsson & Ásbjörnsdóttir 2014). Such study areas are also created by glacial retreat, as rising global temperatures result in the revelation of abiotic areas that were previously covered by ice.

Nutrient availability plays a significant role in facilitating primary succession (Bernasconi *et al.* 2011). While nutrients generally flow from terrestrial to marine habitats, seabirds provide a way of active nutrient transfer in the other direction, by foraging on marine-derived prey, and, upon returning from foraging trips, excreting in the terrestrial habitat they inhabit during the breeding season (De La Peña-Lastra 2021). Studies on Surtsey and two neighboring islands have shown that such nutrient transfers by seabirds can be a major driver of plant succession and soil formation in Iceland (Magnússon *et al.* 2014, Leblans *et al.* 2017).

In this study we examined the effect of avian nutrient transfer from sea to land on primary succession within the Breiðamerkurjökull fore-field, formed by glacial retreat, in SE-Iceland. The fore-field is a part of the Breiðamerkursandur-Fagurhólsmýri nesting ground, where two large seabird species, the great skua (*Stercorarius skua*) and arctic skua (*Stercorarius parasiticus*), breed (Skarphéðinsson *et al.* 2016). These seabirds nest in sparse colonies (Olsen 2013) and their site fidelity to roosting, scouting, and nesting spots have led to the formation of bird hummocks. The bird hummocks tend to be at an elevated ground and form distinct grass-covered landscape features. Previous studies within the Breiðamerkurjökull fore-field have revealed strong effects of avifauna presence on soil chemical properties and colonization by plants shortly after exposure from glacial retreat (Vilmundardóttir *et al.* 2015, Turner-Meservy *et al.* 2022). Building upon this research, we measured vegetation and soil properties as a function of distance from the center of bird hummocks to determine how nutrient transfer affects primary succession and soil development. In addition, we examined the timescale of the effects by accounting for differences in the hummocks' ages. In doing this we aimed to answer the following questions:

1. Does proximity to bird hummocks affect vegetation and soil properties?
2. How far from the bird hummocks do the effects reach?
3. Is there a correlation between vegetation and soil properties?

MATERIAL AND METHODS

Study area

The study was conducted in the proglacial area of Breiðamerkurjökull (N64°02'-05', W16°13'-19'), an outlet glacier from Vatnajökull in SE-Iceland (Fig. 1). As a result of the Little Ice Age (LIA), that occurred between the 14th century and the late 19th century, Breiðamerkurjökull reached its maximum extent around 1890 (Watts 1962). Since that time until the present it has slowly retreated, exposing a land area of approximately 115 km^2 by retreating 4 to 7 km (Guðmundsson *et al.* 2017).

The climate at the study site is highly oceanic, with cool summers but mild winters (Einarsson 1984), with mean annual temperature just below 4.8°C and mean July temperature around 10.6 °C (Unpublished data from the Icelandic Metrological Institute, from the weather station Fagurhólsmýri, mean 1949-2007). Mean annual precipitation is around 3500 mm (Unpublished data from the Icelandic Metrological Institution, from the weather station Kvísker, mean 1960-2011).

The site is classified as an Important Bird Area, partly because it holds one of the largest breeding populations of great skua in Iceland (Skarphéðinsson *et al.* 2016). However, numbers of breeding great skuas in the area seem to have collapsed from an estimated 2,820 pairs in 1884-1885 to 185 in 2018 (Lund-Hansen & Lange 1991, Jóhannesdóttir & Hermannsdóttir 2019). In 2017, the area became part of the largest national park in Iceland, Vatnajökulsþjóðgarður.

The study area is generally characterized by moraines with low vegetation cover and mosses are the dominant plant group (Vilmundardóttir 2015). Scattered throughout the moraines are grassy vegetation islands formed through point-centered influence of seabirds (bird hummocks). The vegetation of bird hummocks differs from that of the adjacent moraines, as they are densely covered by grasses and herbs (Vilmundardóttir 2015, Turner-Meservy *et al.* 2022).

Field sampling was conducted on moraines marking the extent of the glacier in 1994, 1982, 1960, 1945, 1930, and 1890, i.e. the study sites formed a chronosequence (Fig. 1). The outline of the glacial margins had been identified by S. Guðmundsson (see e.g. Guðmundsson 2014 and Guðmundsson *et al.* 2017).

Sampling

The outlines of the former glacial margins were converted to GPS waypoints, and for each moraine five points were randomly selected for vegetation and soil sampling. These points were located in the field and the nearest bird hummock identified as a sampling site, making up for a total of 30 hummocks to be analyzed (Fig. 1).

The diameter of each hummock, as defined by the visible difference between hummock vegetation and the surrounding moraine vegetation, was measured from north to south. On each hummock, a total of nine 50 x 50 cm quadrats were placed, one at the center and the others at four locations adjacent to the center to the north and south, extending 3 m from the center (Fig. 2, Fig. 3 A and B). In each quadrat, all vascular plant species were identified according to Kristinsson (2010) (Fig. 4 A and B). Each species

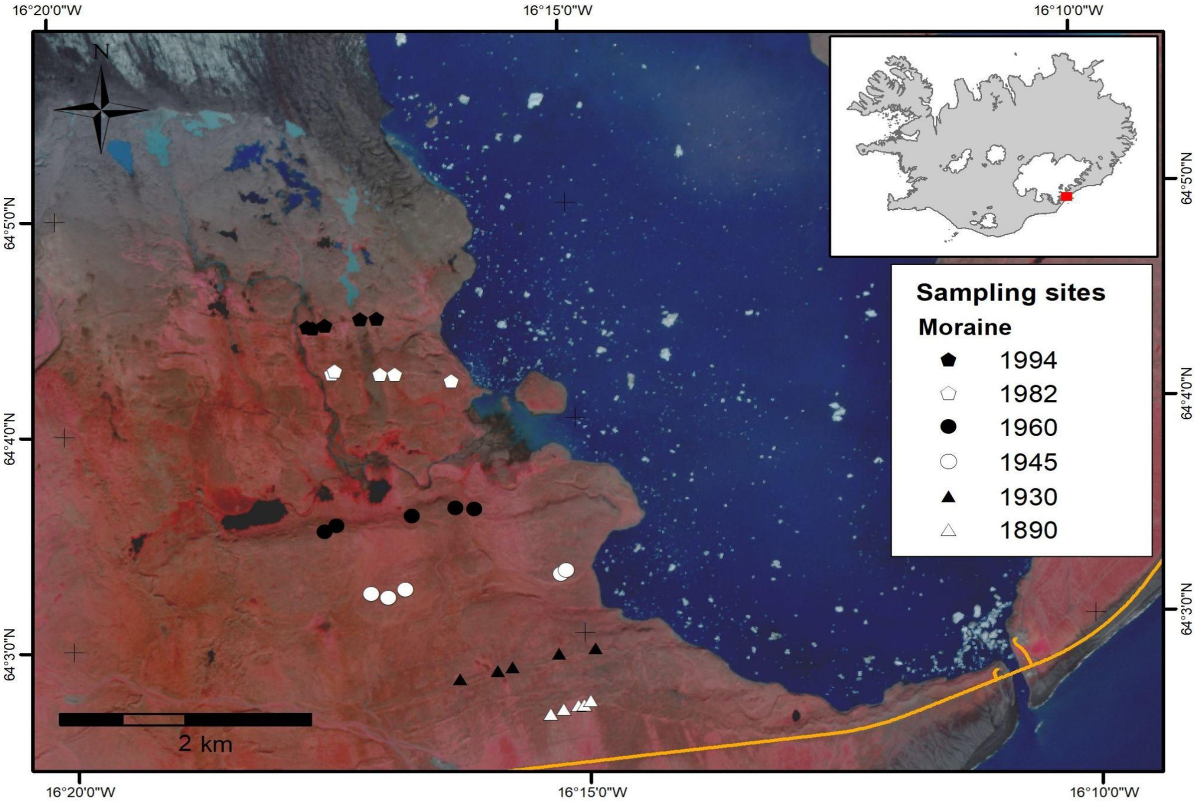

Figure 1. Sampling sites from July 2018 within the glacial fore-field of Breiðamerkurjökull, shown on an infrared Sentinel-2 satellite image from 22 August 2018. The sites are located along the estimated position of the glacier terminus at a given point in time (see e.g. S. Guðmundsson 2014 and S. Guðmundsson et al. 2017).

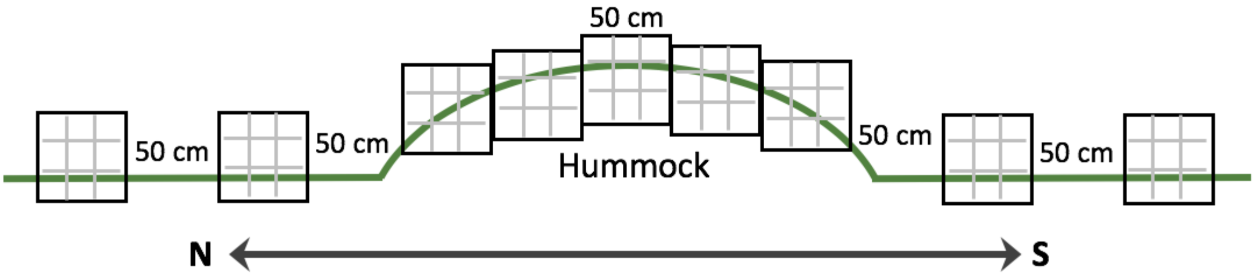

Figure 2. The setup of nine 50 x 50 cm quadrats placed on each bird hummock. One quadrant was placed on the hummock's center while the other eight were lined up to the north and the south up to 3 m distance from the center.

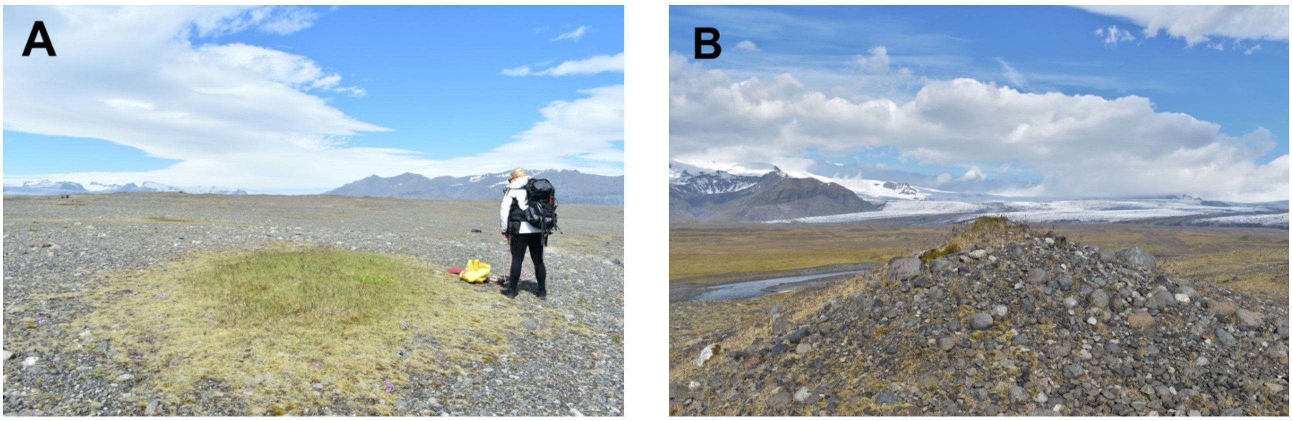

Figure 3. Bird hummocks on moraines of different age within the Breiðamerkurjökull fore-field in SE-Iceland. A. Moraine from the year 1945. B. Moraine from the year 1982. Photos SS, July 2018.

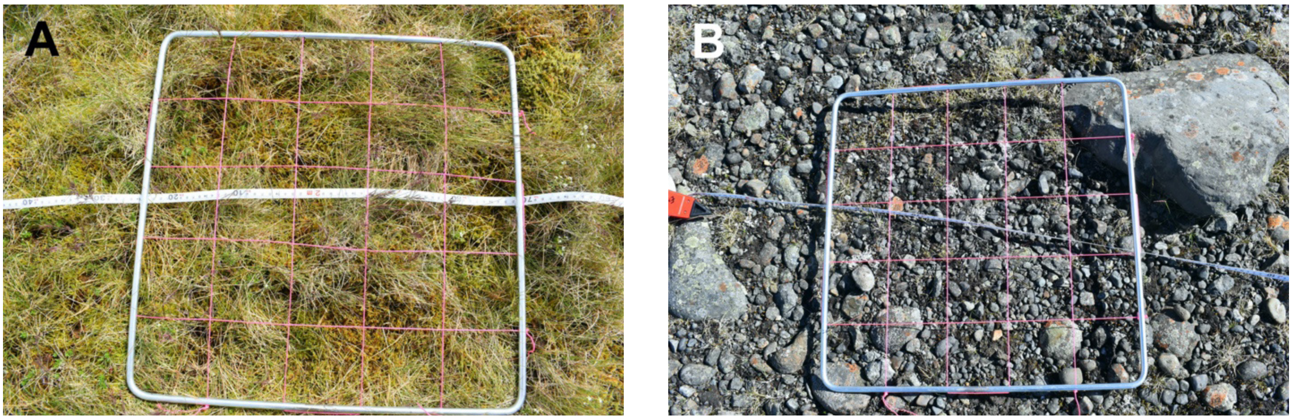

Figure 4. Examples of vegetation quadrats from a sampling site on moraine formed in 1890, within the Breiðamerkurjökull fore-field in SE- Iceland. A. The center of a bird hummock. B. Three meters north of the hummock's center. Photos SS, July 2018.

was categorized according to the following groups: grasses, forbs, shrubs, and ferns. In addition to these categories, total vegetation cover, moss cover, and lichen cover were estimated within each quadrat by using the Braun-Blanquet cover scale (Braun-Blanquet, 1932). Each quadrat was photographed prior to soil sampling for further reference. Soil samples were collected from the top 5 cm within each quadrat, for a total of 270 samples.

Soil sample analysis

Soil samples were analyzed at the University of Iceland, Reykjavík. The samples were air dried at room temperature and sifted through a 2 mm sieve. The organic matter (OM) concentration was measured through loss on ignition (LOI) by combustion at 550°C in a muffle furnace for four hours (Nelson & Sommers 1996). Soil pH in H_2O was measured in deionized water-soil suspension (1:5), shaken for 2 hours and measured by glass electrode (Oakton pH 510 Benchtop Meter). Both OM and pH were measured in duplicates.

Statistical analysis

Effects of bird presence on vegetation and soil were explored with all measured parameters. To examine the relationship between the vegetation and soil factors and the distance to bird hummocks a linear mixed effect models (LMER) fitted by REML. The dependent parameters used in the models were total vegetation cover, cover groups, number of vascular plant species, OM, and pH_{H2O}. In all models, distance from the center of the hummock and the quadratic term of the distance was defined as an independent factor, each moraine as a fixed factor and each hummock set as a random factor (*dependent parameter ~ poly(Distance, 2) + (Moraine) + (Distance|hummock)*. A Tukey's post hoc test was run to examine the difference in dependent variables between moraines. The relationship between vegetation cover, grass cover and forb cover on OM and the relationship between OM and soil pH_{H2O} were explored with linear models (LM).

The extent of the effects of bird presence was examined by comparing the diameter of bird hummocks between moraines of different age with a one way of variance (ANOVA) and a Tukey test.

The statistical analyses were made in R-gui (R Core Team, 2021) using the additional packages lme4 (Bates *et al.* 2015), GGplot2 (Wickham 2016), dplyr (Wickham *et al.* 2022), emmeans (Graves *et al.* 2019,), and MuMIn (Barton 2022).

RESULTS

Vegetation

The diameter of bird hummocks varied significantly with time since deglaciation ($F_{5,24}=7.62, p<.001$) and the change was visible when comparing hummocks from the oldest and youngest moraines (Fig. 3). The diameter was found to increase with age, although the diameter did not vary significantly between the oldest hummocks on moraines from 1945, 1930, and 1890. Hummock diameter was shortest at the 1994 moraine (greatest diameter = 0.5 m), largest at the 1945 moraine (greatest diameter = 3.0 m), and the diameter did not change significantly for the 1930 and 1890 moraines (Fig. 5).

The vegetation on the bird hummocks mostly consisted of dense grass cover and a sparser forb cover, and for this reason we only performed data

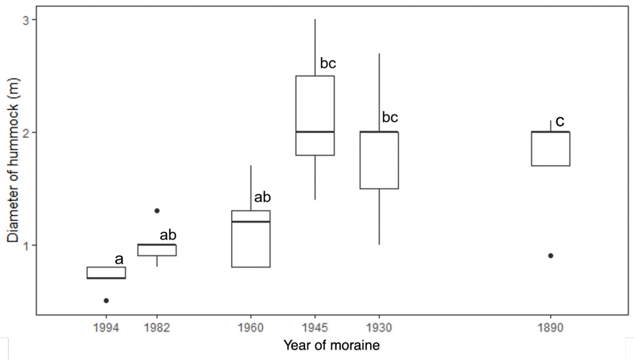

Figure 5. A boxplot comparing the diameter of bird hummocks at different aged moraines within the Breiðamerkurjökull fore-field in SE-Iceland. The letters a, b, and c indicate significant differences between the moraines.

analysis on these two cover groups. In total, 29 species of vascular plants were identified within the quadrats. Of those, 12 were categorized as grasses, 14 as forbs, 2 as shrubs, and 1 as a fern. Some of the most common species were *Festuca vivipara*, *Festuca ricardsonii, Agrostis stolonifera,* and *Galium normanii* (Table 1).

The cover of the two most common plant groups was also plotted against distance from the hummocks' center. Grass cover varied significantly with distance (R_2= 0.77; p < .001; Standard coefficient=0.28). with a stronger relationship than forbs (R_2= 0.46; *p* < .001; Standard coefficient =0.04) and total vegetation cover (R_2= 0.56; *p* < *.001;* Standard coefficient=0.13). Grass

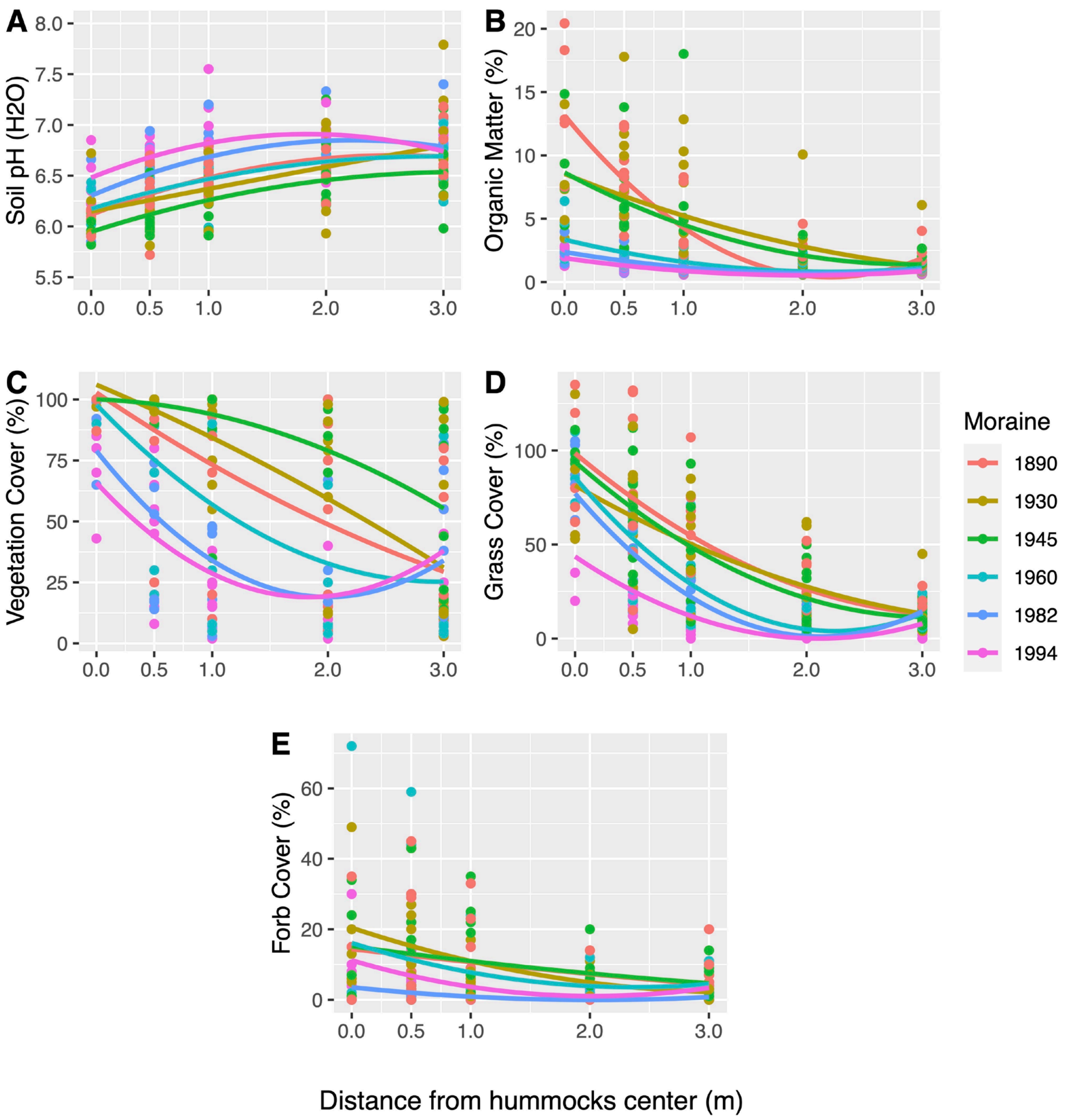

Figure 6. The relationship between measured variables and distance from hummock center at the Breiðamerkurjökull fore-field in SE- Iceland. A) pH (H2O), B) percentage of organic matter, C) vegetation cover (%), D) grass cover, and E) forb cover. The lines are quadratic fits.

Table 1. List of vascular plant species identified within quadrats at the study site, with indicators on which moraine(s) each species was found. The table lists whether the same species have been found at least once on Surtsey as well as species which have established a viable population on Surtsey according to Borgþór Magnússon et al. (2020).

				Breiðamerkurjökull fore-field						**Surtsey**	
Nr.	***Scientific name***	**Species**	**Classification**	1890	1930	1945	1960	1982	1994	At least once	Viable population
1	*Agrostis stolonifera*	Creeping bentgrass	Grass	X	X	X	X	X	X	X	X
2	*Agrostis vinealis*	Brown bentgrass	Grass	X						X	
3	*Alchemilla alpina*	Alpine lady's-mantle	Forb	X		X			X	X	
4	*Arabidopsis petraea*	Northern rock-cress	Forb	X	X		X				
5	*Bistorta vivipara*	Alpine bistort	Forb	X		X					
6	*Botrychium lunaria*	Moonwort	Fern	X			X				
7	*Carex maritima*	Curved sedge	Grass			X				X	X
8	*Cerastium alpinum*	Alpine mouse-ear	Forb	X	X	X					
9	*Cerastium fontanum*	Common mouse-ear chickweed	Forb	X	X	X	X	X	X	X	X
10	*Empetrum nigrum L.*	Crowberry	Shrub	X						X	X
11	*Festuca richardsonii*	Red fescue	Grass	X	X	X	X	X	X	X	X
12	*Festuca vivipara*	Viviparous sheep's-fescue	Grass	X	X	X	X	X	X	X	
13	*Galium normanii*	Slender bedstraw	Forb	X	X	X	X	X	X	X	
14	*Galium verum*	Lady's bedstraw	Forb	X	X	X				X	
15	*Juncus trifidus*	Highland rush	Grass				X				
16	*Juncus triglumis*	Three-flowered rush	Grass		X						
17	*Luzula spicata*	Spiked woodrush	Grass	X	X	X	X	X	X	X	
18	*Plantago maritima*	Sea plantain	Forb				X			X	
19	*Poa alpina*	Alpine meadow-grass	Grass						X		
20	*Poa flexuosa*	Wavy meadow-grass	Grass	X	X	X	X	X	X		
21	*Poa glauca*	Glaucous bluegrass	Grass	X	X	X	X	X	X	X	
22	*Rumex acetosa*	Sorrel	Forb	X						X	X
23	*Rumex acetosella*	Red sorrel	Forb	X	X	X	X	X	X	X	X
24	*Saxifraga aizoides*	Yellow mountain saxifrage	Forb	X							
25	*Sedum annuum*	Annual stonecrop	Forb	X					X		
26	*Silene suecica*	Red Alpine catchfly	Forb	X	X						
27	*Thymus praecox*	Wild thyme	Shrub	X	X	X	X	X	X	X	X
28	*Trisetum sp.*	Spike trisetum	Grass	X		X			X		
29	*Viola canina*	Heath dog-violet	Forb					X			
			Frequency	23	14	16	14	11	14	16	8

cover in relation to distance from bird hummocks was similar between moraines, although the grass cover at the youngest moraine, from 1994, was found to significantly differentiate from the two oldest moraines ($p < .05$). Forb cover did not differentiate between moraines. The total vegetation cover was significantly lower at the two youngest moraines, from 1994 and 1982, compared with the three oldest moraines from 1890, 1930, and 1994 ($p < .005$). The total vegetation cover decreased at the slowest rate from the center of the moraine from 1945 (Fig. 6).

Soil

Concentration of OM significantly increased with proximity to the bird hummocks (R_2= 0.68; $p< .001$; Standard coefficient=0.20). Concentration of OM in relation to distance was not significantly different between the moraines (p>.05). The pH_{H2O} in soil was found to significantly decrease with proximity to the bird hummocks at (R_2= 0.71; $p< .001$; Standard coefficient=-0.18). The relationship between distance and pH_{H2O} was significantly different between the 1945 and 1994 moraines ($p< .001$).

OM concentration was found to be significantly

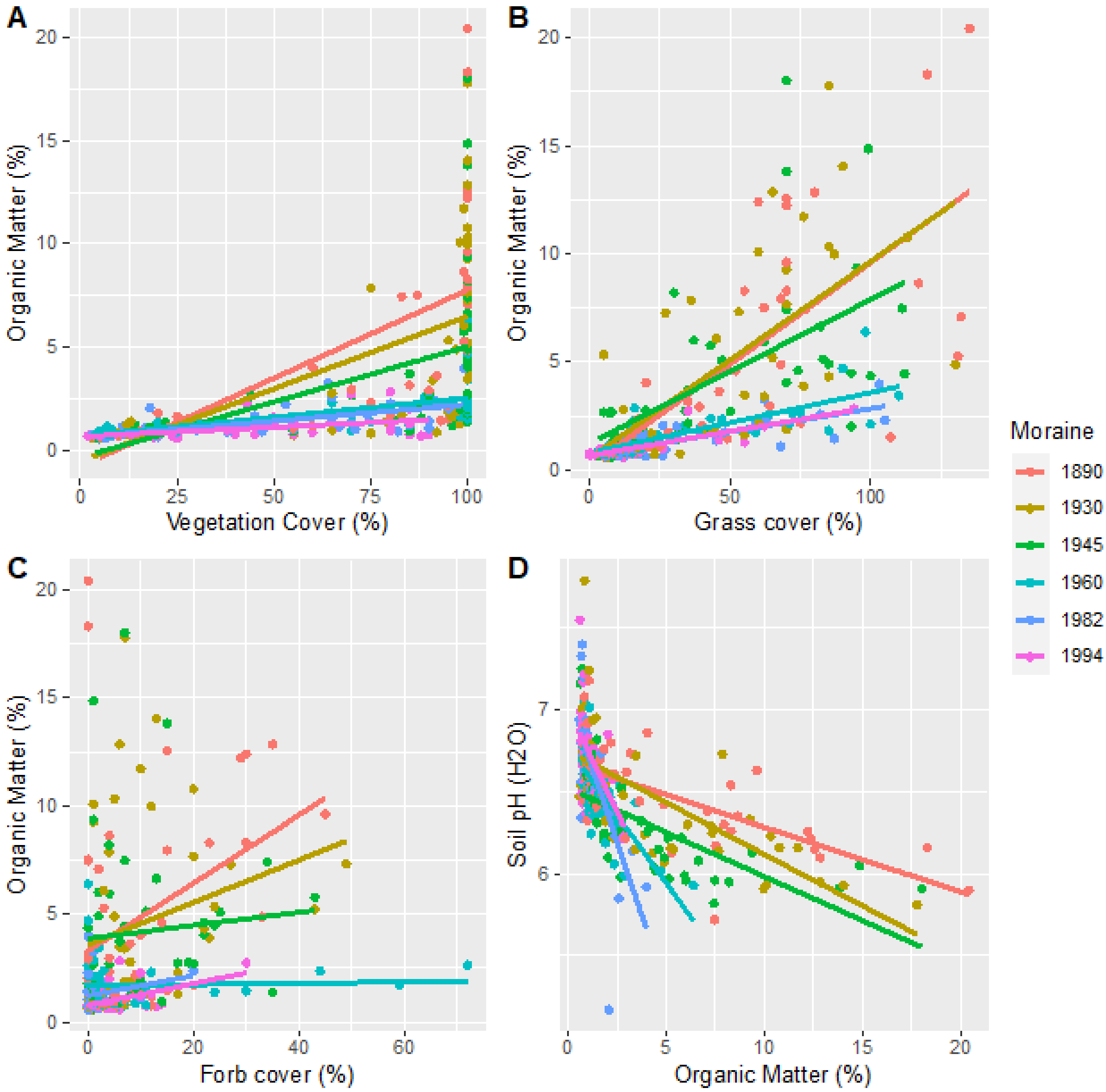

Figure 7. Graphs showing relationships between measured variables and OM concentration within the Breiðamerkurjökull fore-field, SE- Iceland. A) Vegetation cover, B) grass cover, C) forb cover, and D) soil pH $_{H2O}$. The lines are linear regressions.

higher with increased cover of vegetation, grasses, and forbs. The average relationship was strongest for grass cover ($F_{2,266}$ = *127.8;* R^2= 0.49; *p< .001*), then total vegetation cover ($F_{2,266}$ = *82.93;* R^2= 0.38; *p< .001),* and weakest with forb cover ($F_{2,266}$ = *34.15;* R^2= 0.20; *p< .001*) (Fig. 7).

Soil pH_{H2O} was found to have a significantly negative relationship with OM concentration ($F_{6,262}$ = *32.83;* R^2= 0.42; *p< .001*). The relationship between pH_{H2O} and OM was significantly different between moraines ($F_{5,261}$ = *8.09*; *p< .001).*

DISCUSSION

Our results reveal that within the Breiðamerkurjökull fore-field the proximity to bird hummocks significantly impacts vegetation and soil properties.

Grass cover showed the highest estimated relationship to proximity to the hummocks compared to forb cover and total vegetation cover. These results were similar to those from Surtsey, revealing quick response to available nutrients among grasses, caused by their excellent capability at utilizing nutrients with their fine but dense root system (Magnússon *et al.*

2014). Soil OM increased and soil pH_{H2O} decreased with distance from bird hummocks.

Grass cover had the strongest influence on OM concentration of the measured vegetation types. This suggests that accumulation of OM, and therefore soil organic carbon (SOC), at the hummocks is mostly influenced by the grass carbon inputs. When under elevated N inputs, Icelandic grasslands show an increased capacity to store SOC (Leblans *et al.* 2017), a property that could apply to the bird hummocks as well. The correlation between OM concentration and soil pH_{H2O} was also significant, and the degree of the relationship varied between ages of moraines. The lower pH_{H2O} will further enhance plants' capabilities to absorb soil nutrients, resulting in a positive feedback loop between soil properties and vegetation growth. A comparable lowering in pH_{H2O} with stages in primary succession have been observed on Surtsey (Sigurdsson & Magnusson 2010) and on nunataks on Breiðamerkurjökull (Sigurðsson *et al.* 2020).

The extent of the birds' impacts, as interpreted by the diameter of hummocks, showed to increase significantly with age of the moraine where it was located. The hummocks on the 1945 moraine stood out from that pattern, having the largest diameters, while the two oldest were not significantly different (Fig. 5). The diameter also varied within hummocks on the same moraine, which can both be explained by environmental factors, such as degree of slope, and the popularity of a hummock among the birds. Although the ground of hummocks within the same moraine became available for birds at the same point in time, it is unlikely that the accumulated time of bird presence is equal.

Of the 29 plant species that were identified within the quadrates on and around the bird hummocks within the sampling area in this study, 16 have also been found on Surtsey, and eight thereof have been categorized as having viable populations there, according to Borgþór Magnússon et al. (2020). Like on Surtsey, most of the dominant species within the fore-field are thought to have been dispersed by birds, considering the long distance to seed sources and the seed properties of the most common species. All of the 16 vascular plant species found both within the Breiðamerkurjökull fore-field and on Surtsey are common around the country (Kristinsson, H. 2010).

As the Breiðamerkurjökull fore-field was previously found to be characterized by highland vegetation (Sigurðsson et al., 2020), and this study reveals that bird hummocks are primarily characterized by lowland vegetation, this suggests that bird presence is affecting the species composition on the bird hummocks.

Most seabirds breed in colonies, therefore the impact of their presence on the vegetation is often densely restricted to certain areas. The highest biomass of seabirds in Iceland nests on steep cliffs where their deposited marine-derived nutrients have reduced potential to affect vegetation and soil formation (Doughty *et al.* 2016). In comparison, the widespread skua population at the Breiðamerkurjökull fore-field influences a large area with their territorial behavior resulting in local hot spots of plant succession, soil formation, and SOC accumulation. This influence has weakened recently with the collapse of great skuas (Jóhannesdóttir & Hermannsdóttir 2019).

These results enhance our understanding of the interplay between marine and terrestrial ecosystems, which are important with faster retreating glaciers and significant changes in sea bird population. Seabird populations continue to decline at an alarming rate both globally (Dias *et al.* 2019) and in Iceland (Vigfúsdóttir 2021), weakening the link between the land and ocean, and could possibly slow the rate of primary succession in the area.

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