UNIVERSITY OF ICELAND

Master's thesis
in Environment and Natural Resources

Effects of Great Skuas (*Stercorarius skua*) and Arctic Skuas (*Stercorarius parasiticus*) on primary succession at the retreating Breidamerkurjokull glacier, SE-Iceland

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FACULTY OF LIFE AND ENVIRONMENTAL SCIENCES

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This thesis satisfies 60 credits towards an M.S. in Environment and Natural Resources in the Faculty of Life and Environmental Sciences, University of Iceland,
School of Engineering and Natural Sciences

Abstract

Seabirds can play a vital role in primary succession by transferring nutrients from sea to land. Here, the effects of sparse seabird colonies on primary succession at the Breiðamerkurjökull glacial forefield in SE-Iceland were examined. 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 birds. The aim of this study was to assess the influence of bird presence on vegetation and soil properties. This was done by mapping the distribution of skuas and examining how vegetation and soil properties changed with the distance from bird hummocks and the influence of time on that relationship. In total 59 Arctic skuas were recorded with 9 AOTs (Apparently Occupied Territory) and 40 great skuas were recorded and 5 AOTs during bird censuses. The territories of the two skua species did not overlap. Total vegetation cover and grass and forb cover were found to significantly increase with proximity to the hummocks' centers as well as the concentration of soil organic matter, while soil pH_{H2O} significantly decreased. These results demonstrate the importance of seabirds as natural fertilizers in primary succession and early soil formation processes.

Útdráttur

Sjófuglar geta gegnt mikilvægu hlutverki í frumframvindu með því að flytja næringarefni frá sjó til lands. Hér voru skoðuð áhrif strjálla sjófuglabyggða á frumframvindu framan Breiðamerkurjökuls á Suðausturlandi. Svæðið einkennist almennt af gisinni gróðurþekju, þar sem mosar eru ráðandi, með dreifðum, grösugum „eyjum" (fuglaþúfum) sem myndast vegna áhrifa fugla. Markmið þessarar rannsóknar var að leggja mat á áhrif viðveru fugla á gróður- og jarðvegseiginleika. Það var gert með því að kortleggja útbreiðslu ásamt því að kanna hvernig gróður- og jarðvegseiginleikar breyttust með fjarlægð frá fuglaþúfum og áhrifum tíma á það samband. Alls sáust 59 kjóar sem ekki sýndu óðalshegðun, en skráð voru 9 óðöl kjóa þá sáust 40 skúmar sem ekki sýndu óðalshegðun og 5 skúma óðöl voru skráð. Óðöl tegundanna sköruðust ekki. Í ljós kom að heildar gróðurþekju, þekja grasa og annarra blómplantna, auk styrks lífræns efnis í jarðvegi jókst marktækt með nálægð við fuglaþúfurnar en pH_{H2O} lækkaði marktækt með nálægð við þúfurnar. Þessar niðurstöður sýna fram á mikilvægi sjófugla sem náttúrulegir áburðargjafar fyrir frumframvindu og jarðvegsmyndun á fyrstu stigum.

Dedication

This thesis is dedicated to my daughter Margrét Freyja, who came into the world during its making and gave me one more reason to finish it.

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Abbreviations

AOT – Apparently Occupied Territory

FAO – Food and Agriculture Organization of the United Nations

IPCC – Intergovernmental Panel on Climate Change

LIA – Little Ice Age

LOI – Loss on ignition

MDN – Marine-Derived Nutrient

N – Nitrogen

OA – Ocean acidification

OM – Organic matter

P – Phosphorus

SOC – Soil organic carbon

SOM – Soil organic matter

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1 Theoretical background

1.1 Climate change

Throughout Earth's history, there have always been fluctuations between cooling, or glaciation, and warming periods (Mann and Kump, 2008). However, since the Industrial Revolution, anthropogenic greenhouse gas emissions have resulted in global warming that has far exceeded these natural fluctuations (FAO, 2018, IPCC, 2022). These effects are widespread and readily apparent worldwide, from polar to equatorial latitudes. As our understanding and ability to gauge these effects develops, we will undoubtedly discover additional consequences (Field, 2014; IPCC, 2022).

Iceland's ecosystems, considering their mid-Atlantic and sub-Arctic location, are especially vulnerable to climate change (McCarthy et al., 2001), as areas at higher latitudes have experienced greater increases in temperature than those at lower latitudes (Cohen et al., 2014; Stocker, 2014). The direct effects of climate change in Iceland are hardly more evident than the continuous and steady retreat of its glaciers over the past 120 years (Sigurðsson et al., 2007).

1.2 Changes in the land environment

Glaciers are a prominent part of Icelandic landscape, covering 11% of the country's land area and having pronounced effects on nature, particularly soils (Björnsson & Pálsson, 2008). The period roughly between the early 14th century and the late 19th century is referred to as the Little Ice Age (LIA) (Grove, 2001). During the LIA, glaciers advanced globally until reaching a maximum extent around 1890 (Björnsson & Pálsson, 2008). Since then, global temperature increased by about one degree Celsius, resulting in massive ice losses, represented by glacier and sea ice retreat (IPCC, 2022; Paul & Bolch, 2019). Glaciers are expected to continue to retreat, as the majority of glaciers have yet to normalize their reduced extents given the present-day climate, and temperatures are predicted to continue rising (Paul & Bolch, 2019).

In line with the global trend, Icelandic glaciers have rapidly retreated in the 21st century (Eyþórsson et al., 2018). Studies on the effects of the expected climate change have revealed that majority of Iceland's main ice caps will disappear during the next two centuries, isolating glaciers to the highest elevations (Aðalgeirsdóttir et al., 2006; 2011). Since the end of the LIA, from 1890 to 2014, about 2000 km^2 of land have become exposed due to glacial recession in Iceland (Björnsson et al., 2018), resulting in the appearance of vast abiotic areas in the sub-glacial terrain (Sigurðsson et al., 2007).

1.2.1 Primary succession

Primary succession is the process by which an ecosystem develops on new substrate that was previously devoid of life, lacking organic matter or soil. Nutrient availability plays a significant role in facilitating primary succession (Bernasconi et al., 2011). The first species to colonize the area, largely photosynthetic organisms such as algae and lichens, can begin the process of soil formation and allow succession to occur. The detritus from these organisms provides an important source of soil organic matter (SOM) due to decomposition, and plays roles in water retention, cation exchange capacity, and supplies energy and nutrients to microorganisms. During this process, the accumulation of organic matter tends to lower the pH value of the soil (pH measured in water solution, pH_{H2O}), making it more acidic, which affects vegetation growth (Thomas, 1996). This trend has been observed also in Iceland, where newly exposed soil was found to have a neutral or slightly alkaline pH_{H2O} that declined over time and stabilized at 5.5-6 within 100 years (Vilmundardóttir et al., 2014; 2015).

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 emergence of Surtsey, an island in S-Iceland created by a submarine volcanic eruption in 1963, 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. The glacial retried of Breiðamerkurjökull has been well documented through mapping former glacial outlines (Guðmundsson, et al., 2017).

Glacial moraines are formed by the accumulation of soil and other debris when glaciers retreat. Well-defined moraines with documented histories offer a "space-for-time substitution" approach for studying primary succession called chronosequence (Wojcik et al., 2021). The chronosequence approach was first performed in Iceland in the glacial forefields of Skaftafellsjökull more than 50 years ago (Persson, 1964).

In a chronosequence, the only factor differing between areas of comparison is age. Chronosequence has been a widely used method to examine primary succession and soil formation (Jenny, 1941; Johnson & Miyanishi, 2008; Walker et al., 2010). With continuing worldwide trends of glacial retreat, chronosequence has become common for the study of glacial forefields (Wojcik et al., 2021), with one of the oldest such studies having been conducted in Glacier Bay, Alaska (Bormann & Sidle, 1990).

1.2.2 Soil formation

Because of the extended time required for them to form, soils are considered a nonrenewable resource. Soil is considered both a biological and physical phenomenon and can accordingly be considered a significant link between the biological and physical aspects of a landscape (Smith et al., 2018).

The soil formation process at newly exposed surfaces is dependent on a variety of factors: organisms (the available biota), regional climate, topography (including the water table), time, parent material composition, and human activity. These factors are considered as falling into either passive factors (relating to the original state, such as parent material and original topography, as well as time), or active (external sources of change, such as climate and biotic variables) (Jenny, 1941).

In Iceland, the well-documented glacial retreat of Breiðamerkurjökull has provided a reliable timescale for a chronosequence within the glacier's forefield (Guðmundsson et al. 2017;

Vilmundardóttir et al., 2015). Those studies have revealed the accumulation of SOM, leading to lower pH_{H2O} values. Studies in Glacier Bay have revealed that accumulation of SOM and lowered pH_{H2O} can affect the types of plants that can grow in the soil. When under long-term elevated seabird driven nitrogen (N) inputs, Icelandic grasslands show an increased capacity to store soil organic carbon (SOC) (Leblans et al., 2017).

1.2.3 Soils in Iceland

Parent material composition is the fundamental factor in determining the type of soil formed in glacial forefields (Jenny, 1941). Different from most other soils in Europe and the world, the parent material of Icelandic soils is of recent volcanic origin, usually consisting of basaltic material, both rock and tephra (Arnalds, 2008; 2015). Thus, glacial forelands preserve large quantities of these materials (Björnsson & Pálsson, 2008).

Most soils in Iceland are classified as Andosol under the World Reference Base (WRB) soil classification system (IUSS Working Group, 2006), specifically Brown Andosol, which is the soil type that occurs under vegetation in well drained areas (Arnalds, 2015). The main characteristic properties of Andosol are low bulk density, high organic matter content, high hydraulic conductivity and high-water retention, strong phosphate preservation, and variable charge characteristics (Arnalds, 2015). The property of accumulating organic material allows Andosol to store more carbon reserves per unit area than other dryland soils (Batjes, 1996; Eswaran et al., 1993). The pH_{H2O} level in Brown Andosol ranges typically between 5-7. The soils of sparsely vegetated areas, Vitrisols, have very different properties compared to Brown Andosol as they lack the high organic matter content, water holding capacity, and secondary clay minerals, and soil pH_{H2O} is generally higher than 7 (Arnalds, 2015).

Nitrogen (N) is a key limiting factor for plant growth in Iceland (Óskarsson & Sigurgeirsson, 2001; Ritter, 2007) and for plant succession in volcanic deposits in Iceland (Gíslason & Eiríksdóttir, 2004; Gíslason et al., 1996). This is similar to other comparable areas such as Glacier Bay in Alaska, where N and phosphorus (P) both limited the plant growth in pioneer soils (Chapin et al., 1994).

Studies have revealed that soil formation and primary succession is often a slower process in Iceland compared to other cold regions in the world such as the Alps in mid-Europe, Alaska, and Scandinavia (Alexander & Burt, 1996; Dümig et al., 2011; Egli et al., 2010; He & Tang, 2008; Kabala & Zapart, 2012; Vilmundardóttir et al., 2015). This could be explained by comparatively slower vegetation succession, lower summer temperatures, more rapid temperature fluctuations around the freezing point, and possibly grazing.

1.3 Changes in the marine environment

Marine ecosystems are fundamental for the overall health of our planet. They host a great portion of biodiversity, regulate climate, sustain a vibrant economy, and contribute to the world’s food security. Although the impacts of anthropogenic climate change on the world's oceans have not been studied as much as the effects on terrestrial ecosystems, many different trends have been reported (FAO, 2018).

Oceans have taken up roughly one third of anthropogenic carbon dioxide (CO_2) emissions. This uptake increases water acidity through a process called ocean acidification (OA). Studies show that increased acidity hampers calcification in shell-forming invertebrates, such as phytoplankton, crustaceans, and corals (Macko & Fantasia, 2018). Knowledge on evolutionary adaptation to OA is limited, but studies show that it may shift the biodiversity and food web of entire communities (Bopp et al., 2013; Thor & Dupont, 2018).

A further effect of global warming is the influx of cold freshwater from melting glaciers. Not only does this reduce the salinity of seawater, altering the biogeochemical cycles of the world's oceans, but it also has the ability to alter oceanographic features and processes such as currents and stratification. As cold freshwater is less dense than the existing warmer, saline seawater, the seawater can sink deeper, affecting the natural submarine flow of seawater, and therefore nutrient transport overall (Rahmstorf, 2006). Changes in ocean stratification, as well as northward shifting isotherms, have been observed in Icelandic waters in recent decades (Ruiz-Angulo, 2022).

1.3.1 Icelandic marine environment

Iceland is located just south of the Arctic circle, at the junction of the Mid-Atlantic Ridge and the Greenland-Scotland Ridge. The oceanic circulation and consequently the distribution of marine populations around Iceland is influenced by these submarine ridges (Ástþórsson & Vilhjálmsson, 2002; Gíslason, 2005; Jónsson & Valdimarsson, 2005).

The effects of anthropogenic activities in Icelandic waters are evident. A time series conducted in Icelandic waters from 1985-2008 showed a clear trend of increasing ocean acidification (Ólafsson et al., 2009). Sea levels around Iceland are rising by more than 30 mm per year due to climate change (Compton et al., 2015). Furthermore, climate change is expected to have effects on sea temperatures, amount of precipitation, wind patterns, and primary production both on land and in the ocean (Björnsson, 2018 ; Stocker, 2014).

These factors have had noticeable impacts on the distribution and abundance of various organisms. Many geographical shifts have already been documented in numerous fish species, for example the Atlantic mackerel (*Scomber scombrus*) and Atlantic cod (*Gadus morhua*) (Overholtz et al., 2011; Engelhard et al., 2014). An apparent 2005 crash in the population of sandeels (*Ammodytes* sp.), a key prey fish for most seabird populations in Iceland (Lilliendahl et al., 2013; Vigfúsdóttir, 2021), may have also been related to climate change (Bjarnason et al., 2021).

Other indirect effects of climate change might be encroachment by competing species as well as loss of suitable habitats (Finney et al., 1999). Climate change can also alter migration routes, as habitats that lie along these routes face changes (Wauchope et al., 2017).

1.4 Seabirds

Seabirds are generally long-lived, K-selected animals (Russel, 2009). The fact that they are sexually mature for many years and invest proportionally little energy in their offspring makes them more plastic to short-term changes in their environment. Only when unfavorable conditions last for several years will they have an effect on the population size (Weimerskirch, 2001; Coulson, 2002).

In general, seabirds in the northern hemisphere are more negatively affected by climate change on the southern edge of their distribution (Frederiksen et al., 2013; Gaston et al., 2005). As their southern range warms, resulting in nonideal conditions for habitation of both the seabirds and their prey species, seabird distribution shifts northward (Wauchope et al., 2017).

Worldwide, around 47% of seabird species are declining in population size (Dias et al., 2019). This percentage is even higher in Iceland with 16 out of 24, or two-thirds, of seabird species that nest in Iceland in summer on the decline (Vigfúsdóttir, 2021). Because seabirds forage primarily from the near-coastal ocean, changes in ocean conditions related to global climate change could be linked to these declines.

Currently, 28% of all seabird species are listed as threatened globally, making seabirds one of the most threatened groups of birds in the world (Croxall et al., 2012). Other threats to seabird populations include coastal development, loss of breeding grounds, invasive species, pollution, overfishing, and mortality from bycatch.

1.4.1 Skuas

Skuas are predatory seabirds belonging to the monogeneric family Stercorariidae, with all seven species currently classified under the genus *Stercorarius* (Carlos, 2016). Skuas were formerly placed in the Laridae family (Olsen, 2010). Molecular evidence now suggests that they are more closely related to Alcidae (Kuhl et al., 2021). Of the seven species, four are native to the northern hemisphere, while the other three are found in the southern hemisphere.

Family Stercorariidae

Genus *Stercorarius*

1. Great skua, *Stercorarius skua*
2. Chilean skua, *Stercorarius chilensis*
3. South Polar skua, *Stercorarius maccormicki*
4. Brown skua, *Stercorarius antarctica*
5. Arctic skua, *Stercorarius parasiticus*
6. Long-tailed skua, *Stercorarius longicaudus*
7. Pomarine skua, *Stercorarius pomarinus*

The great skua (*Stercorarius skua*) and the Arctic skua (*Stercorarius parasiticus*, American English: parasitic jaeger) are the most common skua species in Iceland, although the long-tailed skua (*Stercorarius longicaudus*) and pomarine skua (*Stercorarius pomarinus*) are regular visitors as well during spring and autumn. Nesting among long-tailed skuas has been recorded since 2003 (Hilmarsson & Yates, 2000).

1.4.2 Great skua

The great skua is endemic to the northeast Atlantic. Great skuas generally breed in sparse colonies or solitary pairs in lowlands on North Atlantic islands (Andersson & Götmark, 1980;

Olsen, 2010). Great skuas are known for their territoriality and aggressively defend their nesting sites from intruders (Furness, 1987).

Great skuas are opportunistic feeders, feeding on virtually all available food. In the Faroe Islands, the diet of great skuas has been noted to include fish, seabirds including kittiwakes, fulmars, and puffins, as well as terrestrial birds and mammals (Hammer et al., 2016). Previous studies suggest that great skuas are often associated with discarded waste from trawlers (Camphuysen & Van der Meer, 2005; Veen et al., 2003). The diminishing fish stocks and enhanced utilization of the catch onboard the fishing vessels have reduced food availability and forced great skuas to turn to alternative prey (Mitchell et al., 2004).

The wintering grounds of those nesting in Iceland were determined with geolocation data-loggers from 11 birds that nested at the Breiðamerkurjökull forefield in 2008. Five of those wintered close to Newfoundland and south of Greenland, two wintered northwest of Africa, two wintered in the Bay of Biscay, and two used both the east and west Atlantic Ocean (Magnúsdóttir et al., 2012).

In surveys during 1984-1985, great skua colonies were found spread throughout S and SE Iceland coastal areas, with additional colonies in Héraðssandur and Öxarfjörður in NE Iceland. At that time the primary breeding grounds for great skua in Iceland was at open glacial plains in the SE, the largest being at the Breiðamerkurjökull forefield, with an estimated 1390-1610 breeding pairs, making it the third largest documented breeding ground of great skua in the world (Lund-Hansen & Lange, 1991).

The most recent population estimate of great skuas, conducted in 2004, determined 16,000 breeding pairs globally (Mitchell et al., 2004). Recent population censuses in S and SE Iceland have documented a collapse in the population in the area (Skarphéðinsson, 2014; Stefánsson, 2014; Jóhannesdóttir & Hermannsdóttir, 2019). Until the 1980s the great skua population had continuously increased, mainly as a result of protection after heavy persecution in the 19th century. The decline thereafter is associated with the decrease in the sandeel population and changes in the commercial fishing industry (Olsen, 2010). Due to this rapid decline, the species' local status was changed from Least Concern (LC) to Critically Endangered (CE) for the first time in Autumn 2018. The evaluation for species red lists in Iceland is conducted by the Icelandic Institute of Natural History, according to the criteria established by the International Union for Conservation of Nature (IUCN) (personal communication, Kristinn Haukur).

1.4.3 Arctic skua

The Arctic skua is the most widely distributed skua species, nesting in Arctic and subarctic areas (Olsen, 2010; Wiley & Lee, 1999). They are mainly a coastal species, but they can also be found in areas such as tundra and barren islands (Svensson et al., 2010).

The European breeding population of Arctic skuas is currently estimated to be 27,100-41,500 pairs, with the largest populations found in Norway, Russia, and Iceland. The breeding population is believed to have declined by 58% between 1987 and 2021 (BirdLife International, 2021). Meanwhile, a study conducted in Scotland revealed a 81% decline since 1992 (Perkins et al., 2018). The Arctic skua is classified as Endangered within the European Union (BirdLife International, 2021).

Arctic skuas are opportunistic feeders during the breeding season, taking small mammals, eggs, invertebrates, other birds, and plant berries. However, arctic skuas in the North Atlantic feed mostly on sandeels by kleptoparasitising other seabirds. Therefore, the population faced a decline in the 1980s during the sandeel collapse (Olsen, 2010). A four-year study on the west coast of Scotland revealed that a population of Arctic skuas was halved, associated with predation pressure from a population of great skuas (Jones et al., 2008). It is currently unknown if Arctic skuas in Iceland face similar pressure.

Arctic skuas make long migrations to southern oceans. The wintering grounds of Arctic skuas in Iceland range from southern South America eastwards to southern South Africa (Hallgrímsson et al., 2015).

1.5 Nutrient transport

Nutrients are critical to any ecosystem, and thus it is necessary to understand the mechanisms of their flow and transport. Mechanisms of nutrient transport in the environment can be classified as either passive or active. The main 'passive' nutrient transport vector is water, such as runoff into oceans via rivers, streams, or precipitation. Meanwhile, 'active' nutrient transport is that which goes against this natural flow, such as biotic vectors (McInturf et al., 2019).

1.5.1 Active nutrient transport via animals

Ecosystems are often studied as being self-contained, such as marine versus terrestrial ecosystems, but mobile species can traverse these boundaries, which gives rise to the concept of the 'meta-ecosystem,' considering multiple ecosystems as a single functioning unit (Loreau et al., 2003). Animals play a significant role in the transport of nutrients across these boundaries, such as when they feed in one area and transfer the resulting nutrients and energy elsewhere through excretion, reproduction, being predated, or dying otherwise (Moss, 2017). Migratory animals regularly transport nutrients and energy between ecosystems and can thus support less productive ecosystems (Polis et al., 1997). Species responsible for such transport can therefore be termed 'ecosystem engineers' as they can significantly modify a habitat (Copp et al., 2010; Polis et al., 2004).

Even within an ecosystem, animal-directed nutrient transfer can have large impacts. Studies have revealed the significant role marine mammals play in distributing nutrients vertically in the ocean (Doughty et al., 2016), for example, how whales drive nutrient cycling by feeding in the deeper layers of the oceans and transporting those nutrients via defecation at the surface (Roman & McCarthy, 2010).

1.5.2 Nutrient transfer between marine and terrestrial ecosystems

While nutrients generally flow from terrestrial to marine habitats via geophysical processes, active nutrient transfer in the other direction has been observed via seabirds, anadromous fish, and marine mammals (González-Bergonzoni et al., 2017; De La Peña-Lastra, 2021). Various studies have revealed impacts on vegetation via deposits of marine-derived nutrients (MDN) at nursing and resting sites of pinnipeds, such as Galapagos sea lions (*Zalophus wollebaeki*) (Fariña et al., 2003) and gray seals on Surtsey (Magnússon et al., 2020). Further, when Pacific salmon species annually travel up rivers for spawning, they accumulate more than 95% of their body mass and nutrients as they grow in the ocean (Groot & Margolis, 1991). When they return to their natal stream to spawn, their MDN are transferred to freshwater, coastal, and terrestrial ecosystems by water movement and by predators, such as otters, bears, and eagles (Reimchen et al, 2003).

Seabirds act as an important link between land and ocean, as they nest on land and forage at sea. Bioenergetic models estimate an annual transport of marine-derived N via seabirds to be approximately 1,100 Gg worldwide (Riddick et al., 2012). The rate of N cycling declined where rats reduced seabird abundance (Wardle et al., 2009). In general, avian nutrient transfer can significantly support plant communities at an early stage of succession and the quality of the land they lay on (Sekercioglu, 2006; Merkel & Barry, 2008; Meltofte et al., 2013).

In a study focusing on little auks (*Alle alle*) in Greenland, it was estimated that MDN fuels more than 85% of aquatic and terrestrial biomass in systems influenced by birds (González-Bergonzoni et al., 2017). It is apparent that this flux of nutrients has decreased in correlation with the decline of monitored seabird populations (Paleczny et al., 2015).

Nutrient transport by animals has been documented to speed up plant succession and soil development (Bockheim & Haus, 2014). Studies conducted on Surtsey show that gulls which nest on the island are the main source of N for the island and their nutrient transfer is a major driver of plant succession and soil formation (Magnússon et al., 2009; Leblans et al., 2017).

2 Study site

Breiðamerkurjökull is the fourth largest outlet glacier from Vatnajökull, SE-Iceland (N64°0 2’-05’, W16°13’-19’) (Björnsson, 1996). Breiðamerkurjökull reached its maximum extent around 1890, when it was less than 250 meters from the coastline (Watts, 1962). This development is historically documented in medieval annals, country records, journals, and geographical maps (Henderson, 1819; Sigurðsson & Cahill, 1978; Thienemann, 1824). Between the last decade of the 19th century and 1930 the glacier slowly retreated from its prominent end moraines (Björnsson et al., 2001). Since that time and up to the present day, Breiðamerkurjökull has only continued its retreat, exposing a land area (forefield) of approximately 115 km^2 by retreating 4-7 km from 1890-2010 (Guðmundsson et al., 2017). The area in front of the glacier has been subject to major glacially induced changes, which have been well documented (Guðmundsson, 2014).

The forefield material is comprised mainly of volcanic basalt and hyaloclastite (Jóhannesson et al., 1998) as well as tephra from subglacial eruptions in Grímsvötn, Katla, Bárðarbunga, and Öræfajökull (Óladóttir et al., 2011). The terminal moraines on the Breiðamerkurjökull forefield mark the maximum (1890) extent of the outlet glacier. Although Breiðamerkurjökull has been steadily retreating since then, the retreat has been interrupted with static periods and/or readvance resulting in large glacial moraine formations.

The climate at the Breiðamerkurjökull forefield is highly oceanic, with cool summers but mild winters (Björnsson & Pálsson, 2008), and the area is relatively isolated from seed sources, making plant colonization in the moraines more challenging. The closest birch forest (the only native plant in Iceland to form continuous forests) is located at Kvísker, ~11 km distance to the west (Vilmundardóttir et al., 2015).

Table 1. Information on the study site at the Breiðamerkurjökull forefield.

Study site	
GPS points	N64°02’-05’, W16°13’-19’
Area	~ 18,000,000 Square Meters
Elevation range	15−70 m a.s.l.
Mean annual temperature 2017	
Kvísker	6.15°C
Höfn í Hornafirði	5.69°C

Both great skuas and Arctic skuas nest at the Breiðamerkurjökull forefield (Skarphéðinsson et al., 2016). The forefield is part of the Breiðamerkursandur-Fagurhólsmýri nesting ground, one of the largest great skua colonies in Iceland (Lund-Hansen & Lange, 1991), although recent population censuses have documented a collapse in the population at the area (Jóhannesdóttir & Hermannsdóttir, 2019).

Previous studies within the Breiðamerkurjökull forefield have revealed point-centered influence of birds on vegetation development (Vilmundardóttir et al., 2015) and strong effects of avifauna presence on soil chemical properties (Turner-Meservy et al., 2022). Skuas nest in sparse colonies (Olsen, 2010) and their site fidelity to roosting, scouting, and nesting spots have led to the formation of bird hummocks. The roosting and scouting spots could be shared with other species which also defend territories. These bird hummocks tend to be on elevated ground and form distinct grass-covered landscape features.

Various other bird species nest at the Breiðamerkurjökull forefield. Currently the most common bird species in the area is the barnacle goose (*Branta leucopsis*). Iceland has been an important staging ground for the species during its migration between wintering grounds in Great Britain and breeding grounds in Northeast Greenland (Percival & Percival, 1997). Barnacle geese were first documented to nest in southeast Iceland in 1988 (Þorsteinsson, 1989). The number of breeding pairs were stable, between 5-6, the next few years. However, the population has rapidly increased in size and distribution (Guðmundsson et al., 2018; Magnússon et al., 2002; Stefánsson et al., 2015). The number of breeding pairs was estimated at ~120 in 2009 in all of Iceland (Skarphéðinsson & Auhage, 2012) and in 2020 there were 1491 breeding pairs on Skúmey, a newly revealed island in the glacial lagoon Breiðamerkurlón, alone (Brynjólfsson, n.d.). Studies conducted on vegetation on Skúmey have revealed effects of the dense breeding population of barnacle geese on primary succession (Óskarsdóttir & Þórisson, 2018).

The Breiðamerkurjökull forefield has been used for a long time for sheep grazing and the area west of Breiðamerkurlón continuous to be grazed by considerable amount. Currently, sheep from the farms Hof and Hnappavöllum graze at the area during the summer, previously also from Kvískerjum (personal communication, Bjarni Diðrik Sigurðsson).

The Breiðamerkurjökull forefield has been listed on the Náttúruminjaskrá, the list of Icelandic protected areas, since 1975. The area is also declared an Important Bird Area by BirdLife International. In the summer of 2017, along with Jökulsárlón, the forefield became part of the Vatnajökull National Park (Guðmundsson et al., 2018). One of the main motives to include the site in the national park was the presence of important breeding grounds for great skuas, barnacle geese, and Arctic terns (*Sterna paradisaea*) (Vatnajökulsþjóðgarður, 2020).

3 Bird census

Bird census, i.e. assessing the number of great and Arctic skua, was performed during 11-13 June 2018 during the nesting period for the two species (Lund-Hansen & Lange, 1991; Stefánsson, 2014). The weather was mild and visibility good for bird spotting. Wind speed was measured between 1-6m/s, and temperature 9-12°C at the weather stations Kvísker and Höfn í Hornafirði (Veðurstofa Íslands, 2018). The sky was mostly clear and there was no precipitation during the field work.

The method used for estimating the number of breeding pairs was Apparently Occupied Territories (AOTs), as recommended for the two skua species in *Seabird monitoring handbook of Britain and Ireland* (Walsh et al., 1995). AOT was scored for any of the following indicators: "a) nest, eggs, or chicks; b) apparently incubating or brooding adults; c) adults distracting or alarm-calling; d) pair or single bird in potential breeding habitat, apparently attached to area. The following were not scored as AOTs: e) bird(s) flying past, en route to somewhere else; f) feeding individual(s); g) single bird (or pair) flushed from an area; h) three or more skuas of same species regularly together but not showing any signs of territoriality." The same method was used for estimating numbers of breeding pairs for other species in the area.

The study site was divided into 15 linear transects. GPS coordinates for each end of the transects were found using Google Maps. The transects varied in length between 0.8 – 5 km. All transects were 200 meters wide, and birds were only recorded if they were 100 meters or less from the transect's middle line. Although special interest was put into finding AOTs, locations of non-breeding birds were also mapped to visualize the distribution of the species in the area. To prevent counting the same bird twice, there was a 100 meter gap between transects. In order to capture the time gradient of the glacial retreat, the transects lay across the glacial moraines, from South to North. Due to the glacial river which runs between 1982 and 1960 moraines, the transects were split into two sections, North and South of the river. Unfortunately, three transects North of the river were inaccessible due to high water volume in the glacial river (Figure 1).

A Garmin 60CSx handheld GPS unit was used to walk in a straight line between transect points and mark GPS units of all recorded AOTs. While walking between the two points in the transect, all birds were counted and behavior recorded. For each sighting, the distance of the bird from the transect was measured using a Nikon Aculon AL11 laser rangefinder.

Common names of bird species observed were recorded in accordance with the BirdLife International (2021).

4 Objectives

The main objective of this study was to determine how nutrient transfer by great skuas and Arctic skuas affects primary succession and soil development at the Breiðamerkurjökull forefield, SE-Iceland. In addition, we examined the timescale of the effects by accounting for differences in the hummocks' ages.

The effects of the seabirds were evaluated by (i) mapping the distribution of skuas and their nest and (ii) measuring vegetation cover and soil properties at and around the bird hummo

5 Results and discussion

5.1 Bird Cencus

The Arctic skua and the great skua were found to be the most common seabirds in the study area, both regarding total number of encounters and of breeding pairs. The two skua species were also second and third most encountered species in total and second and third most common birds in total (Table 2, Figure 1). In total, 59 Arctic skuas and 9 AOTs were recorded, with the roughly calculated nesting density in the area being 0.94 AOTs/km^2. Meanwhile, 40 great skuas and 5 AOTs were recorded, accounting for 0.47 AOTs/km^2 (Figure 2). Birds of both skua species were seen continuously standing or resting at bird hummocks around the site (Figure 3, 4). A presence on bird hummocks was clearly not bound to birds displaying AOT behavior.

Table 2. Total number and number of breeding pairs of bird and mammal species encountered during the bird counting at the Breiðamerkurjökull forefield, SE-Iceland.

Scientific name	Common name	Encounters	Breeding Pairs
Birds			
Anas platyrhynchos	Mallard	1	0
Anser anser	Greylag goose	2	0
Anthus pratensis	Meadow pipit	1	0
Branta leucopsis	Barnacle goose	136	21
Charadrius hiaticula	Common ringed plover	15	7
Corvus corax	Common raven	1	0
Cygnus cygnus	Whooper swan	7	0
Gavia stellata	Red-throated diver	5	3
Lagopus muta	Rock ptarmigan	3	0
Larus fuscus	Lesser black-backed gull	2	0
Numenius phaeopus	Whimbrel	21	19
Plectrophenax nivalis	Snow bunting	6	4
Pluvialis apricaria	Golden plover	17	15
Rissa tridactyla	Black-legged kittiwake	10	0
Somateria mollissima	Common eider	4	0
Stercorarius parasiticus	Arctic skua	59	9
Stercorarius skua	Great skua	40	5
Sterna paradisaea	Arctic tern	23	6
Mammals			
Vulpes lagopus	Arctic fox	2	-
Mustela vison	American mink	1	-

The breeding grounds for the two skua species were found to be divided on each side of the water system which separated the transects, just north of the 1960 moraine (Figure 1, 5).

A group of 12 great skuas was seen on one of the lakes north of 1960 moraine. The birds in the group did not show any signs of AOTs, thus likely to be non-breeding birds. The group is indicated by a diamond in Figure 1 (Figure 6).

At least 3 empty nests (all south of previously mentioned water system), possibly from skuas, were found with no sign of current usage and no birds defending the area. That together with a relatively high number of birds which did not show behavior suggest reduced breeding numbers compared with recent years. This could also be a result of nest predation by for example fox and mink, both of these predators were sighted during the bird census.

The separation of breeding grounds between the two species is clear, with only one Arctic skua AOT south of the water system and no great skua AOTs north of the water system. It is unclear if the separation is due to different feeding approaches, such as if the Arctic skua is gathering a lower proportion of its prey at sea during the hatching time compared to the great skua, or if the great skua is more aggressive and therefore able to claim breeding grounds closer to the sea. If the current distribution represents the distribution of the two skua species in the past, it could be interpreted that the initial formation of bird hummocks is more driven by Arctic skuas and later, long after the hummocks have formed, great skuas further extending the effects of the birds.

The most commonly sighted species was the barnacle goose, with 136 sightings. Sightings of barnacle geese were mostly recorded on the transects closest to the Breiðamerkurlón glacial lagoon (Figure 7). Fast rising numbers of the species have been shown to have noticeable effects on the vegetation around their most dense nesting grounds in the Breiðamerkurjökull forefield, Skúmey, both by providing nutrients to the area via excretion and limiting growth of certain plant types by grazing (Guðmundsson et.al, 2018). However, the barnacle goose was not of significant interest to this study, as they do not forage at sea and are unlikely to spend significant time on the bird hummocks, as they are not territorial and were not seen occupying the hummocks during this study.

Although the aim with this study was to access the impact of active nutrient transfer from sea to land via seabirds, it is also likely that other birds recorded contribute to the formation of the bird hummocks in the area. In general, birds which display territorial behavior on the ground can cause point centered effects on their surroundings. Of the species listed in table 2, whimbrel (*Numenius phaeopus*), rock ptarmigan (*Lagopus muta*) and golden plover (*Pluvialis apricaria*) could be mentioned. All of these species were recorded at bird hummock during the counting. AOTs of both whimbrels and golden plovers were more numerous than AOTs of the two skua species, although total numbers of the skuas were considerably higher. The presence of these birds likely affects the results of soil and vegetation properties on the hummocks, and the extent of that effect could be examined in further research in the area.

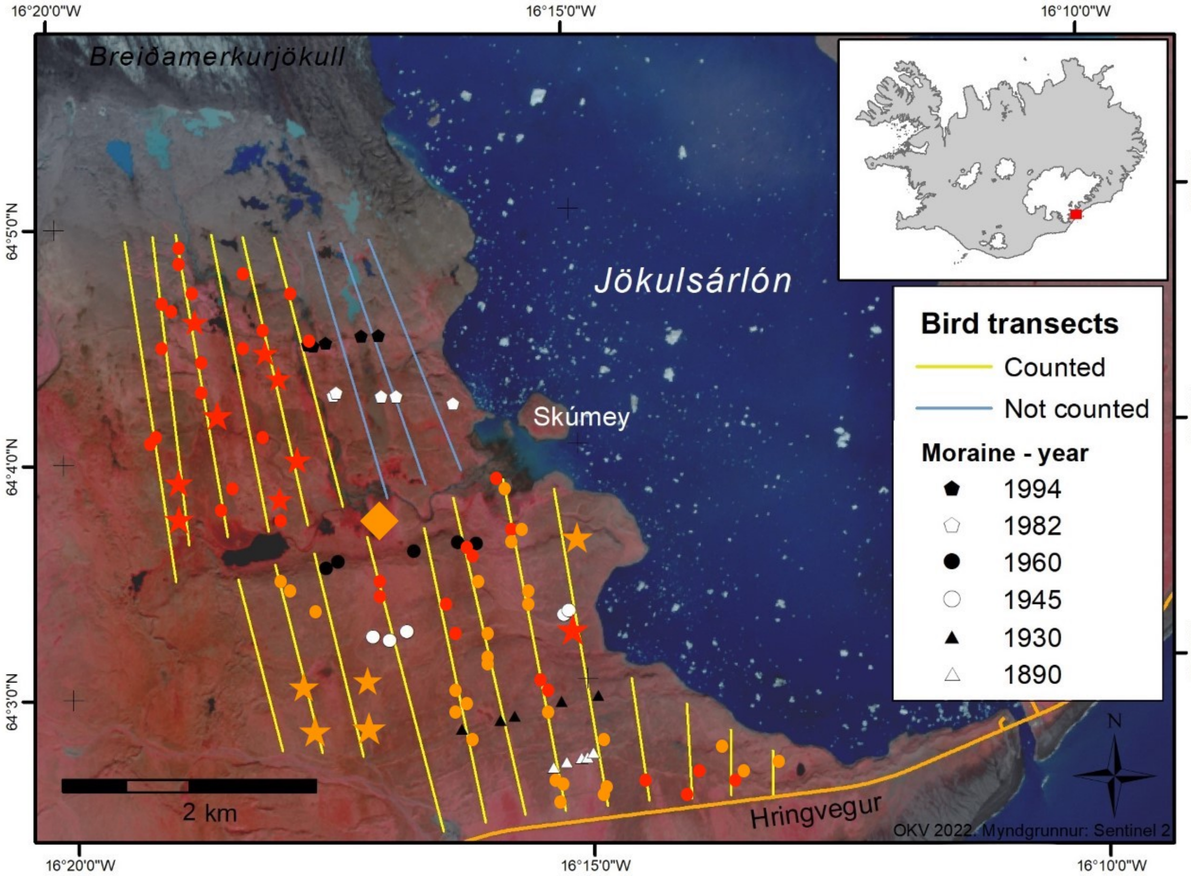

Figure 1. Distribution of great skuas (orange) and Arctic skuas (red) within the Breiðamerkurjökull forefield in SE-Iceland. AOTs for each of the species are indicated with a star. The diamond indicates a sighting of a group of 12 great skuas. Lines mark the linear transects, yellow were counted and blue were not counted.

Figure 2. Great skua nest on the 1890 moraine. A. Two great skua eggs, B. Territorial behavior by great skua. Photos SS, June 2018.

Figure 3. Great skuas occupying bird hummocks. A. Pair of great skuas south of 1890 moraine, B. Great skua resting on the 1890 moraine. Photos SS, June 2018.

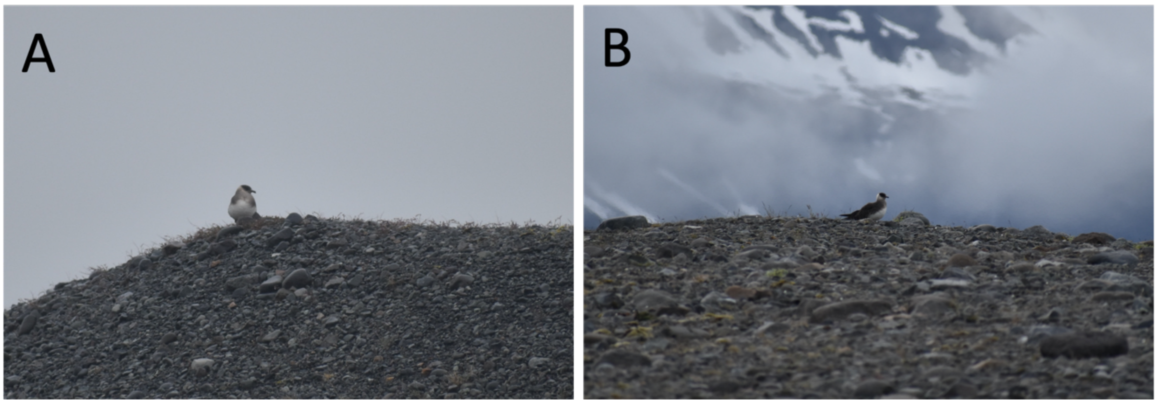

Figure 4. Arctic skuas scouting on grassy hummocks. A. Arctic skua on the 1982 moraine. B. Arctic skua on the 1994 moraine. Photos SS, June 2018.

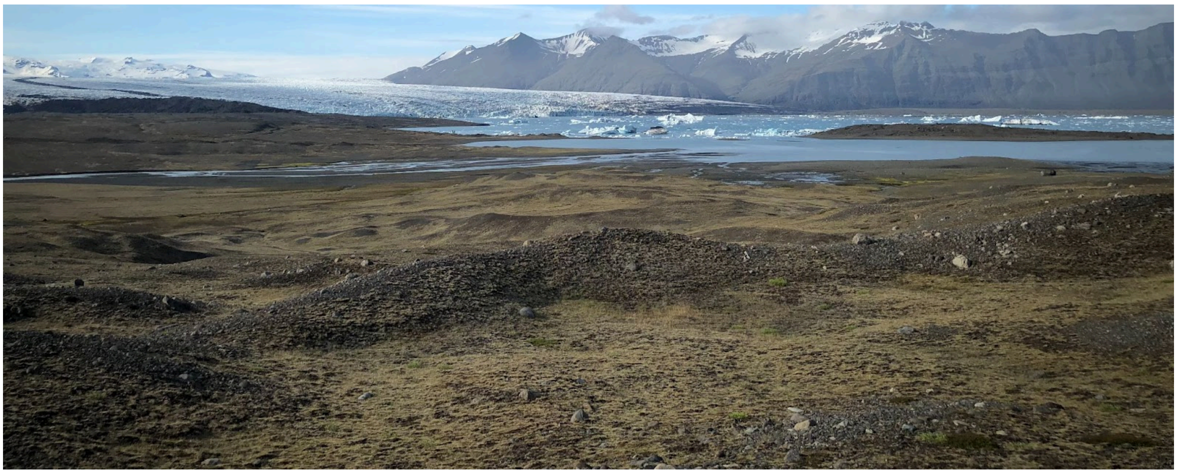

Figure 5. Looking over the water system which separated the majority of the skua species nesting grounds, the island Skúmey and the Breiðamerkurlón glacial lagoon. Picture taken on the 1960 moraine. Photo SS, June 2018.

Figure 6. Part of a group of 12 non-breeding great skuas. Photo SS, June 2018.

Figure 7. 17 Barnacle geese (+1 chick) and one eider duck at Breiðamerkurlón. Photo SS, June 2018.

5.2 Soil and Vegetation Inventory

The results and discussion regarding soil and vegetation analysis are found in a scientific paper which was published independently from the other results. The paper begins on page 29 and results begin on page 33.

6 Conclusions

The most common bird species was found to be the barnacle goose. As this species generally does not use the bird hummocks for scouting, the distribution was not mapped. The most common seabirds at the site were the Arctic skua and the great skua. Of all Arctic skuas, 59 were recorded as unlikely breeders and 9 displayed AOT behavior. Of all great skuas, 40 were recorded as unlikely breeders and 5 with AOT behavior. Both species were recorded to use bird hummocks for scouting and resting. Bird hummocks were occupied both by birds displaying AOTs and by birds that did not. Nesting sites were found to be divided by the water system just north of the 1960 moraine.

The results reveal that within the Breiðamerkurjökull forefield, vegetation and soil properties were significantly impacted by proximity to the hummocks' centers. Coverage of grasses showed the highest estimated relationship with proximity when compared to forbs and total vegetation cover. Furthermore, SOM increased with proximity to the hummocks while soil pH_{H2O} decreased with proximity.

By foraging at sea and nesting on land, seabirds form an essential link between marine and terrestrial ecosystems. In opposition to the natural flow of nutrients from land to sea via passive nutrient vectors, seabirds serve as active vectors, introducing a significant amount of MDN into their nesting sites via excretion. These nutrients alter soil chemistry and pH_{H2O}, providing for increased plant nutrition. This nutrient transport is especially relevant in newly exposed areas, where MDN can serve as the primary nutrient source and therefore contribute to primary succession.

The results of this study enhance our understanding of the interplay between marine and terrestrial ecosystems, which grows more important given the acceleration of glacial retreat and significant declines in seabird populations both worldwide (Dias et al., 2019) and in Iceland (Vigfúsdóttir, 2021). These declines weaken the essential link seabirds provide, and could potentially slow the rate of primary succession in the areas they nest in. As the Breiðamerkurjökull forefield is an area experiencing both primary succession after glacial retreat and significant declines in great skua populations (Jóhannesdóttir & Hermannsdóttir, 2019), it deserves further research in these areas to provide us with insights on how this link might be re-established should it be severed.

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8. 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 km2 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 Meteorological Institute, from the weather station Fagurhólsmýri, mean 1949-2007). Mean annual precipitation is around 3500 mm (Unpublished data from the Icelandic Meteorological 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).

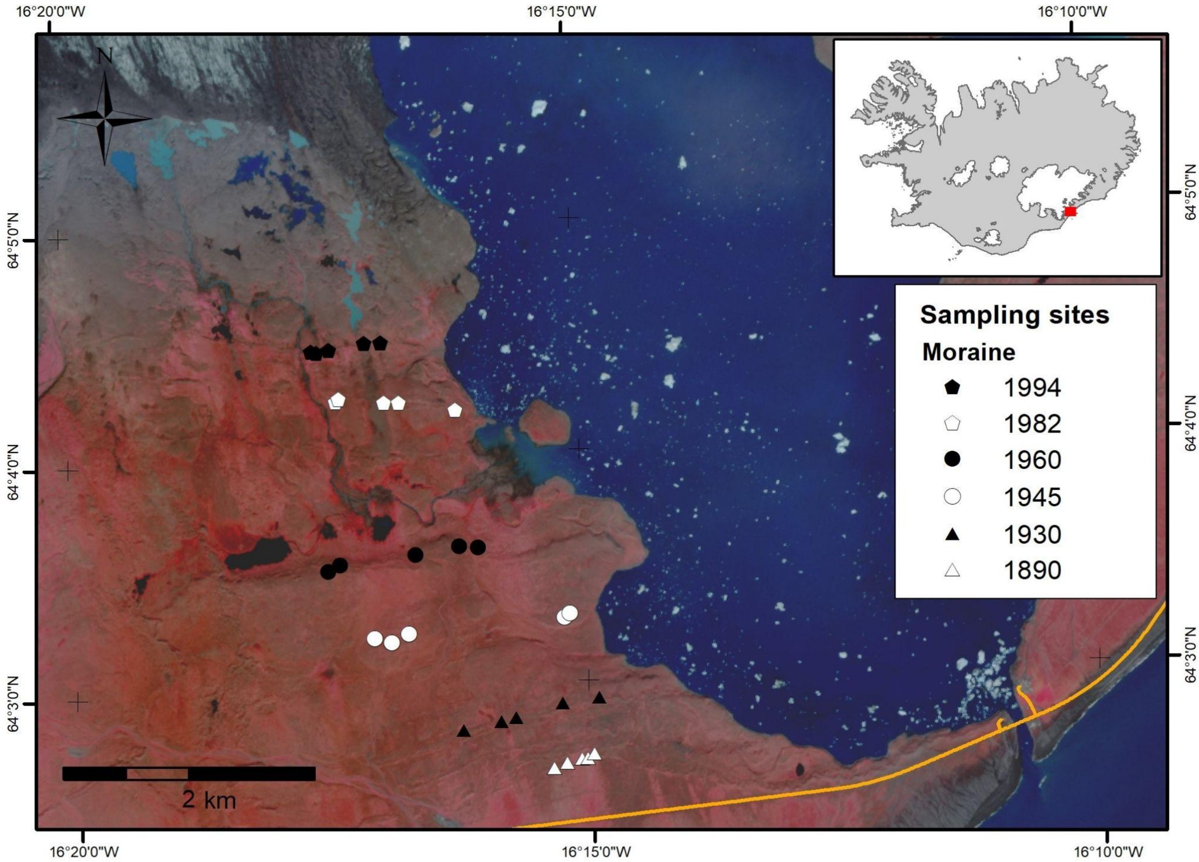

Figure 1. Sampling sites from July 2018 within the glacial fore-field of Breiðamerkurjökull, shown on an infrared Sentinel-2 satellite image from 22 August 2018. The sites are located along the estimated position of the glacier terminus at a given point in time (see e.g. Guðmundsson, 2014 and Guðmundsson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

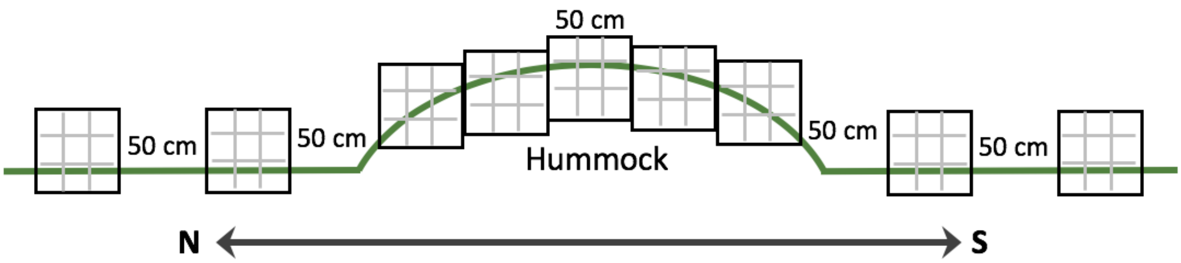

Figure 2. The setup of nine 50 x 50 cm quadrats placed on each bird hummock. One quadrant was placed on the hummock's center while the other eight were lined up to the north and the south up to 3 m distance from the center.

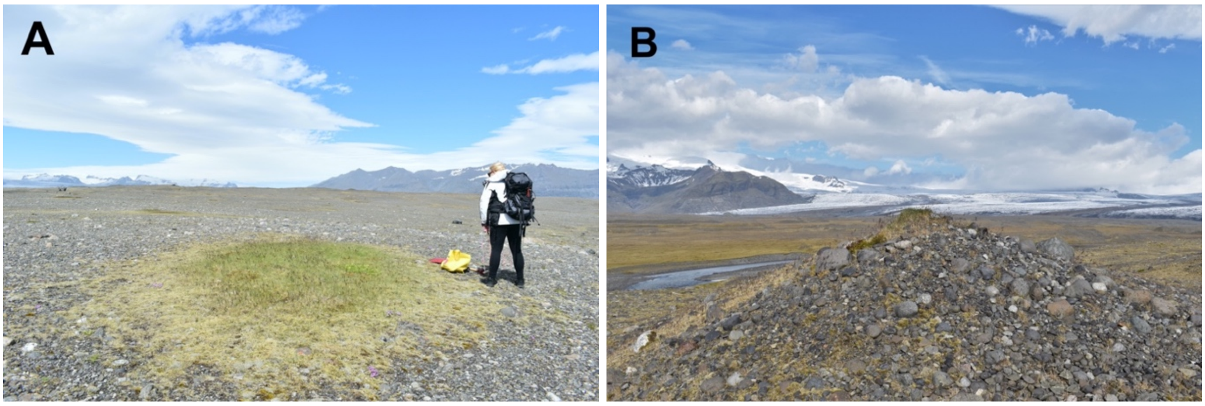

Figure 3. Bird hummocks on moraines of different age within the Breiðamerkurjökull fore-field in SE-Iceland. A. Moraine from the year 1945. B. Moraine from the year 1982. Photos SS, July 2018.

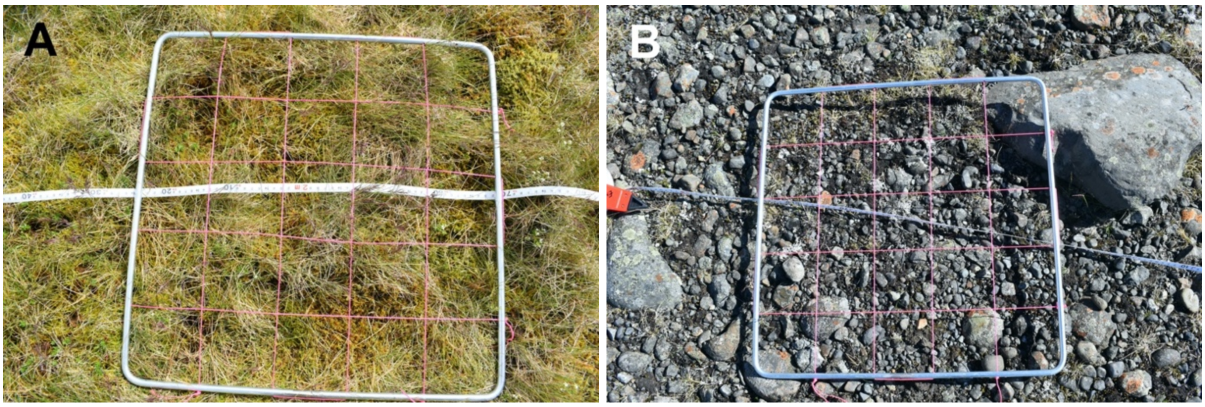

Figure 4. Examples of vegetation quadrats from a sampling site on moraine formed in 1890, within the Breiðamerkurjökull fore-field in SE-Iceland. A. The center of a bird hummock. B. Three meters north of the hummock's center. Photos SS, July 2018.

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 was performed. 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) (Fig. 5).

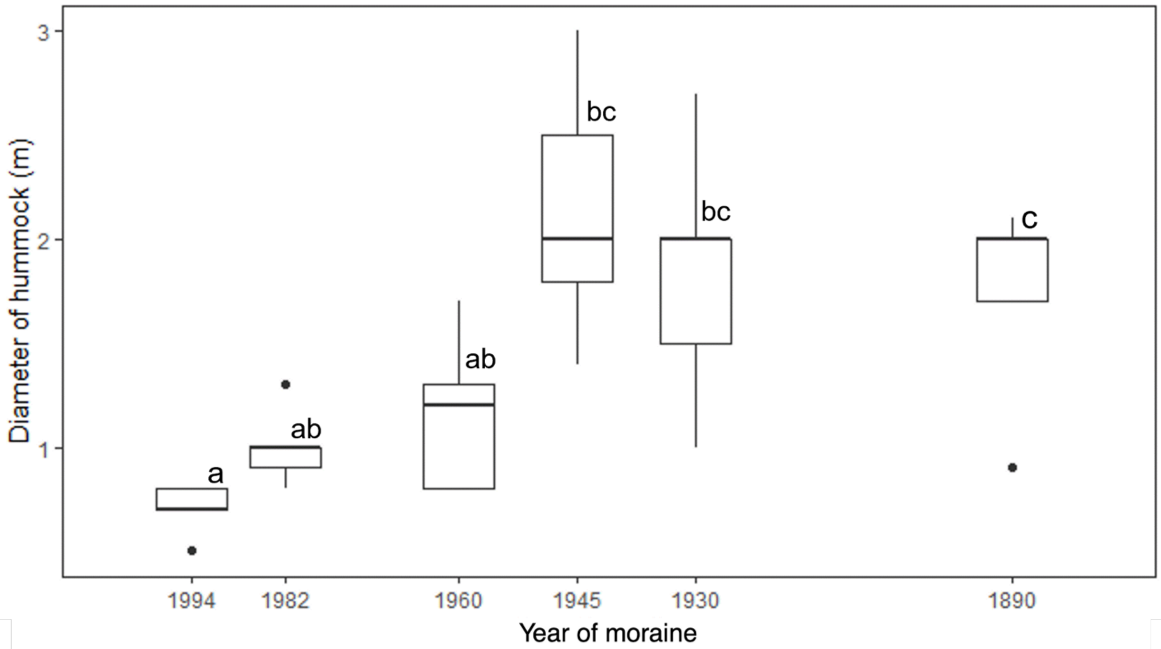

Figure 5. A boxplot comparing the diameter of bird hummocks at different aged moraines within the Breiðamerkurjökull fore-field in SE-Iceland. The letters a, b, and c indicate significant differences between the moraines.

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 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 richardsonii*, *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 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).

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 est 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 Popu-lation**
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

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).

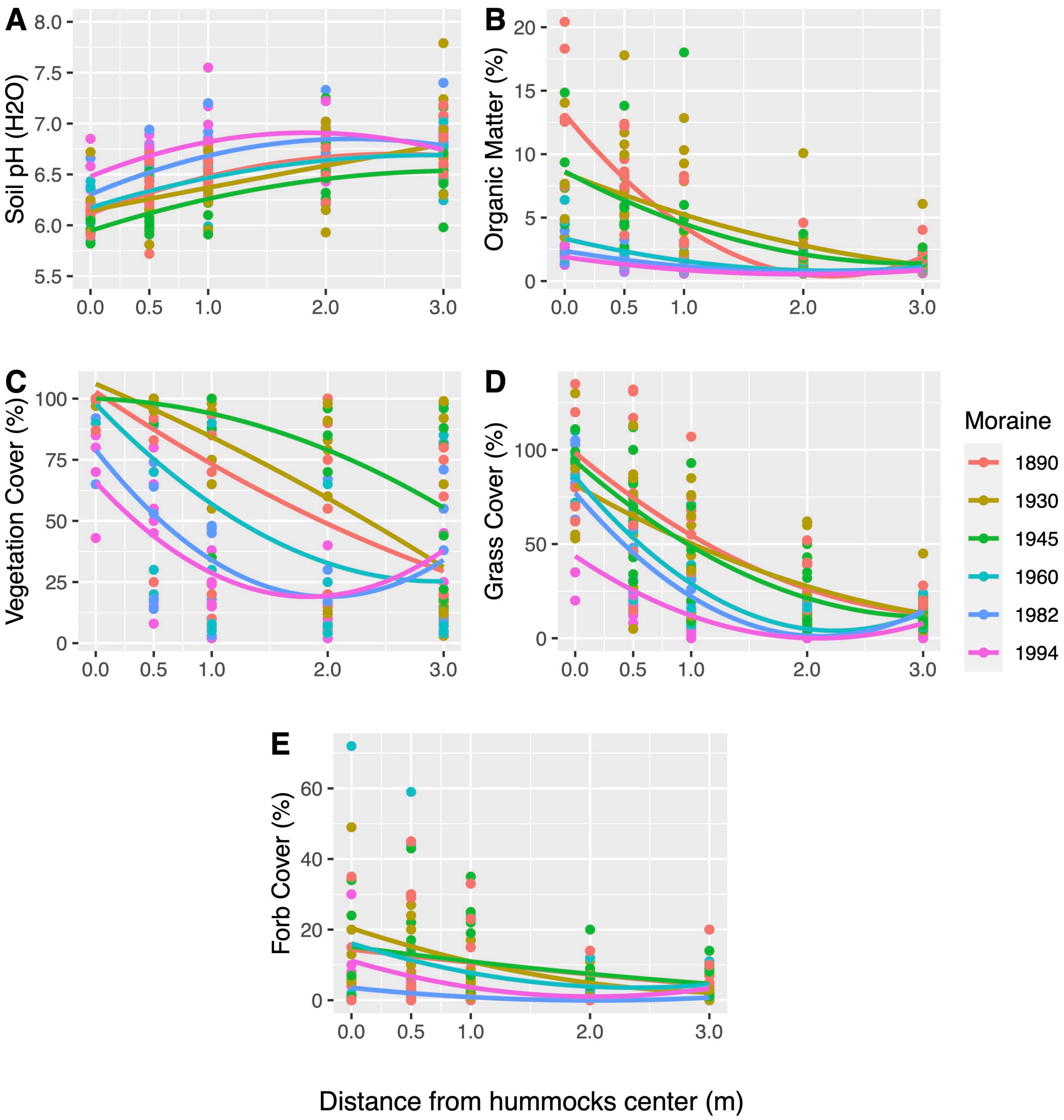

Figure 6. The relationship between measured variables and distance from hummock center at the Breiðamerkurjökull fore-field in SE-Iceland. A) pH_{H2O}, B) percentage of organic matter, C) vegetation cover (%), D) grass cover, and E) forb cover. The lines are quadratic fits.

OM concentration was found to be significantly 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; R2= 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*).

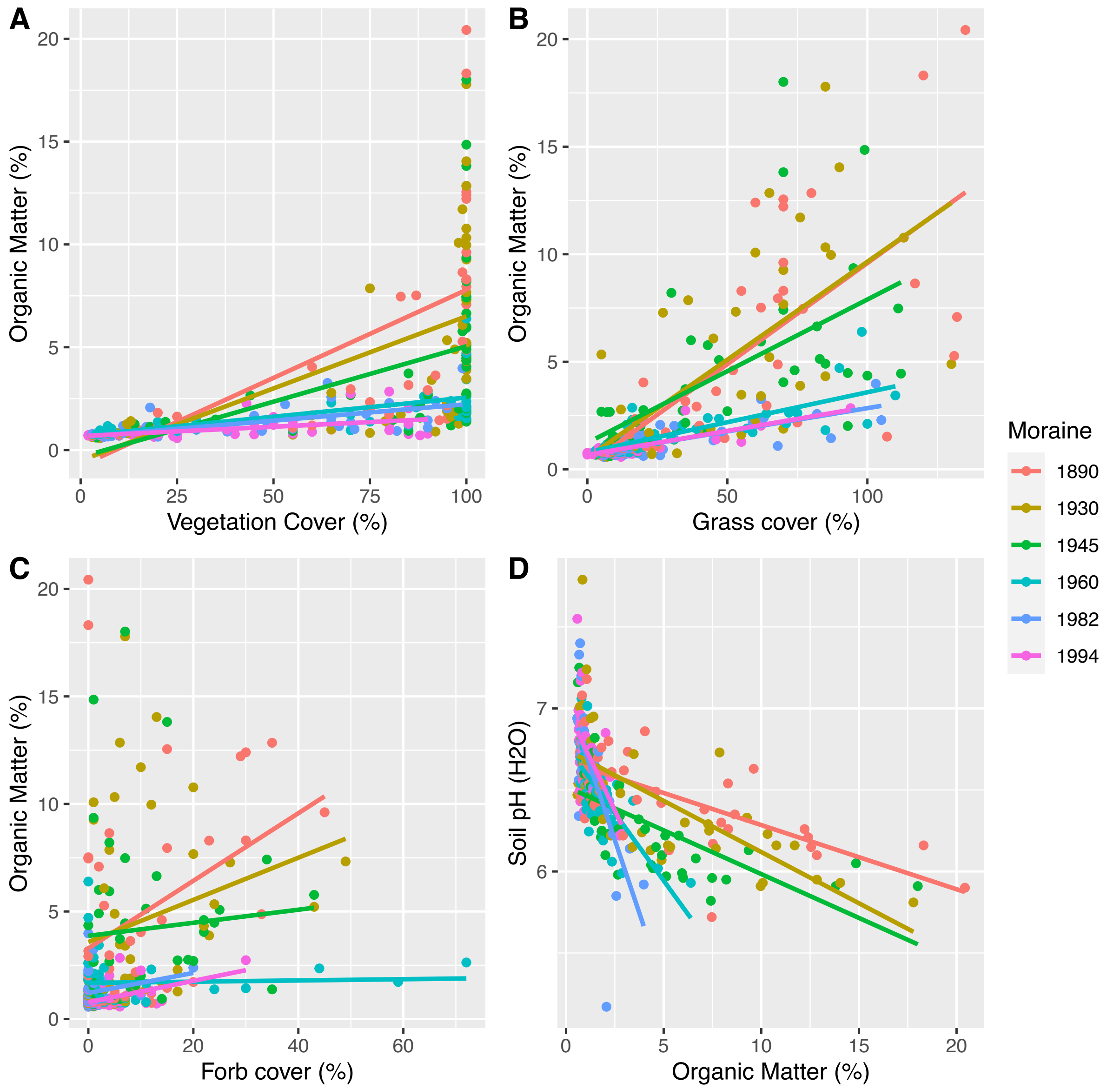

Figure 7. Graphs showing relationships between measured variables and OM concentration within the Breiðamerkurjökull fore-field, SE-Iceland. A) Vegetation cover, B) grass cover, C) forb cover, and D) soil pH_{H2O}. The lines are linear regressions.

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 indicated by the diameter of hummocks, showed to increase significantly with age of the moraines where they were located. However, hummock diameters on the three oldest moraines did not differ significantly from one another (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, 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.

Acknowledgements
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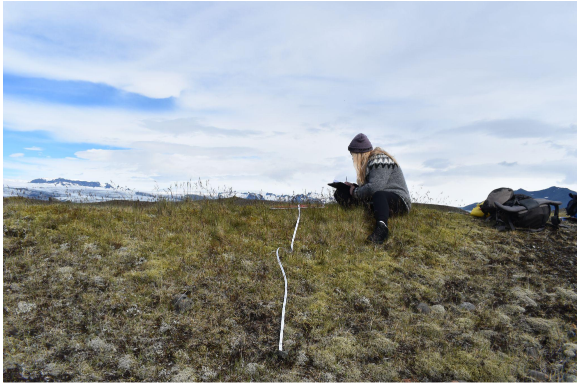
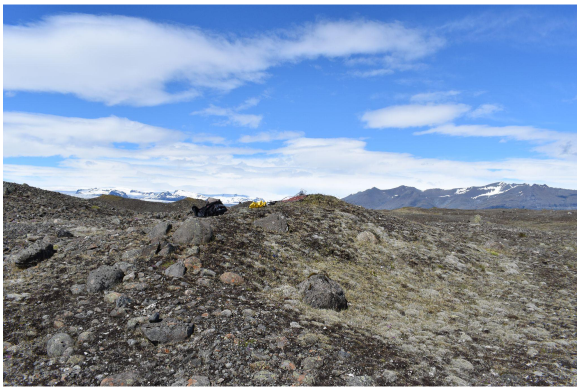
Appendix

Photos of Hummocks on 1890 Glacial Moraine

 1890_1	 1890_2
 1890_3	 1890_4
 1890_5	

Photos of Hummocks on 1930 Glacial Moraine

1930_1

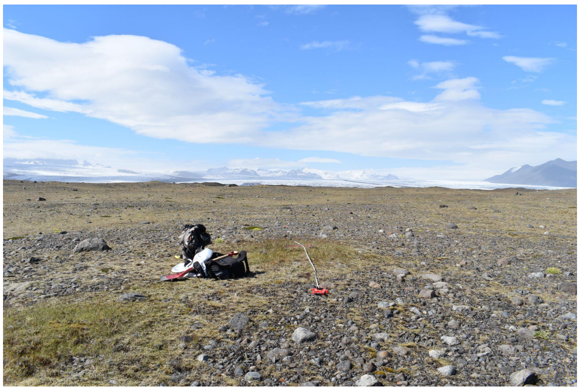
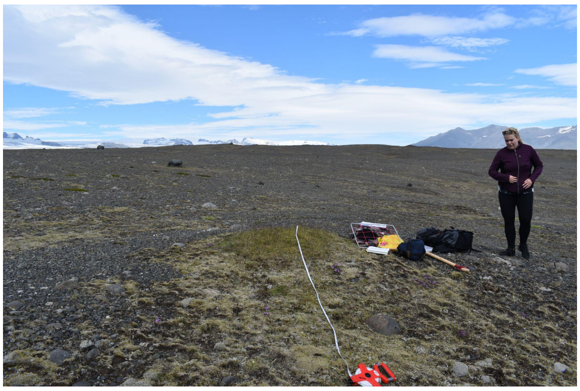
1930_2

1930_3

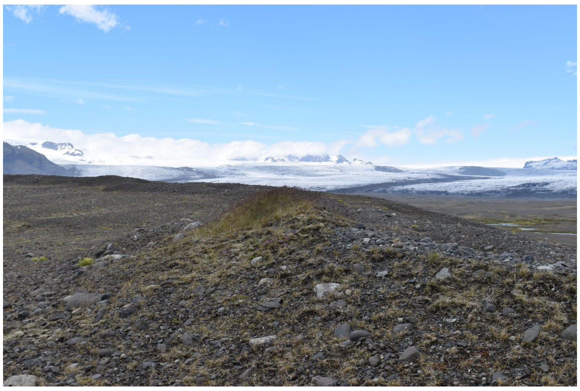
1930_4

30_5

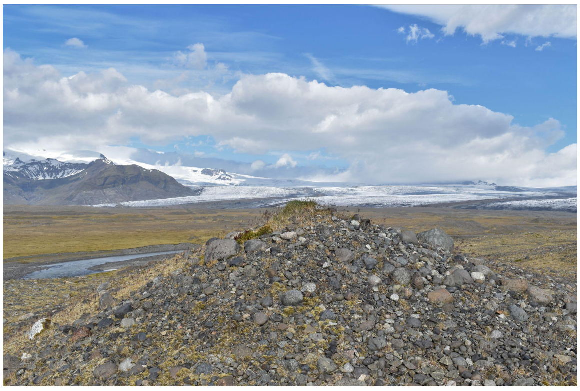
Photos of Hummocks on 1945 Glacial Moraine

 1945_1	 1945_2
 1945_3	 1945_4
 1945_5	

Photos of Hummocks on 1960 Glacial Moraine

 1960_1	 1960_2
 1960_3	 1960_4
 1960_5	

Photos of Hummocks on 1982 Glacial Moraine



1982_1

1982_2

1982_3

1982_4

1982_5

Photos of Hummocks on 1994 Glacial Moraine

1994_1

1994_2

1994_3

1994_4

1994_5