SURTSEY RESEARCH

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Cover page: Bryophytes studied on Elliðaey, which is the third largest island in the Vestmannaeyjar archipelago, after Heimaey and Surtsey. It is ca. 5900 years old and gives a glimpse of how Surtsey will develop into the future. The people are Nils Cronberg and Gróa Valgerdur Ingimundardóttir from Lund University in Sweden.

Photo: Borgthór Magnússon, July 20, 2018.

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Introduction

In the fall of 2022, we publish the 15th volume of *Surtsey Research* which includes nine papers in the fields of terrestrial biology, marine biology, and geology. The papers are written by about 30 authors taking part in research on Surtsey or other related Icelandic environments in the last few years.

Research activity and monitoring on Surtsey has continued annually from the time the island rose from the sea in 1963. A unique record of geological and biological data has been accumulated making Surtsey one of the best monitored volcanoes in the world. The research activity and interest in the island was naturally greatest during the years following the eruption, aswell as funding for establishing new research and facilities on the island.

The Surtsey Research Society, with the support of several research institutions and universities in Iceland, has through the years ensured that the research activities on the island have continued. In recent years it has anything but declined. Young and enthusiastic scientists, the third generation, have taken over and broadened the research taking place on the island. The results of some of their works can be seen in the current and latest volumes of Surtsey Research.

We acknowledge the work of Bjarni D. Sigurðsson, the current editor in chief of Surtsey Research and his team of co-editors, Karl Gunnarsson, Kristján Jónasson Lilja Gunnarsdóttir, Lovísa G. Ásbjörnsdóttir, Olga K. Vilmundardóttir and Tobias Björn Weisenberger. The continuous research expeditions to Surtsey through the years have not the least been made possible by the persistent assistance from the Icelandic Coast Guard, both on sea and in the air.

In 2023 sixty years will have passed from the beginning of the Surtsey eruption. It is of importance to continue research on the island and maintain its conservation and status as a World Heritage Site. Only the first chapters in the Surtsey story have yet been written.

On behalf of the Surtsey Research Society

Borgthór Magnússon
vice-chairman 2009 - 2022

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TERRESTRIAL BIOLOGY

Vascular plant colonisation, distribution and vegetation development on Surtsey during 1965–2015

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ABSTRACT

Since Surtsey was formed in 1963–1967, colonisation of vascular plants has been recorded by locating the first colonists of each species within a 1 ha (100x100 m) quadrat grid system of the island. The abundance of individual vascular plant species was further recorded within the grid in 1996-1997, 2005-2006, and 2014-2015 using a three graded abundance scale from rare to common.

During 1965–2015, a total of 74 vascular plant species were found on Surtsey. The colonisation was considerable between 1965–1979 followed by a stagnation period. After the establishment of a dense seagull colony on the southern part of the island in 1986, colonisation increased greatly and peaked between 1992–1995. The colonisation differed greatly between surface types, being highest on sandy lava and barren lava, relatively low on eolian sand and coastal sediments, and none on palagonite tuff. By classification and ordination six main vegetations types were identified over the period 1996–2015, forming a gradient from scattered, species poor pioneer vegetation to a dense, lush vegetation developed under by high nutrient input from breeding seagulls. Over this period major vegetation changes occurred. Areas with pioneer vegetation have greatly decreased, while areas with Honckenya and gravel flat vegetation, and forb rich grassland have increased. The number of species per ha increased on average from 4.8 to 7.2 and 10.4 in the years 1996-1997, 2005-2006, 2014-2015 respectively. Despite the great influence of seabirds within their breeding colony, most of the island still has sparse vegetation cover. The colonising species differed greatly in their rate of dispersal. Species with the greatest rate were *Honckenya peploides*, *Poa annua* and *Silene uniflora*, followed by *Sagina procumbens, Puccinellia coarctata, Cerastium fontanum, Arabidopsis petraea, Leymus arenarius* and *Rumex acetosella*. They are either pioneers and/or ruderals and are common on the mainland of Iceland, where they grow in sparsely covered, rocky or sandy areas or on land that has been disturbed.

INTRODUCTION

Surtsey was formed in a submarine eruption in 1963–1967 and became the westernmost island of the Westman Islands archipelago and the southernmost island of Iceland. The island was considered unique and therefore it was of great interest to follow geological and geomorphological changes of the island and the colonisation of life and primary succession on the new land (Norrman J.O. 1970, Jakobsson et al. 2000, Baldursson & Ingadóttir 2007, Romagnoli & Jakobsson 2015). Therefore, in 1965, Surtsey was protected by law in order to minimize the effect of human activities (Baldursson & Ingadóttir 2007). Various types of research have been performed on Surtsey and in 2008 the island was accepted onto the UNESCO World Heritage List due to its unique nature and the research activities taking place there (Hermannsson 2009).

Colonisation of plants and animals has been intensively studied on Surtsey ever since the island was formed. The first organisms to establish on the island were probably bacteria and fungi (Schwabe 1970). Vascular plants were also early colonisers

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with the first individuals found in 1965 (Fridriksson 1966). During the first two decades colonisation and succession was characterised by coastal plants as the species *Honckenya peploides* and *Leymus arenarius*[1] were forming a sparse vegetation in sandy areas (Fridriksson 1992, Magnússon et al. 2009). Mosses were first observed in 1967 and lichens in 1970 (Jóhannsson 1968, Kristinsson 1972). These two groups have formed continuous cover in a few spots on the island. However, vascular plants have been of far greater significance in vegetation development on the island (Kristinsson & Heiðmarsson 2009, Ingimundardottir et al. 2014, Magnússon et al. 2014.

Colonisation by invertebrates and birds has been studied on Surtsey (Ólafsson & Ingimarsdottir 2009, Petersen 2009). The first records of invertebrates were in 1964 (Friðriksson 1964) and the first birds started breeding in 1970 (Petersen 2009).

From 1990 vegetation succession and soil development has been investigated in permanent plots distributed in different habitats on the island (Magnússon & Magnússon 2000, Magnússon et al. 2009, 2014). Subsequently, these plots have also been used for studies of invertebrate fauna, ecosystem functions and density of seabird nests. (Magnússon et al. 2009, Ólafsson & Ingimarsdóttir 2009, Sigurdsson 2009, Sigurdsson & Magnússon 2010, Leblans et al. 2014).

Significant changes have taken place in the vegetation of Surtsey with time, largely due to a breeding colony of seagulls that started forming in 1986 on the southern lava fields of the island. The colony remained spatially well confined during the first years but has since expanded in area (Magnússon et al. 2014). After 1986 the colonisation by new plant species increased significantly on the island (Magnússon et al. 2014). Comparison of plots inside and outside the seagull colony indicate a great influence of the birds on plant succession and soil development. They show an increase in vegetation cover, ecosystem respiration, soil carbon and nitrogen content, lower soil pH and soil temperatures in plots within the colony (Sigurdsson & Magnússon 2010).

Since the formation of the island, colonisation of vascular plants has been closely monitored in annual visits by scientists using a 100 x 100 m grid system, which was established on the island in order to accurately map the location of individual plants (Fridriksson & Johnsen 1968). In 2015 a total of 74 species had been discovered on Surtsey, or 15% of Iceland’s native vascular plant flora. Of them 64 were found living that year (Magnússon et al. 2020).

In the years 1996-1997 the abundance of all vascular plants on the whole island was mapped within the grid. This was repeated in 2005-2006 and again in 2014-2015. The purpose of this mapping was to obtain information on the distribution of vascular plants on the island and to monitor the rate of dispersal and distribution of individual species. In this paper we describe the colonisation and distribution of the vascular plant species on Surtsey, where and in what types of land they were found. We also describe the main vegetation types found on the island in 2015 and how the vegetation has changed over time.

STUDY AREA

Surtsey is the southernmost of the Westman Islands and is 32 km off the south coast of Iceland (Fig. 1). It was formed during an eruption from the sea floor that lasted from 1963 to 1967. During the eruption, two main tephra cones were built up from two craters on the northern part of the island, while the southern part was formed by lava flows which are mainly of the smooth pahoehoe type, though rugged aa flows are also found (Baldursson & Ingadóttir 2007). At the end of the eruption in 1967 the island had reached an area of 2.65 km^2 and a height of 174 m a.s.l. (Jakobsson et al. 2000). Over time, the island has changed greatly. Large parts of the lava fields on the southern part have disappeared due to marine abrasion and erosion (Jakobsson et al. 2000, Óskarsson et al. 2020). On the northern and leeward side, a spit was formed by accumulation of eroded costal sediments (Fig. 1). In addition, the tephra cones have gradually been transformed into denser palagonite tuff (Jakobsson et al. 2000, Óskarsson et al. 2020). In 1972 the area of the island had decreased to 2.25 km^2, in 1996 to 1.54 km^2, and in 2014 1.31 km^2 (Fig. 1). In 2014 the highest point on the island was 154 m above sea level and thus was 20 m lower than at the end of the eruption in 1967. During 1972–1996, the island decreased on average by 3 ha per year and by 1.3 ha per year during 1996–2014. These changes have been greatest in areas below 60 meters (Fig. 1). Due to the heavy marine abrasion, high cliffs have formed around the island except at the leeward northeastern side. With time the surface characteristics have also changed considerably. The highest cones around the

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[1] Nomenclature follows Wąsowicz 2020.

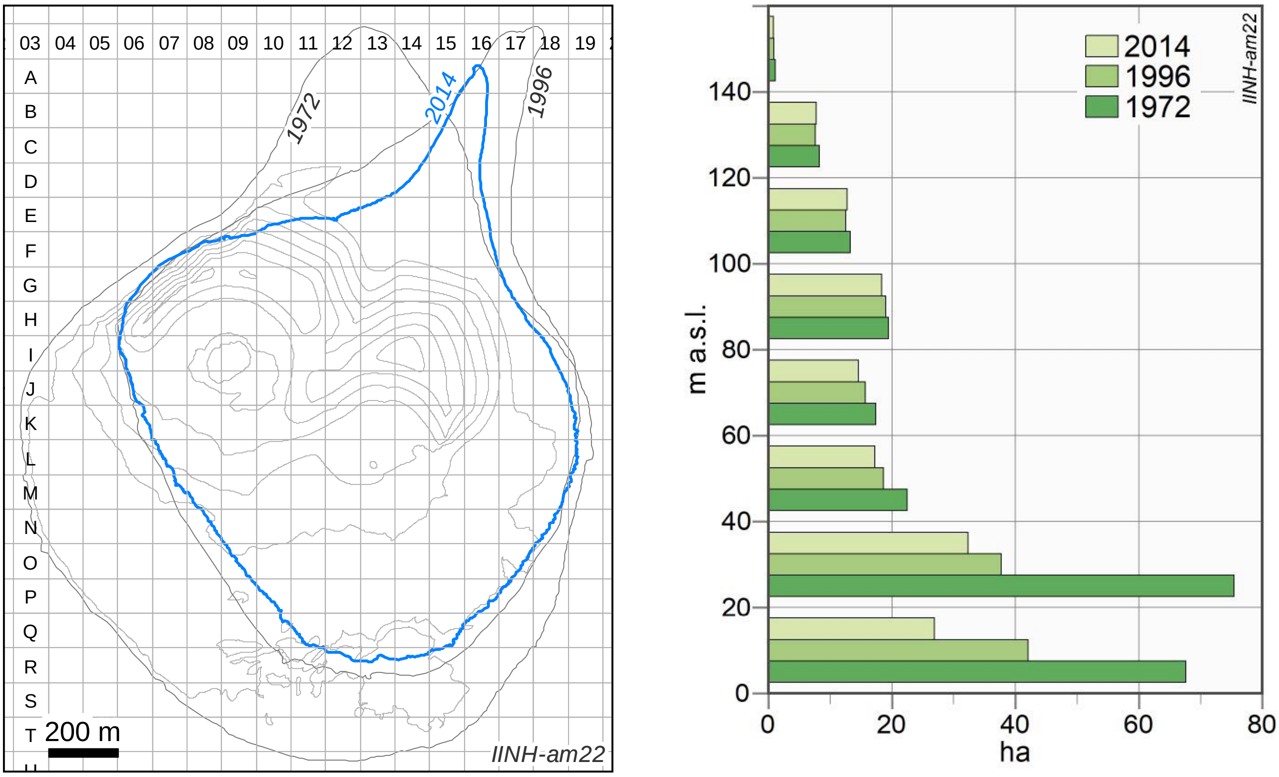


Fig. 1. (A) Map showing the size and outline of Surtsey in 1972, 1996 and 2014. Contour lines (20 m) are based on data from 1972. Also shown is a 100 x 100 m grid system that has been used since the end of the eruption in 1967 to map the distribution of plants on the island. (B) Area of Surtsey by altitude in 1972, 1996 and 2014.

craters now consist of a hard but relatively smooth surface, with a thin layer of gravel and tephra in the most sheltered places. Tephra and sand have also been moved by wind and water from the upper to lower areas and accumulated on lower slopes and the lava below (Óskarsson et al. 2020). However, on the southernmost parts of the lava only fine material is found.

Based on data from an automatic weather station (2009–2019) the climate on Surtsey is relatively mild but windy, with a monthly mean temperature above freezing during all calendar months and wind speed exceeding 20 m/s for 30 days a year on average (Petersen & Jónsson 2020). The warmest month is August with a mean of about 11.3 °C and December the coldest with an average temperature of 3.2 °C. The mean annual precipitation is about 1000 mm, the summer months being the driest and October, on average, the wettest. According to the temperature data, the growing season on Surtsey is long compared to other sites in Iceland as a daily mean temperature above 4 °C generally begins in the middle of April and lasts until November.

METHODS

Plant colonisation and establishment

In 1967 a 100 x 100 m grid system covering the whole island was established in order to map and monitor accurately the location of individual plants (Fridriksson & Johnsen 1968) (Fig. 1). During the first decade all new individuals found were also precisely marked, usually with a wooden stake and given a number. In the first years the fate of all plants was also assessed. By 1979 new individuals had become so numerous that their marking was no longer possible. After that, only the first individuals of new species on the island were systematically marked. From 1998, the location of new colonists has also been recorded by GPS coordinates (Magnússon et al. 2009).

In the present study the relationship between plant colonisation and different surface types on the island was explored by examining in what surface type the first two individuals of each species were found. The classification was based on a modified geological map from 2004 made by Jakobsson (2006). Due to surface changes of the island, this classification is not accurate in all cases, but should still give a good overview of the main types of land in that plants have colonised. Seven of the tagged plant locations were in areas that had been destroyed by marine abrasion before 1996. These places were classified based on a geomorphological map of Surtsey from 1972 (Norrman et al. 1974).

Abundance and distribution

The abundance of individual vascular plant species was systematically examined on the whole island, first in 1996-1997, then in 2005-2006 and finally in 2014-2015. Steep slopes and cliffs not accessible on foot were left out. In each quadrat of the 100 x 100 m grid system the plant species found were classified according to the following abundance scale:

1. Rare - Five or less individuals within a quadrat, or the total cover of a species is less than 2 m^2
2. Medium - More than 5 individuals within a quadrat, or the total species cover ≥ 2 m^2. Species found within less than half of the quadrat.
3. Common - Species found at several sites and distributed within more than half of the quadrat.

The quadrats by the sea were not all of full size. They were nevertheless examined like other quadrats, but only if their size was at least 1/3 of full size (100 x 100 m). Distribution in these quadrats was assessed in the same way as elsewhere but based on the area that was available.

In the study years 1996-1997, 2005-2006 and 2014-2015, a total of 135, 139 and 116 quadrats were examined respectively. The island had decreased considerably during this period, but according to measurements in 1998, 2006 and 2016, its area was 148.1, 137.7 and 128.3 ha in these years respectively (Icelandic Institute of Natural History unpublished data). Differences in the number of quadrats between surveys is due to the fact that the island is constantly shrinking, but also that areas, especially on steep slopes, are differently accessible mainly depending on weather conditions. In order to display the distribution of individual species on the island, maps were made for each species based on their abundance in the quadrats at the different times.

Data analysis

Relationship between vegetation in individual quadrats and trends in plant succession on Surtsey were analysed by classification and ordination. Data from all the quadrats and years was included, 381 in total and 69 vascular plant species. Classification was performed with the two-way indicator species analysis program TWINSPAN (Hill & Šmilauer 2005) and the pseudospecies cut levels set to 1, 2 and 3 based on how common the species were. Ordination was carried out with the Canoco 5 program (ter Braak & Šmilauer 2012). Abundance of vascular plant species in the quadrats was subjected to detrended correspondence analysis DCA. In the analysis detrending was by segments and downweighting of rare species performed. Five supplemental variables were passively projected into the ordination space, namely: normalized difference vegetation index (NDVI) in 1996, 2006 and 2015; number of species per quadrat; shortest distance to sea; distance from the initial center of the seagull colony; and height a.s.l. As the height a.s.l. of the quadrats had not changed significantly from 1996 to 2015, the height model of 1998 was used for all years. The two distances were based on quadrat midpoints.

NDVI data was downloaded from U.S. Geological Survey (USGS), calculated from atmospheric corrected Landsat 5, Landsat 7, and Landsat 8 satellite images acquired on August 17 1996; July 20 2006 and August 6 2015. The data was cut along shorelines to minimise the impact of the sea and an average calculated for each quadrat based on 30 m pixel size. NDVI is an indicator of the magnitude of photosynthetically active vegetation and is usually given in values from -1 to 1 (Rouse et al. 1974). It is calculated with the formula: $NDVI = (R-IR)/(R+IR)$, where R is red reflectance and IR is infrared reflectance where R is red reflectance and IR is infrared reflectance.

Descriptive statistics were performed using the JMP software 9.01 (SAS Institute Inc. 2010). The relationship between supplemental variables and TWINSPAN-classes were analysed with one way ANOVA. Non-normal parameters were log-transformed prior to analysis followed by Tukey's Pairwise Significant Difference test at $\alpha = 0.05$. When transformation was not sufficient for normal distribution requirements, a non-parametric Wilcoxon test was performed and pairwise comparisons made using rank sum test at $\alpha = 0.05/8 = 0.00625$. The relationship between the different surface types on Surtsey and colonisation of vascular plants was tested with Pearson chi-square test.

RESULTS

Colonisation in time

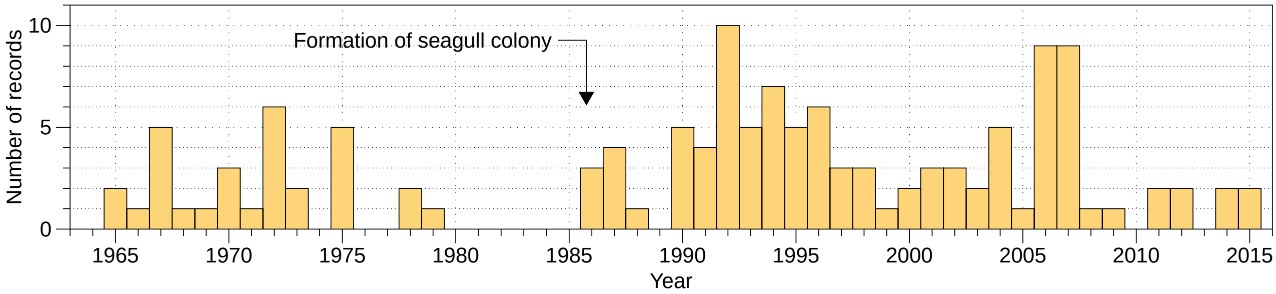


Fig. 2. Vascular plant colonisation on Surtsey during 1965–2015 based on the first two records of each species. Total number of records = 130, of these, 56 species have been recorded at two locations and 18 at one.

During 1965–2015, a total of 74 vascular plant species were found on Surtsey. The results show that plant colonisation has changed over time (Fig. 2). Based on the first two records of each species, the colonisation was considerable between 1965–1979, the first years after the island rose from the sea. Then six years passed without any new colonisation being noticed. Following 1986 there was, however, a sharp increase in colonisation that peaked during 1992–1995 after which it declined again. A new peak occurred in 2006–2007. It should be noted that new plant species are not always found in their first year of growth on the island. In some cases, they may be several years old when they are discovered.

Relationship between surface types and colonisation

The colonisation of plants on Surtsey has varied in time and space (Fig. 4). The first plants (1965–1967) were found on the northern spit of the island and on nearby slopes. During the following years (1968–1980) the colonisation does not seem to be strongly restricted to any particular area but was spread over a large part of the island. However, no colonisation was observed on the highest hills or on steep slopes (Fig. 4).

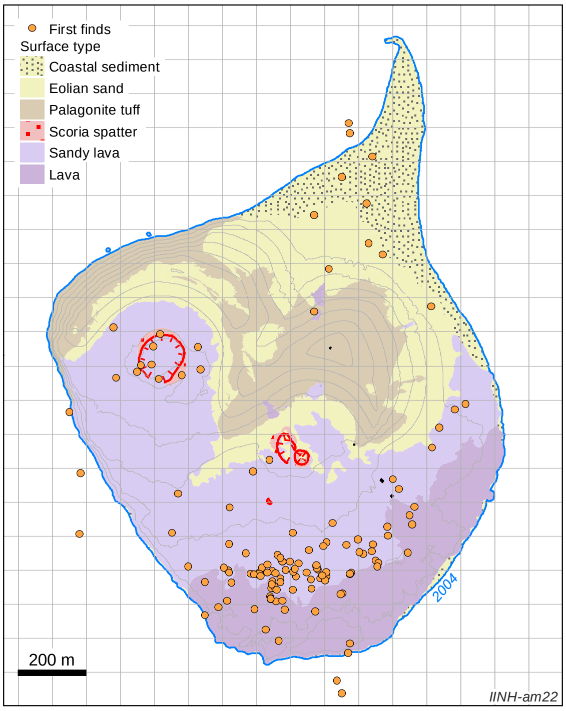


Fig. 3. Map showing the main surface types on Surtsey in 2004, based on Jakobsson (2006) and the sites of first two records for each vascular plant species found on the island 1965-2015. Points outside the coastline of 2004 were on land that had eroded.

In the years 1986–1995, after a break of six years, a new period of colonisation began and now the new colonisers were mainly confined to two areas. Firstly, in and around the western crater and secondly, and to a much greater extent, in the southern part of the island where seagulls started nesting in great numbers in 1986. New plant species were also found to the east of that site. From 1995, the main area of colonisation has been within and at the eastern edges of the seagull colony. Limited colonisation has occurred within the western crater area (Fig. 4).

Plant colonisation differed significantly between surface types (chi-square = 76,87, n =5, p < 0.0001). Colonisation was highest on sandy lava but was also considerable on lava (Fig. 5). No colonisation was observed in areas classified as palagonite tuff and relatively low on aeolian sand and coastal sediments.

Given that the seagulls clearly have a great influence on the colonisation of new species on Surtsey, it was interesting to explore whether colonisation differs on the land types before and

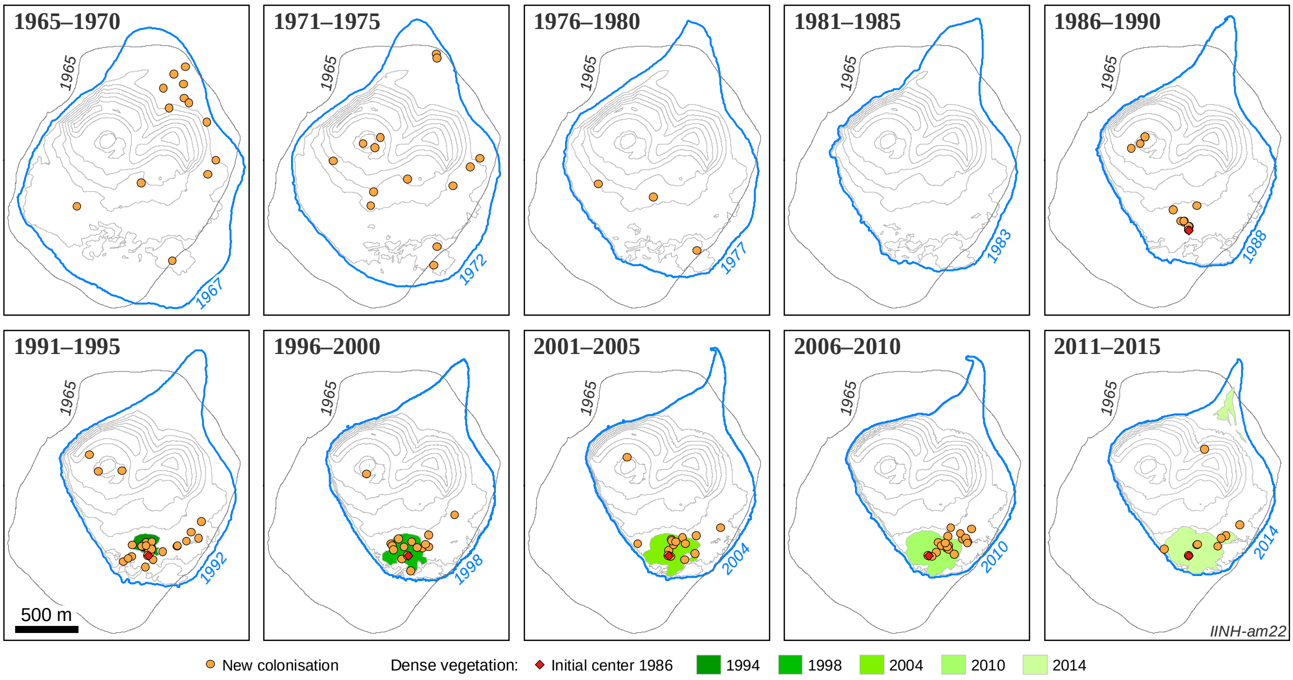


Fig. 4. Maps showing colonisation locations of vascular plants on Surtsey at five years intervals, based on the first two records of each species. The red spot indicates the initial center of the seagull colony established in 1986. The green areas indicate the development of dense vegetation on the island, outlined from aerial photographs.

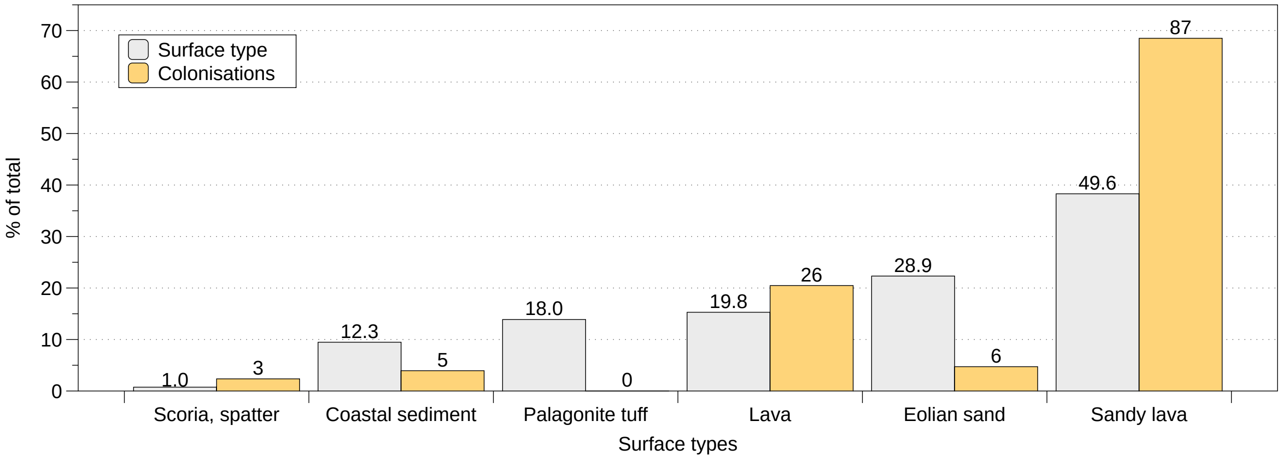


Fig. 5. The relationship between area of different surface types on Surtsey and colonisation of vascular plants. Colonisation is based on the first two records of each species during the period 1965–2015. The area of different surface types is calculated from the size of the island in 2004 and based on map from Jakobsson (2006). Note that records in eroded areas outside the island (6 in total) at that time are excluded (see Fig. 3). Numbers above bars show the area of the different surface types (total size of island 2004 is 129.6 ha) and records of colonisation respectively (127 in total).

after the formation of the seagull colony in 1986. Due to few records (low expected values) it was only possible to compare the colonisation on lava and sandy lava. The results, however, did not show a significant difference between these categories after the arrival of the birds (chi-square = 1.01, df = 1, Ns).

The vegetation types on Surtsey

TWINSPAN-classification of the 381 quadrats studied revealed a great difference in the vegetation of the island (Fig. 6). In the first division two main groups were formed with seven species as positive indicators. Therefore, two main types of vegetation can be recognized. The first (TW1-TW4, 172

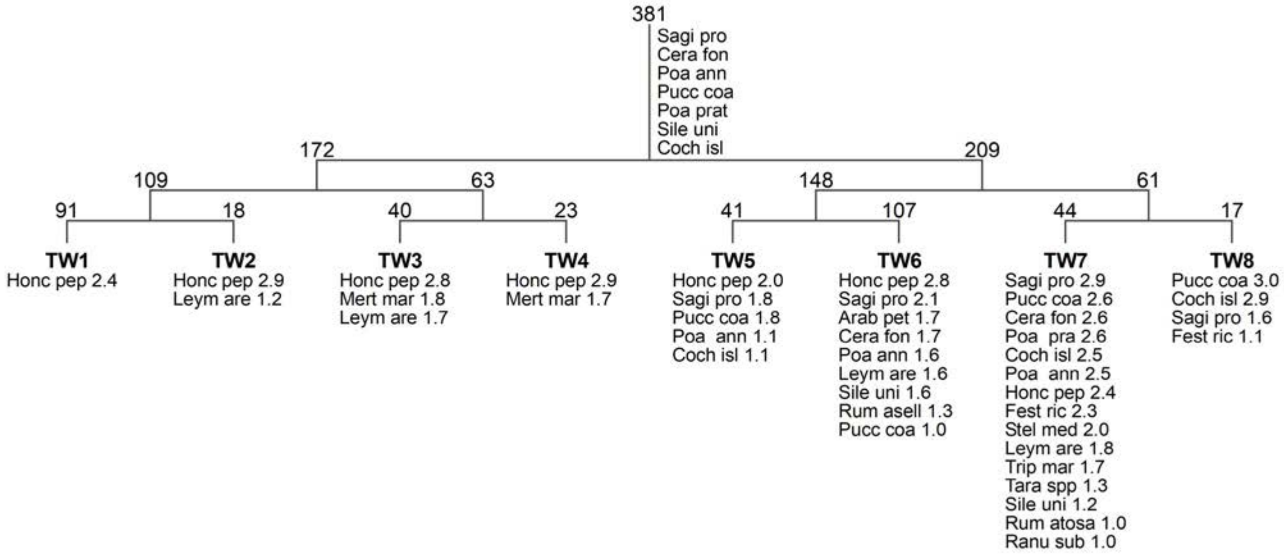


Fig. 6. Result of a TWINSPAN-classification of all quadrats studied on Surtsey based on the abundance of vascular species in 1996-1997, 2005-2006 and 2014-2015. The number of quadrats in each class is shown and so are indicator species for the first division. For each class, the most common species are shown based on average abundance (≥1.0) for each species.

quadrats) is characterized by the pioneer species *H. peploides, Mertensia maritima* and *L. arenarius*. In the second (TW5-TW8, 209 quadrats) the pioneers of the first main group are still part of the vegetation but several other species characterize the vegetation like the forb species *Sagina procumbens, Cerastium fontanum, Silene uniflora* and *Cochlearia islandica* but also the grass species *Poa annua, Puccinellia coarctata and Poa pratensis.* Further divisions resulted in eight classes TW1-TW8 (Fig. 6). The five environmental parameters tested show that there was a great variation between the groups (Table 1). Species richness was very low in TW1 but slightly higher in TW2 or 1.8 and 2.8 species/quadrat respectively. Although low, the richness was significantly higher in TW3 and TW4 (4.1 and 4.7 species/quadrat). The species richness was higher in groups TW5 and TW8 (5.7 and 6.8) and still higher in group TW6 (9.7). However, the group TW7 had by far the highest richness or 18.1 species/quadrat.

Table 1. The six vegetation types on Surtsey and the averages ± SE for vegetation and supplemental variables for the eight TWINSPAN-classes, TW1-TW8. Numbers within parentheses are min-max. Capital letters indicate if differences are significant between classes. Examples of the vegetation types are shown in Fig. 7.

	Honckenya pioneer vegetation		*Honckenya-Mertensia-Leymus* vegetation		*Honckenya-Sagina-Puccinellia* vegetation	*Honckenya* and gravel flat vegetation	Forb rich grassland	*Cochlearia* see-cliff vegetation
	TW1 n=91	TW2 n=18	TW3 n=40	TW4 n=23	TW5 n=41	TW6 n=107	TW7 n=44	TW8 n=17
Number of species*	1.8±0.08E (1-4)	2.8±0.26D (2-6)	4.1±0.19C (3-7)	4.7±0.23C (3-7)	5.7±0.33C (1-11)	9.7±0.29B (4-18)	18.1±0.82A (10-31)	6.2±0.83C (2-13)
NDVI**	-0.019±0.005 E (-0.164-0.076)	0.004±0.008 CDE (-0.078-0.050)	0.051±0.022 C (-0.442-0.520)	-0.017±0.015 E (-0.311-0.061)	0.026±0.006 CD (-0.045-0.122)	0.044±0.006 C (-0.130-0.382)	0.420±0.031 A (0.020-0.804)	0.198±0.039 B (-0.046-0.548)
Height a.s.l. m**	48±3.7CDE (4-138)	55±5.2BC (10-92)	32±6.4EF (4-146)	91±5.7A (14-136)	49±6.8CD (2-146)	71±3.3B (18-146)	26±0.8D (18-42)	21±0.4DF (18-24)
Distance from shore, m**	217±16AB (0-570)	188±33ABC (14-441)	146±23C (0-535)	239±25AB (59-534)	189±27ABC (0-522)	245±12A (6-522)	157±12BC (14-309)	30±10E (0-121)
Distance from the initial center of gull colony, m**	839±31A (235-1491)	605±43BC (348-1055)	908±47A (295-1370)	764±43AB (386-1057)	616±32BC (189-953)	610±22C (173-1057)	191±20D (36-809	232±23D (113-429)

* ANOVA
** Nonparametric comparisons, Wilcoxon.

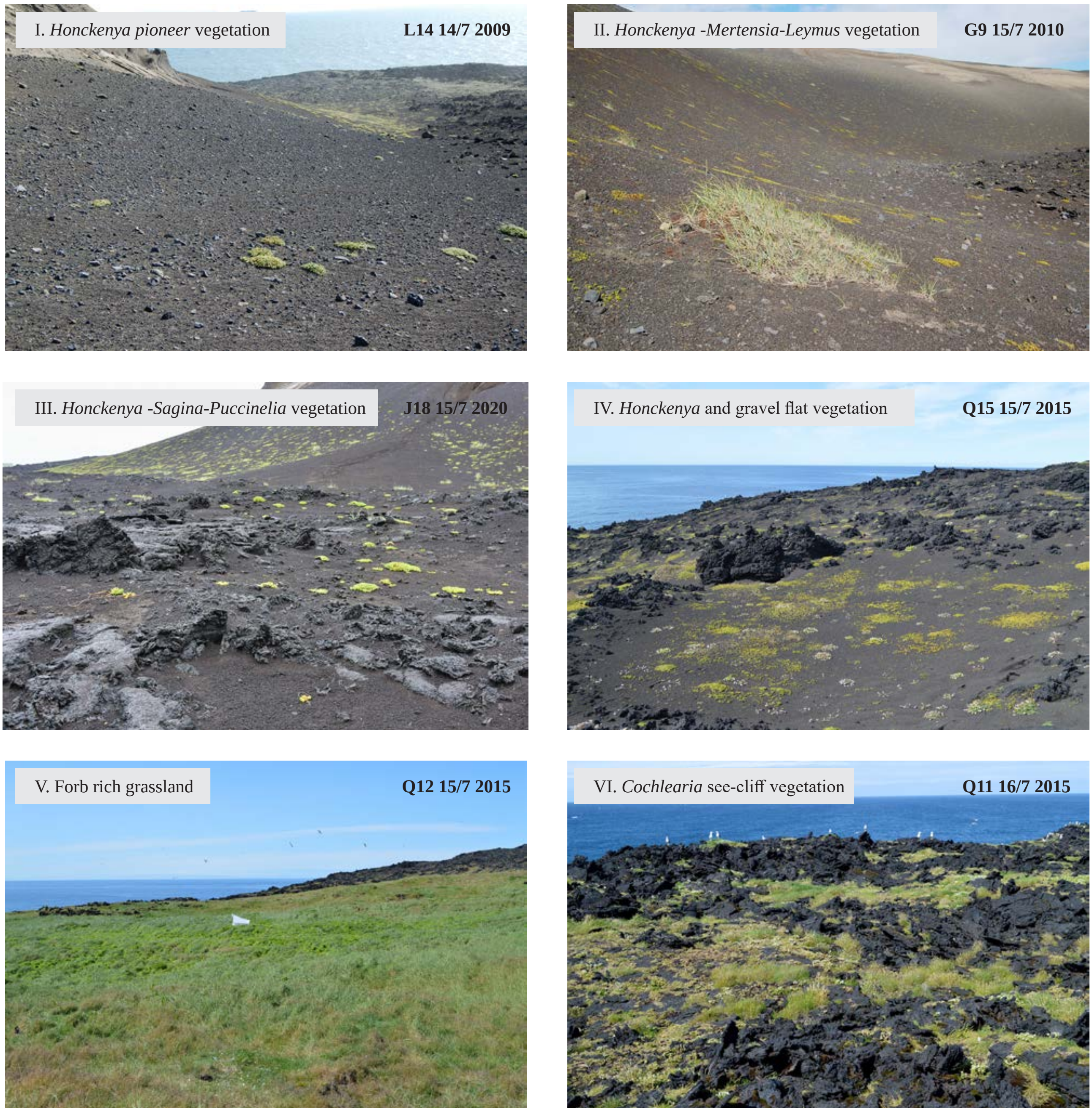


Fig. 7. Examples of the six main vegetation types on Surtsey in 1996–2015. Information on species richness and dominating species is given in Table 1 and Fig. 6.

NDVI values were very different by groups (Table 1). They were lowest in group TW1, TW4 and TW2 (- 0.019, -0.017 and 0.004). Groups TW5, TW6 and TW3 all had fairly similar values, or in the range 0.026–0.051. Much higher values were in category TW8 (0.198). NDVI values were by far highest in group TW7 (0.420).

Based on species composition and abundance of the vascular plants measured in the quadrats between 1996 to 2015, six main vegetation types can be identified on the island (Fig. 7).

I. *Honckenya* pioneer vegetation. This type is represented by the TWINSPAN-classes TW1-TW2. Although very sparse *H. peploides* is the only abundant species in this type.

II. *Honckenya-Mertensia-Leymus* vegetation. The next vegetation type is represented in groups TW3-TW4. This vegetation is closely related to type I but is considerably richer in species. In addition to *H. peploides*, *Mertensia maritima* and *L. arenarius* are common.

III. *Honckenya-Sagina-Puccinellia* vegetation. The third type consists of group TW5. *H. peploides* and *S. procumbens* are abundant, but also the grass species *P. coarctata* and *P. annua*.

IV. *Honckenya* and gravel flat vegetation. The fourth vegetation type is represented by group TW6. *H. peploides* is common as well as *S. procumbens*, but this type is characterised by *Arabidopsis petraea*, *S. uniflora* and *Rumex acetosella*, all common species on gravel flats in Iceland (Kristinsson 2010).

V. Forb rich grassland. The fifth vegetation type corresponds to the group TW7. It differs significantly from all other vegetation types on Surtsey mainly due to high species richness and production. Many coastal plants are still present but additional species adapted to nutrient rich habitats are found. Grass species are common such as *P. pratensis*, *P. annua*, *Festuca richardsonii* but also forbs such as *C. fontanum*, *Stellaria media*, *Rumex acetosa* and *Ranunculus subborealis*.

VI. *Cochlearia* see-cliff vegetation. The sixth vegetation type on Surtsey is represented by group TW8. The most common species are *P. coarctata*, *C. islandica*, *S. procumbens* and *F. richardsonii*.

Ordination

The ordination revealed the variation in the vegetation on Surtsey and the changes that have occurred from 1996-1997 to 2014-2015 (Fig. 8). The eigenvalues for the first three axes were 0.36, 0.14 and 0.10 respectively. The main difference in the vegetation is along Axis 1, which clearly separates the quadrats in the species poor and sparsely vegetated quadrats (TW1-TW4) from those species richer and with denser vegetation (TW7-TW8) (Fig. 8). Intermediate along the axis are quadrats of the classes TW5-TW6. The diagram shows that they have much in common with the quadrats with high scores on Axis 1. Axis 2 mainly separates quadrats in TW5 and TW8 from other classes but both of these classes have relatively low values on the axis. The species *P. coarctata*, *C. islandica* and *S. procumbens* are relatively common in the quadrats (Fig. 9).

Based on the ordination and the environmental variables tested the main gradient in the vegetation data is related to NDVI, species number and distance to the initial center of the seagull colony (Fig. 9). On average both the number of species and NDVI increased along axis 1, but the opposite was true for the distance to the initial center of the seagull colony. The correlation between NDVI and coordinates on axis 1 was 0.61 ($r^2 = 0.37$; $n = 381$; $p < 0.0001$) but the corresponding coefficients for number of species and distance from the initial center of the seagull colony were 0.69 ($r^2 = 0.48$; $n = 381$; $p < 0.0001$) and -0.48 ($r^2 = 0.60$; $n = 381$; $p < 0.0001$) respectively. Distance from shore and h.a.s.l showed much lower correlation with the two ordination axis.

There are also some differences in vegetation depending on the location on the island (Table 1; Fig. 6 & 10). The quadrats in group TW4 are mainly found in the relatively high-lying areas. In addition, the quadrats belonging to TW8 are unique as they are generally close to the shore, or on average 30 m. It is also clear that the vegetation on the island is strongly related to the distance from the initial center of the seagull colony, but the quadrats classified in TW8 and TW7 are on average close to the site where the gulls began to nest in 1986 or 232 and 191 m respectively.

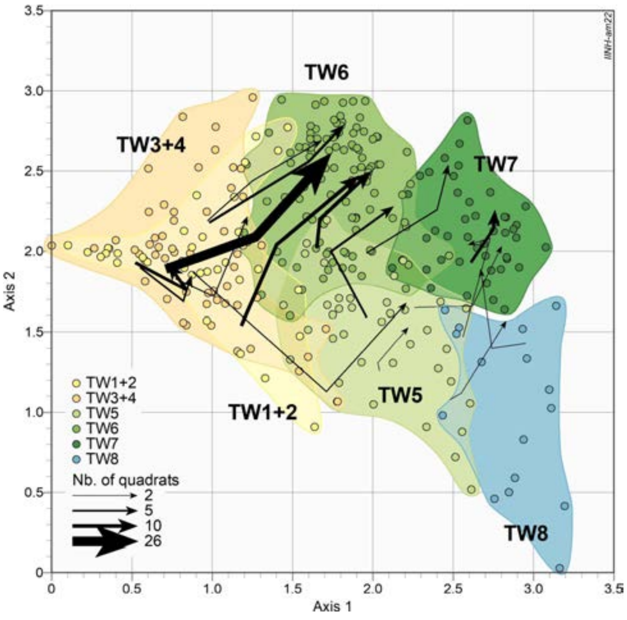


Fig. 8. DCA-ordination of quadrats on Surtsey based on abundance of vascular plant species in quadrats sampled in 1996-1997, 2005-2006 and 2014-2015. Lines enclose the six vegetation types: TW1-TW2, TW3-TW4, TW5, TW6, TW7 and TW8. The arrows denote the main vegetational change with time representing quadrats which transfer between TW-classes in a similar way. Arrow thickness is proportional to the number of quadrats behind each arrow.

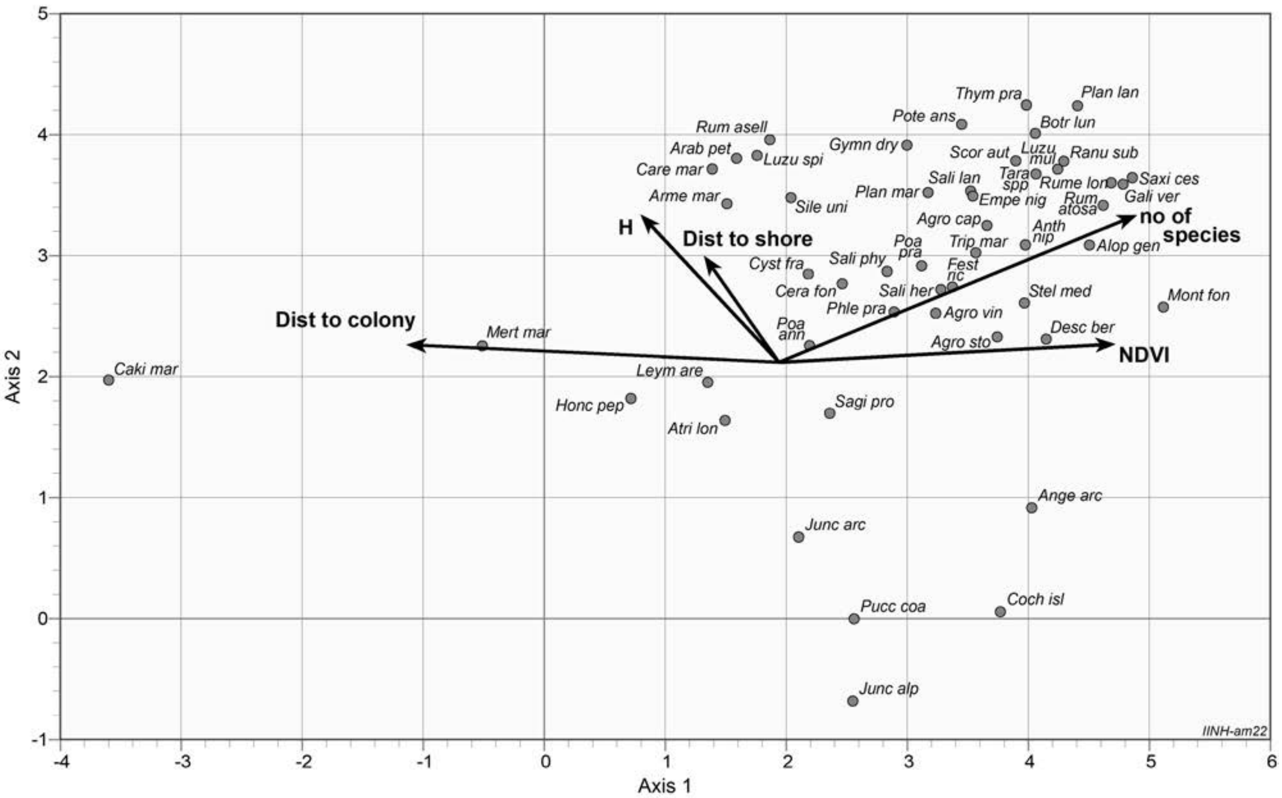


Fig. 9. Results of DCA-ordination of species based on species abundance in quadrats measured in 1996-1997, 2005-2006 and 2014-2015. Only 50 species with the greatest effect on the ordination are shown. Relationship between environmental variables and the DCA-ordination is denoted with arrows where arrow length indicates the relative importance of the variables in explaining the vegetational variation. H is the hight (m) above sea level measured in 1998. Full names of the species are given in Appendix I.

Vegetation changes in time and space

During the study period, major vegetational changes took place on Surtsey, but they vary depending on the location (Fig. 8 & 10).

In the years 1996-1997 the entire northern part of the island had either *Honckenya* pioneer vegetation or *Honckenkia-Mertensia-Leymus* vegetation (classes TW1-TW4). Better vegetated and more species-rich areas (TW5-TW8) were at that time mostly confined to an area on the southern part of the island mainly close to and around the seagull colony (Fig. 10).

Over time, the distribution of the species poor pioneer vegetation (TW1-TW4) has decreased significantly. In 2014-2015 it was only found in the northeastern part of the island (Fig. 10). Instead, other and more species rich vegetation types increased considerably on the island. The most fertile and species-rich areas (TW7) had e.g., increased from about 10 ha in the years 1996-1997 to almost 18 ha in 2014-2015. The largest increase was in *Honckenya* and gravel flat vegetation (TW6), which covered only about 14 ha in the first survey in 1996-1997 but was found in more than 60 ha in 2014-2015 and covered more than half of the island (Fig. 10).

The transfer of quadrats between TW classes provides a good overview of the main vegetation changes that have taken place on Surtsey (Figs. 8 and 10). Changes can be divided into three categories. First, areas that have hardly changed. These are mainly quadrats in classes TW1 and TW2, *Honckenya* pioneer vegetation, which are high on the southeastern slopes of the island and in coastal quadrats on the west side. There conditions are extremely severe due to erosion and transport of sand and tephra. Only very few species can survive under these conditions. e.g. *H. peploides* and *L. arenarius*. Secondly, many quadrats of almost all TWINSPAN-classes all over the island had developed to varying degree towards vegetation class V that characterizes the seagull colony. There the vegetation is relatively dense and rich in species (Fig. 8 & 9). Thirdly, there were a few quadrats by the south coast where the sea constantly erodes the island and affects the vegetation so that salt-tolerant species such as *C. officinalis, P. coarctata and S. procumbens* dominate (*Cochlearia* see-cliff vegetation) while others retreat (Fig. 10).

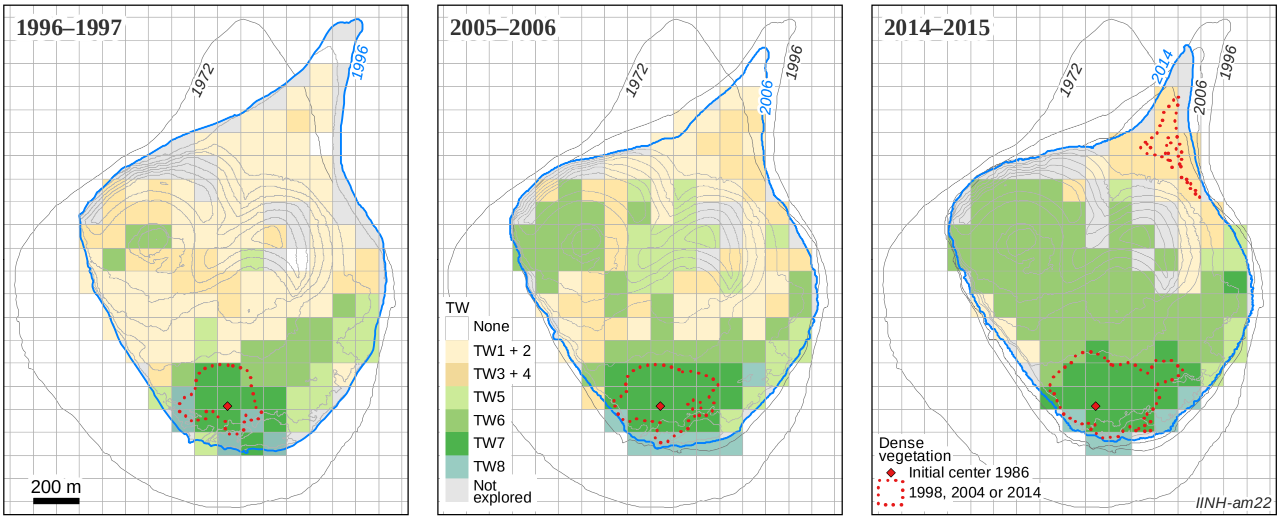


Fig. 10. Maps showing changes in the distribution of the TW-classes on Surtsey. The red dot indicates where the seagulls started to nest on the island in 1986. The dotted lines enclose areas with dense vegetation estimated from aerial photographs.

Changes in the number of species

On Surtsey, the number of species per quadrat has increased substantially during the study period (Fig. 11). In the quadrats that have been sampled in the three surveys (n = 113), the average number of species has increased from 4.8 (min-max 0-22) species/quadrat in the years 1996-1997 to 7.2 (1-26) in the years 2005-2006 and to 10.4 (1-31) in the years 2014-2015. The largest increase occurred on the southern part of the island where the seagulls began to nest, especially in an area extending 300–400 meters to east of the site. A substantial increase also occurred within and around the large crater on the northwestern part of the island (Fig. 11). The increase in species numbers was relatively low on the northeastern part of the island, especially on the low spit and on the steep slopes of the palagonite tuff crater. However, a decrease was found in some quadrats, especially in the western part of the seagull colony and in quadrats close to the sea to the west of that site. There, the number of species declined the most by 8 species per quadrat (from 17 to 9).

There was a strong relationship between the distance from the initial center of the seagull colony and the number of species (Fig. 12). The number of species was highest close to the seagull colony but decreased with increasing distance from that site. In 1996-1997, these effects were visible up to 500 m from the site, and with time they increased and were approximately 600 m at the end of the study period.

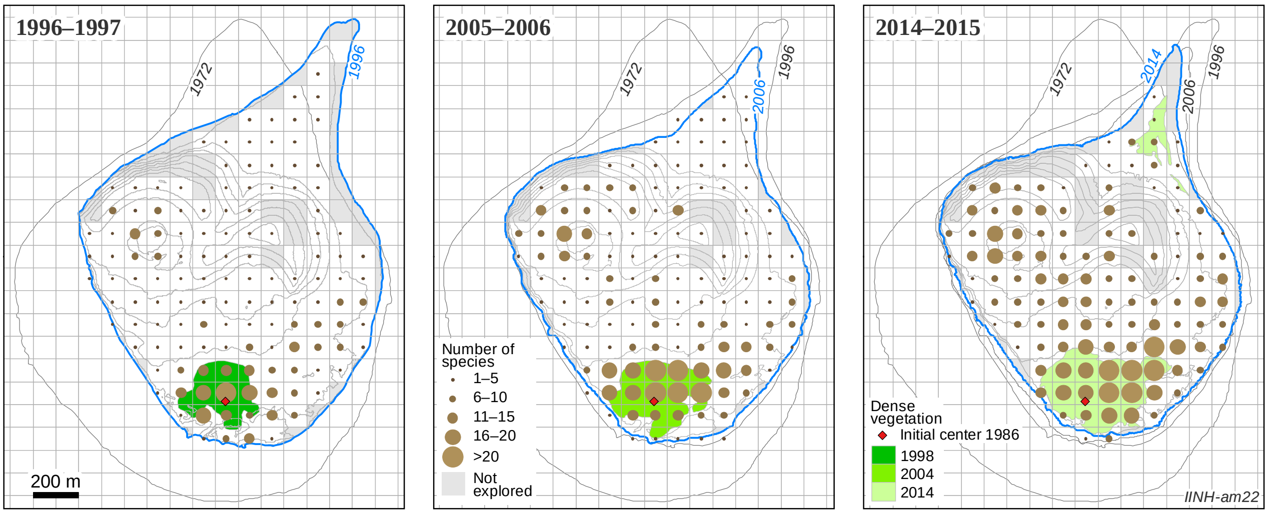


Fig. 11. Maps showing the number of species in quadrats at different times on Surtsey. A red dot indicates where seagulls started nesting on the island in 1986. The green areas denote a dense vegetation estimated from aerial photographs.

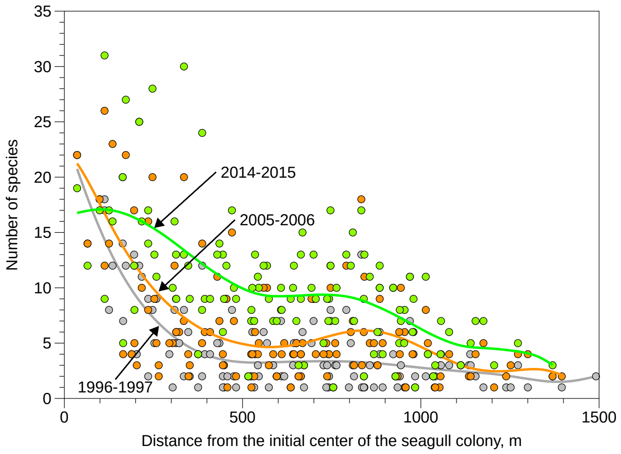


Fig. 12. Changes in the number of species with time related to distance from the initial center of the seagull colony on Surtsey. The lines are fitted with the LOESS method (locally estimated scatterplot smoothing).

NDVI and distance from the seagull colony

The results showed that the NDVI-values were very variable on the island. They were highest within the seagull colony but decreased rapidly with increasing distance (Fig. 13). At ca 500 m distance the effect had become rather low. The NDVI-values have increased over time, especially from 2006 to 2015. The results also showed that NDVI had risen sharply at a distance of 1100–1300 m.

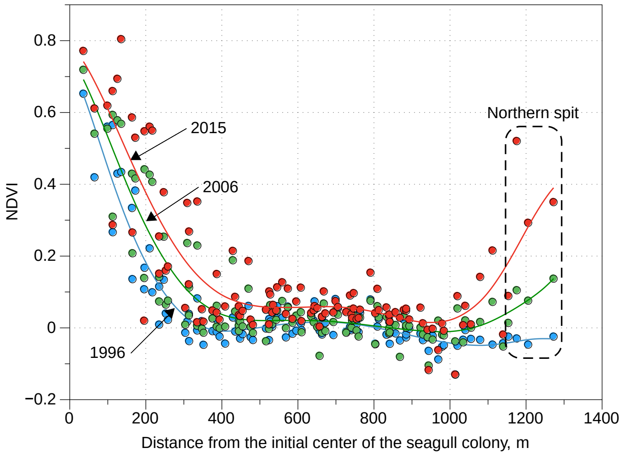


Fig. 13. NDVI-values on Surtsey 1996, 2006 and 2015 related to distance from the initial center of the seagull colony. Data is only shown for those quadrats that were sampled in the three surveys. Quadrats on the northern spit are marked with a rounded box. The lines are fitted with the LOESS method (locally estimated scatterplot smoothing).

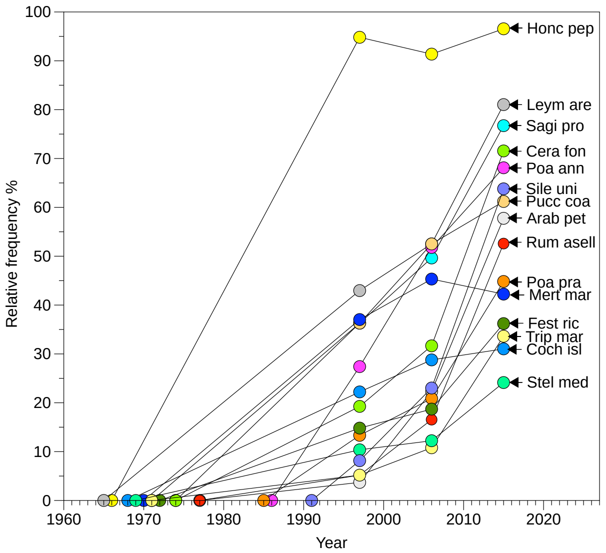


Fig. 14. Relative frequency of the 15 most common vascular plant species on Surtsey in 2014-2015 related to their year of colonisation. The frequency is shown as a percentage of quadrats with species out of the total number of quadrats inspected in, 1996-1997, 2005-2006 and 2014-2015. In these years 135, 139 and 116 quadrats were inspected respectively. Full names of the species are given in Appendix I.

Distribution of species

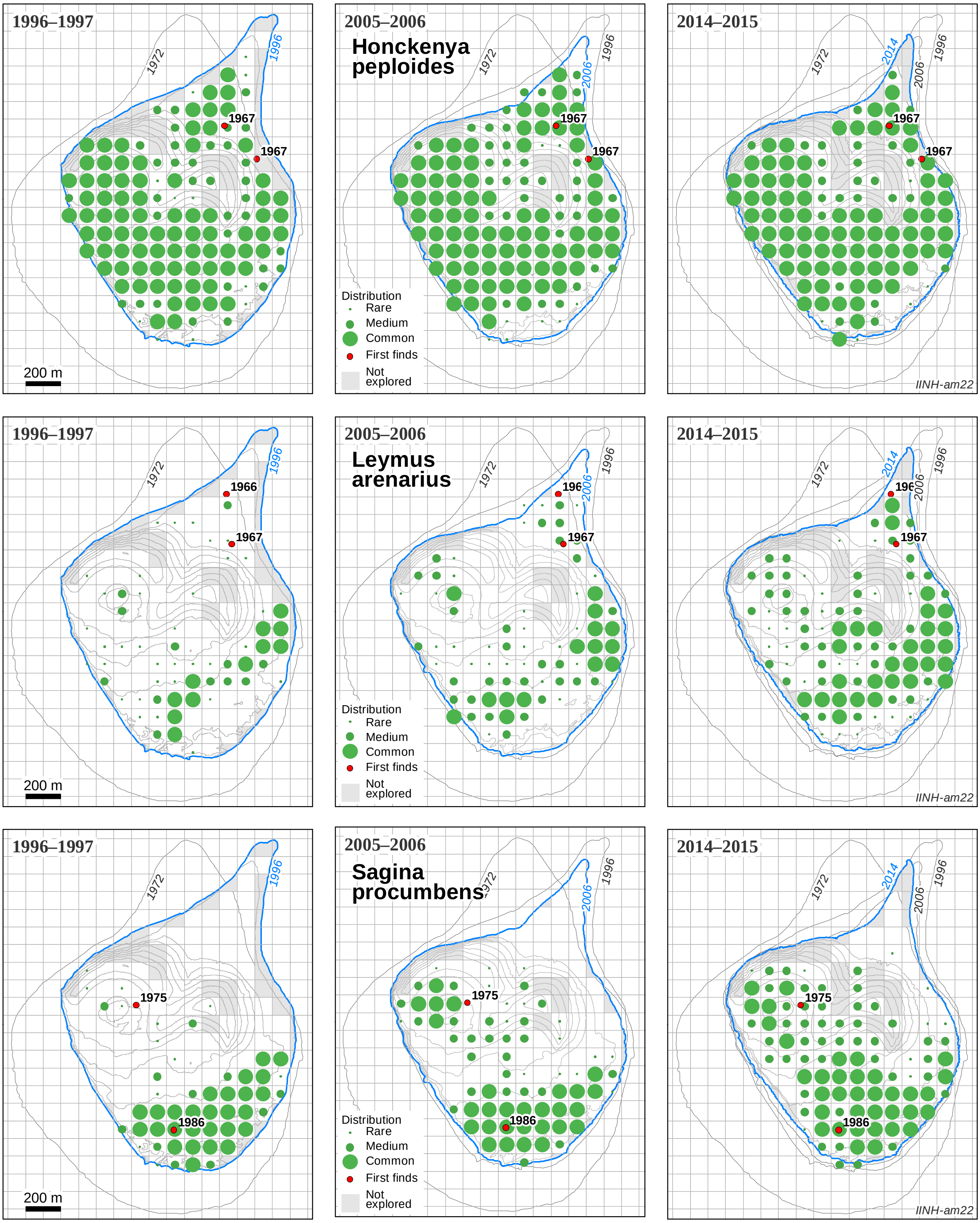
The results shown on Figs. 14 & 15 illustrate how the distribution of the most common species in 1996-1997 has increased during the subsequent study periods, and the largest increase generally occurring between 2006 and 2015. *H. peploides* is an exception, as the species had more or less colonised the whole island in 1996-1997. Then it was already found in 95% of the quadrats studied and its distribution has not changed considerably from that time. (Fig. 14). The species next in rank, *L. arenarius*, *S. procumbens* and *C. fontanum* had a much lower distribution in our first survey, but they have all spread widely during the research period as they were found in over 70% of the quadrats in the last survey. Other common species were *P. annua, S. uniflora, P. coarctata, A. petraea* and *R. acetosella*, all of which were found in over 50% of the quadrats studied in the last survey. The other exception to the general trend was *Mertensia maritima*, but its distribution decreased slightly from 2006-2007 to 2014-2015 (Fig. 14).

Based on frequency of the species on Surtsey they can roughly been divided into four categories:

I. High dispersal rate species. This category includes *H. peploides, P. annua* and *S. uniflora*, which had spread to over 50% of quadrats in less than 20 years.

II. In the second category are species that had reached this level in 35–40 years, namely *S. procumbens*, *P. coarctata*, *C. fontanum*, *A. petraea*, *L. arenarius* and *R. acetosella*. *P. pratensis* could also be included in this category, as the species showed similar rate of dispersal, but it had only been on the island for 29 years in the last survey (Fig. 14).

III. In the third category are several species that



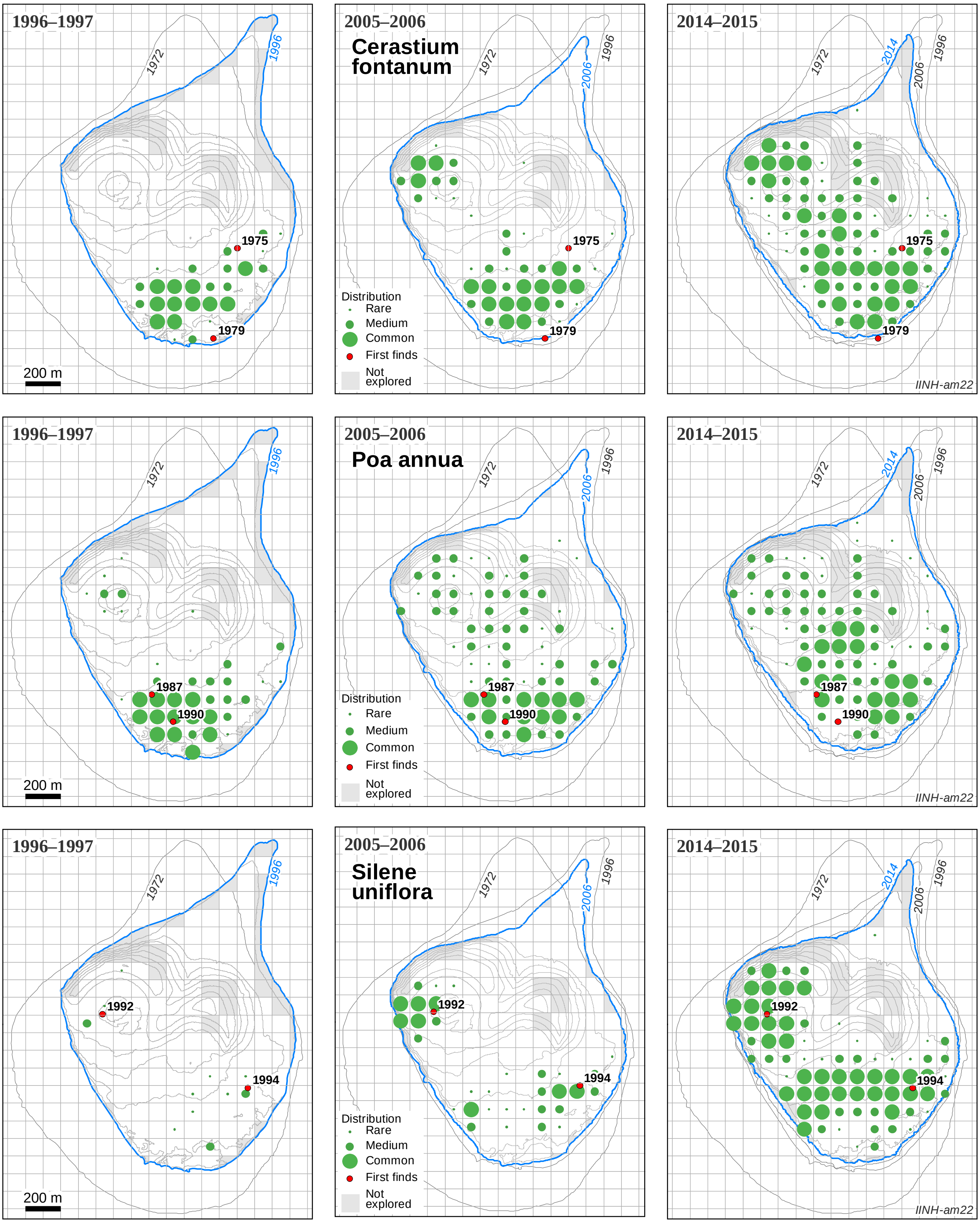


Fig. 15. A-B Map showing development in distribution of the six species that had become most common on Surtsey in the survey of 2014-2015; The red dots indicate the locations of the first two findings of the species on the island. Note that distribution maps for all plant species are given as supplementary information.

all had been on the island for over 40 years but spread rather slowly. In the last survey they were in 17–42% of the quadrats. These are the species, *Carex maritima, S. media, C. islandica, Tripleurospermum maritimum, F. richardsonii* and *Mertensia maritima.*

IV. In the fourth category are species that have either been on Surtsey for a long time without spreading to any extent or species that have been on the island for a relatively short time. Therefore, it is not known yet how they will respond. In the first group are e.g., *Cystopteris fragilis*, *Cakile maritima* and *Armeria maritima*. The habitats for the first two are of rather limited extent on Surtsey. *C. fragilis*, a perennial species, is found mainly in caves and caverns, while *Cakile maritima*, which is an annual, is confined to the northern coastline.

In the second group are e.g., *Taraxacum spp.*, *Empetrum nigrum, R. acetosa, Ranunculus subborealis* and *Scorzoneroides autumnalis.* In the last survey in 2014-2015 these species had been for 20–25 years on the island and had limited distribution.

DISCUSSION

Dispersal routes

In 2015, a total of 74 vascular plant species had been registered on Surtsey, which is about 16% of the native vascular flora of Iceland, which includes about 480 species (Kristinsson 2010). That means that the potential species pool for Surtsey is limited. Dispersal to Surtsey is certainly limiting for plant colonisation not least due to the isolation and distance from the nearest seed sources.

Northeast of Surtsey are older islands (4.8–16.4 km distance) formed in a similar way as Surtsey (Magnússon et al. 2014). They have all undergone major geomorphological changes, differ in area (0.02–0.25 km2) and are species poor (4–24 species/island). On these islands a total of 27 species of vascular plants has been recorded (Magnússon et al. 2014). Of these, only one (*Saxifraga rivularis*) has not been found on Surtsey by 2015. Therefore, of the species registered on Surtsey by 2015, at least 49 originate from a greater distance than 17 km.

Further away but in the same direction are three islands, Heimaey (18.3 km), Bjarnarey (25.5 km) and Elliðaey (27.1 km). Heimaey is by far the largest of all the Westman Islands (13.4 km^2). More than 180 species of vascular plants have been recorded there (Icelandic Institute of Natural History 2022). On Bjarnarey (0.32 km^2) and Elliðaey (0.46 km^2), a total of 33 species of vascular species have been registered, all but one (*Epilobium hornemanii*) also found on Heimaey. When the flora of Surtsey is compared to the flora of all these islands, it can be assumed that at least seven species (*Calamagrostis neglecta, Eleocharis quingeflora, Juncus alpinus, Gymnocarpium dryopteris, Salix arctica and Salix lanata*) originate from the mainland of Iceland as none of them have been recorded on the other Westman Islands.

Dispersal mode for individual species to Surtsey is not known, but the main transport is by sea, wind and birds (Magnússon et al. 2014). Human-mediated dispersal may have occurred although strong measures have been taken to prevent it. The location of the first colonisers, which all were coastal plants and found near the northern shore, strongly indicates that they were dispersed by sea (Fridriksson 1966, Magnússon et al. 2014). It can also be assumed that bird-mediated dispersal has been very important as species colonisation greatly increased after the formation of a seagull colony on the island (Magnússon et al. 2014, Fig. 2–4). Wind has probably been an active transport agent since the island was formed. Due to the long distance, however, it is not likely that many species have been wind-dispersed. The most likely are *Epilobium, Salix and Taraxacum* or species with particularly light seeds such as *Platanthera* and also the cryptogames like *Cystopteris, Equisetum, Botrychium* and *Polypodium*.

Both on Surtsey and Heimaey, easterly winds prevail (Petersen and Jonsson 2020, Veðurstofa Íslands 2015) which means that large-scale wind-dispersal from Heimaey or from the mainland of Iceland to Surtsey is not very likely. Seed rain is also generally highest in September and October, a period of high precipitation, which will reduce the possibility of transporting seeds by wind over long distances. Based on data from 2013 it has been estimated that about 9% of species in Surtsey were dispersed by sea, 75% by birds and 11% by wind (Magnússon et al. 2014).

Surface characteristics and plant colonisation

Colonisation of plants on Surtsey has varied in space and time (Fig. 4). It is clear that both the import of seeds to the island and the conditions for colonisation have changed since the first plants were found in

1965. Although this study did not explore seedling establishment it is clear that surface characteristics are very important for establishment of plants (Fig. 3).

Save sites for seedling establishment differ greatly by surface type. Palagonite tuff is clearly a difficult place for plants to establish. Although the surface has narrow cracks in places, it is usually smooth and without soil. These areas are relatively high on the island and are often steep. Therefore, seeds that land on palagonite tuff are likely to move elsewhere with wind and water. Erosion, infertility and desiccation are all negative factors preventing successful establishment on palagonite tuff.

Eolian sand is mainly found on the steep slopes below the palagonite tuff areas (Fig. 3). These sites are also very severe habitats for seedling establishment. Surface stability is very low and abrasion by sand movement and accumulation of sand are factors that work against seedling establishment. This habitat is also nutrient poor which makes the establishment of plants difficult (Sigurdsson & Leblans 2020). On sandy lava and lava, the conditions for colonisation are clearly better than on palagonite tuff or on aeolian sand (Fig. 3–5). However, on sandy lava there is a lot of sand that drifts and tears or abrades plants. In sheltered places such as in the western crater, seeds accumulate to some extent and moisture conditions are better that in the more exposed habitats which explains the relatively high colonisation (Fig. 3).

Although there is a significant variation within lava areas, the conditions for colonisation on this surface type are relatively favourable (Fig. 5). In depressions fine material, sand and ash will accumulate and make favourable conditions for plant establishment. On the aa or block lava close to the sea on the southern part of the island this kind of sedimentation is limited. There is also a large effect of salt spray, which probably has unfavourable effects on plant colonisation (Maun 2009).

There was a great increase in species colonisation following the establishment of the seagull colony in 1986 (Fig. 4). This can be attributed to increased import of diaspores and to improved conditions for seedling establishment (Magnússon et al. 2014). As vegetation became denser in the seagull colony, new plant colonisation however slowed down but increased in sparsely vegetated or semi-vegetated areas on the outer edge of the colony, especially to the east. This indicates continued import of new species and a presence of suitable microsites for seedling establishment. Outside this area new colonisation was rather low and sporadic (Fig. 4).

Vegetation types and changes in time

The present study showed that during the research period 1996–2015 there has been very large vegetation changes on Surtsey. As previous studies have shown seabirds were the main drivers of plant succession (Magnússon et al. 2009, Magnússon et al. 2014). The birds have clearly had a great impact on the soil fertility and created conditions for species which otherwise could hardly thrive on the island

The six main vegetation types on Surtsey described in this article reflect results of previous analysis of vegetation on the island, based on small permanent plots (10x10 m) (Magnússon et al. 2009, Magnússon et al. 2020). The present study, however, describes conditions on the whole island and how they have changed over time. The vegetation types I, II and III are all quite similar, i.e. species poor pioneer vegetation (Fig. 6 & 7). The three types were under relatively low influence from seabirds and its area decreased on the island during 1996–2015 (Fig. 10). While vegetation that is clearly affected by the birds, i.e. types V and VI, had expanded significantly.

In general, there was a clear increase in NDVI from 1996 to 2015, which indicates that chlorophyll had increased almost over the whole island (Fig. 13).

The areas on the island that do not seem to have changed over time are steep slopes in the north-eastern part of the island. There the vegetation is still at its early stages (Fig. 10) due to ongoing erosion from the slopes which maintains pristine conditions on that part of the island (Óskarsson et al. 2020).

The increase of dense vegetation has not only occurred within and around the seagull colony. A change has also been observed on the northern spit mainly after 2006 (Fig. 10 & 11, 13). This occurred without a considerable change in plant species number (Fig. 11 & 12). The reasons for this increase can partly be traced to seals breeding on the spit and their transfer of nutrients from sea to land (Magnússon et al. 2020). The fact that this has not yet had a significant effect on species number can maybe be attributed to the fact that seals, unlike seagulls, probably do not carry plant diaspores into the area. Also, the area is flooded by seawater in winter, conditions that few plants are adapted to.

Table 2. The main characteristics of the fast-spreading species on Surtsey.

	Life-form	Established strategy	Vegetative reproduction	Seed production	Coastal species	Gravel flat species	Invasive
Arabidopsis petraea	Perennial					× [a]	
Cerastium fontanum	Perennial	R CSR [b]		High [c]	× [a]		× [d, e]
Honckenya peploides	Perennial		High [f, g]		× [a, h]		
Leymus arenarius	Perennial		High [i]		× [a, i]		× [j]
Poa annua	Annual	R [b]		High [k, l]			× [e, m]
Puccinellia coarctata	Perennial				× [a, h]		
Rumex acetosella	Perennial	CSR-stress tolerant ruderal [b]	High [n, o]	High [n]		× [a]	× [n, p, q]
Sagina procumbens	Perennial	R CSR [b]		High [b, e, r]			× [r, s, e, t]
Silene uniflora	Perennial				× [a]	× [a, h]	

[a] Magnússon, S.H. et al. 2016
[b] Grime, J.P. et al. 1988
[c] Salisbury, E.J. 1964
[d] Global Invasive Species Database 2022a
[e] Ryan, P.G. et al. 2003
[f] Sánchez-Vilas, J. et al. 2012
[g] Sánchez-Vilas, J. & R. Retuerto 2017
[h] Kristinsson, H. 2010
[i] Hubbard, C.E. 1968
[j] Midwest Invasive Species Information Network
[k] Hutchinson, C.S. & G.B. Seymour 1982
[l] Warwick, S. 1979
[m] Global Invasive Species Database 2022b
[n] Stopps, G.J. et al. 2011
[o] Houssard, C. et al. 1992
[p] Global Invasive Species Database 2022c
[q] Ferreiro, N. et al. 2020
[r] Cooper, J. et al. 2011
[s] Visser, P. et al. 2010
[t] Global Invasive Species Database 2022d

Characteristics of individual species

On Surtsey, the species *H. peploides*, *P. annua* and *S. uniflora* have spread relatively fast. The same can be said of the species *S. procumbens, P. coarctata, C. fontanum, A. petraea, L. arenarius* and *R. acetosella* (Fig. 14 & 15). Although vegetation conditions on Surtsey have changed considerably since the island was formed, it can be concluded that conditions for germination, seedling establishment and growth have in general been relatively suitable for these species. Which are the main characteristics of these species? All are common on the mainland of Iceland. They usually grow in sparsely covered, rocky or sandy areas or on land that has been disturbed. The species are either pioneers and/or ruderals (Table 2). Many of them are also coastal plants such as *H. peploides, S. uniflora, P. coarctata* and *L. arenarius* and are therefore adapted to soil salinity to some extent. Others are common on gravel flats, even far from the sea, such as *A. petraea* or are found close to the sea but also further inland, like *S. uniflora* and *R. acetosella* (Table 2, Magnússon e.t. al 2016). Based on the behaviour of these species on Surtsey, it is clear that they can withstand harsh conditions like strong winds, unstable and nutrient poor soils, and drought.

Two of the fast-spreading species are short-lived, i.e., *P. annua* which is annual and *S. procumbens* which has been classified as perennial or perhaps even winter-annual (Grime et al. 1988) but the others are long-lived. The species *C. fontanum*, *P. annua*, *R. acetosella* and *S. procumbens* are all known for high seed production (Table 2). Personal observations on Surtsey also suggest that the same is also true for *H. peploides, S. uniflora, P. coartata, A. petraea* and *L. arenarius* especially at the margins of seagull colony.

Many of the fast-spreading species on Surtsey do not only spread by seed but also vegetatively. *H. peploides*, *L. arenarius* and *R. acetosella* have a great potential to spread vegetatively (Table 2). However, the distribution of species on Surtsey is probably mostly due to seed dispersal, although the increase in vegetation cover can in many cases be attributed to vegetative spread.

Many of the species with the highest distribution rate on Surtsey have in general high colonisation ability elsewhere. The species *C. fontanum, P. annua, R. acetosella* and *S. procumbens* have all proved to be active colonisers in areas outside their natural ranges, especially in the southern hemisphere, and have there been classified as invasive (Table 2). For example, *C. fontanum, P. annua* and *S. procumbens* have all spread in the Sub-Antarctic region (Ryan et al. 2003). There they have affected the native flora of the subantarctic Prince Edward Island which is of relatively recent volcanic origin. *R. acetosella*, which is native to Europe and southwestern Asia, has spread throughout many regions of the globe and is considered very invasive in several areas (Stopps et al. 2011, Ferreiro et al. 2020, Global Invasive Species Database 2022c). *L. arenarius*, native to Europe, has been introduced at sites by the Great Lakes in North America. There it has been described as invasive on beaches and dunes (Midwest Invasive Species Information Network 2022).

At least three of the species that have established on Surtsey seem to be very dependent on the seagull colony as they are almost exclusively found within it. These are *Ranunculus subborealis, R. acetosa* and *Taraxacum* spp. All are common on the mainland of Iceland where they grow mainly in nutrient rich grasslands and pastures and in a habitat type classified as Atlantic sea-cliff communities (Kristinsson 2010, Magnússon et al. 2016). Outside Iceland, these species are also common in meadows and pastures, often in fertile, disturbed habitats (Grime et al. 1988).

Future prospects

Despite the great influence of seabirds on the vegetation of Surtsey and some influence of seals, the island is far from being fully vegetated. Most of the island has still very sparse vegetation. It is expected that the vegetation cover will gradually increase, mainly due to the fertilizing effects of birds.

The results of this study indicate that the birds have significantly increased the number of plant species. This is not surprising as seabirds are powerful environmental modulators, generating major changes in soil properties and vegetation in of their breeding colonies (De La Peña-Lastra et al. 2021). Relatively low bird density can increase biodiversity, plant biomass and plant height, as well as to enhance seed dispersal (Anderson & Polis 1999, Sánchez-Piñero & Polis 2000, Otero et al. 2018). Examples of this can now be seen in and at the edges of the seagull colony on Surtsey. However, it is likely that high density of birds will gradually lead to a reduction in species number due to “eutrophication”. This can already be seen in the area where the seagull colony started on Surtsey in 1986. There *F. richardsonii and P. pratensis* have become completely predominant (Magnússon et al. 2009, Magnússon et al. 2014). If the effects of birds become even greater, i.e., increased eutrophication together with increased bird activity like burrowing, trampling and uprooting of plants, it is likely to lead to increase ruderal and nitrophilous species (Kamijo & Hoshino 1995, Baumberger et al. 2012, De La Peña-Lastra et al. 2021). Examples of this can be found in puffin colonies on the older Westman islands (Magnússon et al. 2014).

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SUPPLEMENTAL INFORMATION

Maps showing development in distribution of individual species of vascular plants found on Surtsey in 2014-2015 are available in Supplement S1.

REFERENCES

Anderson, W.B. & G.A. Polis, 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118, 324–332.

Baldursson, S. & Á. Ingadóttir (editors), 2007. Nomination of Surtsey for the UNESCO World Heritage List. Icelandic Institute of Natural History, Reykjavík. 123 p.

Baumberger, T., L. Affre, F. Torre, E. Vidal, P.J. Dumas & T. Tatoni, 2012. Plant community changes as ecological indicator of seabird colonies’ impacts on Mediterranean Islands. Ecological Indicators 15, 76–84.

Cooper, J., R. Cuthbert, N. Gremmen, P.G. Ryan & J.D. Shaw, 2011. Earth, fire and water: applying novel techniques to eradicate the invasive plant, procumbent pearlwort Sagina procumbens, on Gough Island, a World heritage Site in the South Atlantic. International Conference on Island Invasives, 162–165.

De La Peña-Lastra, S., C. Gómes-Rodrígues, A. Pérez-Alberti, F. Torre & X.L. Otero, 2021. Effects of a yellow legged gull (Larus michahellis) colony on soils and cliff vegetation in the Atlantic Islands of Galicia National Park (NW Spain). Catena 199, 105115.

Ferreiro, N., P. Satti, E. Castán, L.Á. Soria & M.J. Mazzarino, 2020. Lupinus polyphyllus Lindl. and Rumex acetosella L. effects on nutrient accumulation and microbial activity on tephra from the Puyehue–Cordón Caulle eruption (2011). Austral Ecol 45, 968–976.

https://doi.org/10.1111/aec.12911

Friðriksson S. & B. Johnsen, 1968. The colonization of vascular plants on Surtsey in 1967. Surtsey Research Prog. Rep. IV: 31–38.

Fridriksson, S., 1964. [The colonization of the dryland biota of the island of Surtsey off the coast of iceland]. Um adflutning lífvera til Surtseyjar. Náttúrufraedingurinn 34, 83–89, (in icelandic with English summary).

Fridriksson, S., 1966. The pioneer species of vascular plants on Surtsey, *Cakile edentula*, Surtsey Res. Progr. Rep. II, 63–65.

Fridriksson, S,. 1992. Vascular plants on Surtsey 1981–1990, Surtsey Res. Progr. Rep. 10, 17–30.

Global Invasive Species Database, 2022a. Species profile: Cerastium fontanum. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1422 on 23-03-2022.

Global Invasive Species Database, 2022b. Species profile: Poa annua. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1418 on 23-03-2022.

Global Invasive Species Database, 2022c. Species profile: Rumex acetosella. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1342 on 23-03-2022.

Global Invasive Species Database, 2022d. Species profile: Sagina procumbens. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1394 on 23-03-2022.

Grime, J.P., Hodgson, J.G. & R. Hunt, 1988. Comparative plant ecology. A functional approach to common British species. Unwin Hyman, London.

Hermannsson, S., 2009. Introduction. Surtsey Res. 12, 5–6.

Hill, M.O. & P. Šmilauer, 2005. *TWINSPAN for Windows version 2.3*. Huntingdon and Ceske Budejovice: Centre for Ecology and Hydrology and University of South Bohemia.

Houssard, C., J. Escarré & N. Vartanian, 1992. Water stress effects on successional populations of the dioecious herb, Rumex acetosella L. New Phytol 120, 551–559.
https://doi.org/10.1111/j.1469-8137.1992.tb01805.x

Hubbard, C.E., 1968. Grasses: A guide to their structure, identification, uses and distribution in the British Isles. Revised edn. Penguin Books; Harmondsworth, Middlesex, England.

Hutchinson, C.S. & G.B. Seymour, 1982. Biological flora of the British Isles - Poa annua L. Journal of Ecology 70, 887–901.

Icelandic Institute of Natural History, 2022. Observational database of Icelandic plants. Occurrence dataset https://doi.org/10.15468/u85y6t accessed via GBIF.org on 2022-04-28.

Ingimundardottir, G. V., H. Weibull & N. Cronberg, 2014. Bryophyte colonization history of the virgin volcanic island Surtsey, Iceland. Biogeosciences 11, 4415–4427.
https://doi.org/10.5194/bg-11-4415-2014

Jakobsson, S.P., 2006. Geological map of Surtsey, scale 1: 5000. Second edition 2006. Icelandic Institute of Natural History, Reykjavík.

Jakobsson, S.P., G. Guðmundsson & J.G. Moore, 2000. Geological monitoring of Surtsey, Iceland 1967-1998. Surtsey Research 11, 99–108.

Jóhannsson, B., 1968. Bryological observation on Surtsey, Surtsey Res. Progr. Rep. IV, 61.

Kamijo, T. & Y. Hoshino, 1995. Effects of short-tailed shearwater on vegetation in Great Dog, Little Dog and Little Green Islands, Tasmania. Wildlife Conservation Japan 1, 127–135. https://doi.org/10.20798/wildlifeconsjp.1.3_4_127

Kristinsson, H., 1972. Studies on lichen colonization in Surtsey 1970, Surtsey Res. Progr. Rep. VI, 77.

Kristinsson, H., 2010. [Flowering Plants and Ferns of Iceland] Íslenska plöntuhandbókin. Blómplöntur og byrkningar. Mál og menning, Reykjavík (in Icelandic).

Kristinsson, H. & S. Heiðmarsson, 2009. Colonization of lichens on Surtsey 1970–2006. Surtsey Research 12: 81–104.

Leblans, N. I. W., B.D. Sigurdsson, P. Roefs, R. Thuys, B. Magnússon & I. A. Janssens, 2014. Effects of seabird nitrogen input on biomass and carbon accumulation after 50 years of primary succession on a young volcanic island, Surtsey. - Biogeosciences 11, 6237–6250.
https://doi.org/10.5194/bg-11-6237-2014

Magnússon, B. & S.H. Magnússon, 2000. Vegetation succession on Surtsey during 1990–1998 under the influence of breeding gulls. Surtsey Research 11, 9–20.

Magnússon, B., S.H. Magnússon & S. Friðriksson, 2009. Developments in plant colonization and succession on Surtsey during 1999–2008. Surtsey Research 12, 57–76.

Magnússon, B., S.H. Magnússon, E. Ólafsson & B.D. Sigurdsson, 2014. Plant colonization, succession and ecosystem development on Surtsey with reference to neighbour islands. Biogeosciences 11, 5521–5537.
https://doi.org/10.5194/bg-11-5521-2014

Magnússon, B., G.A. Guðmundsson, S. Metúsalemsson & S. Granquist, 2020. Seabirds and seals as drivers of plant succession on Surtsey. Surtsey Research 14, 115–130.

Magnússon, S.H., B. Magnússon, Á. Elmarsdóttir, S. Metúsalemsson & H.H. Hansen, 2016. [Habitat types of Iceland] Vistgerðir á landi. In: Ottósson, J.G, Sveinsdóttir, A. & M. Harðardóttir (editors.), 2016. Vistgerðir á Íslandi. Fjölrit Náttúrufræðistofnunar Íslands 54, 17–168 (in Icelandic with English summary).

Maun, M.A., 2009. The Biology of Coastal Sand Dunes. Oxford University Press Oxford.
https://doi.org/10.1093/oso/9780198570356.001.0001

Midwest Invasive Species Information Network, 2022. Lymegrass (Leymus arenarius). http://www.misin.msu.edu/facts/detail/?id=28 on 23-03-2022.

Norrman, J.O., 1970. Trends in post-volcanic development of Surtsey island. Progress report on geomorphological activities in 1968. Surtsey Research Progress Report V, 95–112.

Norrman, J.O., B. Calles & R.Å. Larsson, 1974. The geomorphology of Surtsey Island in 1972. Surtsey Research Progress Report VII, 61–71.

Otero, X.L., S. Peña-Lastra, A. Pérez-Alberti, T.O. Ferreira & M.A. Huerta-Diaz, 2018. Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. Nature Communications, 1–8.

Ólafsson, E. & M. Ingimarsdottir, 2009. The land-invertebrate fauna on Surtsey during 2002–2006. Surtsey Research 12, 113–128.

Óskarsson, B. V., K. Jónasson, G. Valsson & J.M.C. Belart, 2020. Erosion and sedimentation on Surtsey island quantified from new DEMs. Surtsey Research 14, 63–77.

Petersen, A., 2009. Formation of a bird community on a new island, Surtsey, iceland. Surtsey Research 12, 133–148.

Petersen, G.N & T. Jónsson, 2020. The climate of Surtsey. Surtsey Research 14, 9–16.
https://doi.org/10.33112/surtsey.14.1

Romagnoli, C. & S.P. Jakobsson, 2015. Post-eruptive morphological evolution of island volcanoes: Surtsey as a modern case study. Geomorphology 250: 384–396.
https://doi.org/10.1016/j.geomorph.2015.09.016

Rouse, J.W., R.H. Haas, J.A. Schell & D.W. Deering, 1974. Monitoring Vegetation Systems in the Great Plains with ERTS. In: Third Earth Resources Technology Satellite-1 Symposum. Volume 1, Technical Presentations, section A. https://ntrs.nasa.gov/archive/nasa/casi.ntrs.nasa.gov/19740022614.pdf

Ryan, P.G., V.R. Smith & N.J.M. Gremmen, 2003. The Distribution and Spread of Alien Vascular Plants on Prince Edward Island. African Journal of Marine Science 25, 555–562.
https://doi.org/10.2989/18142320309504045

Salisbury, E.J., 1964. Weeds and aliens 2. edn. London Collins.

SAS Institute Inc., 2010. Using JMP 9. Cary, NC, SAS Institute Inc.

Sánchez-Piñero, F. & G.A. Polis, 2000. Bottom-up dynamics of allochthonous input: Direct and indirect effects of seabirds on islands. Ecology 81, 3117–3132.
https://doi.org/10.1890/0012-9658(2000)081[3117:BUDOAI]2.0.CO;2

Sánchez-Vilas, J., R. Bermúdez & R. Retuerto, 2012. Soil water content and patterns of allocation to below- and above-ground biomass in the sexes of the subdioecious plant Honckenya peploides. Ann. Bot. 110, 839–848.
https://doi.org/10.1093/aob/mcs157

Sánchez-Vilas, J. & R. Retuerto, 2017. Sexual dimorphism in water and nitrogen use strategies in Honckenya peploides: Timing matters. Journal of Plant Ecology 10, 702–712.
https://doi.org/10.1093/jpe/rtw072

Schwabe, G. H., 1970. On the algal settlement in craters on Surtsey during summer 1968. Surtsey Res. Prog. Rep. 5, 51–55.

Sigurdsson, B.D., 2009. Ecosystem carbon fluxes of Leymus arenarius and Honckenya peploides on Surtsey in relation to water availability: a pilot study. Surtsey Research 12, 77–80.

Sigurdsson, B.D. & B. Magnússon, 2010. Effects of seagulls on ecosystem respiration, soil nitrogen and vegetation cover on a pristine volcanic island, Surtsey, Iceland. Biogeosciences 7, 883–891.
https://doi.org/10.5194/bg-7-883-2010

Sigurdsson, B. D., & N. I. W. Leblans, 2020. Availability of plant nutrients and pollutants in the young soils of Surtsey compared to the older Heimaey and Elliðaey volcanic islands. Surtsey Research, 14, 91-98.
https://doi.org/https://doi.org/10.33112/surtsey.14.8

Stopps, G.J., S.N. White, D.R. Clements & M.K. Upadhyaya, 2011. The Biology of Canadian Weeds. 149. Rumex acetosella L. Can J Plant Sci, 1037–1052.
https://doi.org/10.4141/cjps2011-042

Ter Braak, C.J.F. & P. Šmilauer, 2012. CANOCO reference manual and user's guide. Software for ordination (version 5.0). Microcomputer Power, Ithaca, New York.

Visser, P., H. Louw & R.J. Cuthbert, 2010. Strategies to eradicate the invasive plant procumbent pearlwort Sagina procumbens on Gough Island, Tristan da Cunha. Conservation Evidence 7, 116–122.

Veðurstofa Íslands, 2015. Wind rose BIVM 2005-2014. https://www.vedur.is/media/vedur/BIVM_windrose_2005-2014.pdf

Warwick, S., 1979. The biology of Canadian weeds 37 Poa annua L. Canadian Journal of Plant Science: 59, 1053–1066.
https://doi.org/10.4141/cjps79-165

Wąsowicz, P., 2020. Annotated checklist of vascular plants of Iceland. Fjölrit Náttúrufræðistofnunar nr. 57. Garðabær: Náttúrufræðistofnun Íslands.
https://doi.org/10.33112/1027-832X.57

APPENDIX I

Abbreviations and full names of species

Agro cap	*Agrostis capillaris* L.
Agro sto	*Agrostis stolonifera* L.
Agro vin	*Agrostis vinealis* Schreb.
Alop gen	*Alopecurus geniculatus* L.
Ange arc	*Angelica archangelica* L.
Anth nip	*Anthoxanthum nipponicum* Honda
Arab pet	*Arabidopsis petraea* (L.) V.I. Dorof.
Arme mar	*Armeria maritima* (Miller) Willd.
Atri lon	*Atriplex longipes* Drejer
Botr lun	*Botrychium lunaria* (L.) Sw.
Caki mar	*Cakile maritima* Scop.
Care mar	*Carex maritima* Gunnerus
Cera fon	*Cerastium fontanum* Baumg.
Coch isl	*Cochlearia islandica* Pobed.
Cyst fra	*Cystopteris fragilis* (L.) Bernh.
Desc ber	*Deschampsia beringensis* Hultén, Fl. Kamtchatka
Empe nig	*Empetrum nigrum* L.
Fest ric	*Festuca richardsonii* Hook.
Gali ver	*Galium verum* L.
Gymn dry	*Gymnocarpium dryopteris* (L.) Newman
Honc pep	*Honckenya peploides* (L.) Ehrh.
Junc alp	*Juncus alpinoarticulatus* Chaix
Junc arc	*Juncus arcticus* Willd.
Leym are	*Leymus arenarius* (L.) Hochst.
Luzu mul	*Luzula multiflora* (Ehrh.) Lej.
Luzu spi	*Luzula spicata* (L.) DC.
Mert mar	*Mertensia maritima* (L.) Gray
Mont fon	*Montia fontana* L.
Phle pra	*Phleum pratense* L.
Plan lan	*Plantago lanceolata* L.
Plan mar	*Plantago maritima* L.
Poa ann	*Poa annua* L.
Poa pra	*Poa pratensis* L.
Pote ans	*Potentilla anserina* L.
Pucc coa	*Puccinellia coarctata* Fernald & Weath.
Ranu sub	*Ranunculus subborealis* Tzvelev
Rum asell	*Rumex acetosella* L.
Rum atosa	*Rumex acetosa* L.
Rume lon	*Rumex longifolius* DC.
Sagi pro	*Sagina procumbens* L.
Sali her	*Salix herbacea* L.
Sali lan	*Salix lanata* L.
Sali phy	*Salix phylicifolia* L.
Saxi ces	*Saxifraga cespitosa* L.
Scor aut	*Scorzoneroides autumnalis* (L.) Moench
Sile uni	*Silene uniflora* Roth
Stel med	*Stellaria media* (L.) Vill.
Tara spp	*Taraxacum spp*
Thym pra	*Thymus praecox* Opiz
Trip mar	*Tripleurospermum maritimum* (L.) W.D.J. Koch

Vegetation cover, gross photosynthesis and remotely sensed vegetation indices in different aged sub-arctic volcanic islands in the Vestmannaeyjar archipelago

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ABSTRACT

Surtsey and the older islands in the Vestmannaeyjar archepelago offer a unique possibility to study how sub-Arctic ecosystems develop from unvegetated mineral volcanic substrate to grasslands with thick Brown Andosol soils. The present study was carried out on 24 study plots distributed across six different ecoystems on Surtsey, Heimaey and Elliðaey islands and involved field measurements of soil volumetric water content (VWC), vascular plant cover (VPC) and instantanious rate of gross primary production (GPP). Remote sensing was also used to determine the vegetation indices of normalized difference vegetation index (NDVI), photochemical reflectance index (PRI) and chlorophyll/carotenoid index (CCI) of each plot and find their relationships to the measured VPC and GPP. Nýjahraun on Heimaey and the area not affected by seabirds on Surtsey were not significantly different in any measured variable. During their initial 48-58 years of primary succession, they had reached ca. 3% (VPC) to 12-13% (GPP, VWC) of the measured variables in the 5900-year-old Lyngfellisdalur on Heimaey, which has negligible seabird nutrient inputs. However, the measured VPC and GPP had reached similar levels in only 58 years in the seabird-affected parts of Surtsey as measured on the 5900-year-old seabird-affected Elliðaey. This shows how seabirds can greatly speed up ecosystem development by oceanic nutrient inputs into terrestrial ecosystems. Significant relationships were found between NDVI and VPC and between CCI and GPP, which may become important tools to track ecosystem development in space and time on the islands.

INTRODUCTION

Surtsey volcanic island, formed in an eruption during 1963-1967, is one of most studied ecosystems in Iceland (cf. Baldursson & Ingadóttir 2007). Most ecological studies on Surtsey have focused on community changes in flora, fauna and microbes (e.g. Magnusson *et al.* 2014, Ilieva-Makulec *et al.* 2015, Marteinsson *et al.* 2015) and only few have focused on the underlying ecosystem processes and soil development (e.g. Sigurdsson & Magnusson 2010, Sigurðsson 2011, Leblans *et al.* 2017, Sigurdsson *et al.* 2020). From these studies, it is clear that the establishment of a seabird colony on Surtsey in 1986 had a large impact on plant succession and ecosystem processes on the new island.

Now, almost 60 years after Surtsey emerged from the ocean and after both plant succession and soil development are under way, comparison to older volcanic islands in the archipelago is of interest to clarify how far ecosystem structure and function on Surtsey has reached. In the past few years, papers have been published where plant communities (Magnusson *et al.* 2014), soil development (Leblans *et al.* 2017) and nutrient availability (Sigurdsson & Leblans 2020) has been compared between Surtsey and older neighboring islands. It is, however, noteworthy that no ecological studies have so far taken place on the younger lavafield of Nýjahraun on Heimaey. The lava is from an eruption in Jan-Jul 1973.

Multispectral remote sensing captures the spectral reflectance properties of surfaces caught by the sensors that can be e.g. hand held or mounted on drones, airplanes or satellites. The reflectance can be related to plant function (e.g. Ustin *et al.*, 2009). Therefore, the use of remotely sensed vegetation indices as proxies of plant function can be exploited to parameterize relationships for estimating rates of GPP (Wong *et al.* 2019, 2020). Such relationships can then be used as means to extrapolate plot-level GPP data to larger areas.

The first aim of this study was to compare measurements in areas in the Vestmannaeyjar archipelago that differed both in age and if they had high seabird nutrient inputs (Surtsey, 58 years; Elliðaey, 5900 years) or not (Surtsey, 58 years; Nýjahraun, Heimaey, 48 years; Lyngfellisdalur, Heimaey, 5900 years: Table 1). By including all these sites we were interested to see how far the ecosystem parameters had reached in the younger lavafields, compared to the older islands where the grassland ecosystems can be considered fully developed. The second aim was to compare the Nýjahraun and Surtsey ecosystems. The third and final aim was to establish relationships between VPC and GPP and the measured vegetation indices (NDVI, PRI, CCI). Such relationships can be of high value when using remote sensing to estimate ecosystem structure and function in space and time.

METHODS

Study area

This study was performed on three islands of the volcanic Vestmannaeyjar archipelago (63°250N, 20°170W; south Iceland; Fig. 1) in mid-July 2020 and 2021. The main vegetation type on the Vestmannaeyjar archipelago is lush grassland, except in areas that are unsuitable for seabird colonization, where heathlands, herb slopes or dry meadows can be found or where the surface is in early stages of primary succession after a volcanic eruption (Magnússon *et al.* 2014). Five sites were studied with low and high natural seabird inputs and of different age (Fig. 1).

At Surtsey and Nýjahraun on Heimaey the soils and vegetation were at an early successional stage (48 and 58 years old, respectively), but Lyngfellisdalur on Heimaey and Elliðaey have well-developed soils on bedrocks that both date from eruptions that took place ca. 5900 years ago. As Nýjahraun is located on the only inhabited island in the archipelago, Heimaey,

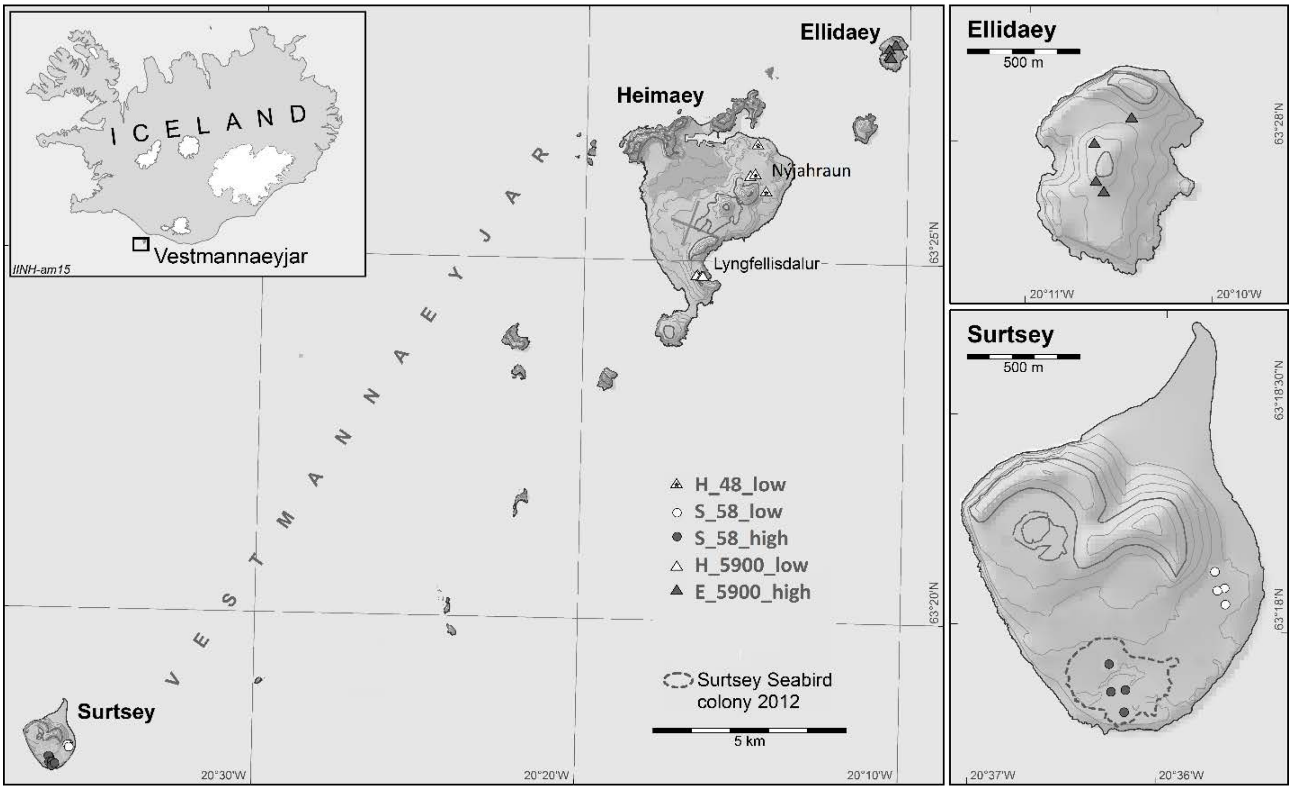

Figure 1: Location of the Vestmannaeyjar archipelago at the southwest coast of Iceland, including the three study islands, Surtsey, Heimaey and Elliðaey. The smaller two maps show the islands Elliðaey and Surstey in a greater detail. Circles show study plots on Surtsey and triangles plots on the older Heimaey and Elliðaey. The number in the site label stands for age of site in 2021 (years) and "low" or "high" stand for relative seabird nutrient inputs. Map by Anette Th. Meier.

parts of it have been heavily influenced by human activities; especially the spread of the N-fixing exotic plant species *Lupinus nootkatensis* (Sims) Donn. Parts of it remain, however, relatively intact and those were used in the study. The soil profiles at Lyngfellisdalur, Heimaey and Elliðaey were undisturbed at least since 395 AD, which was determined from the precence of an ash layer from that time <1 m below the surface (Leblans *et al.* 2017). The Surtsey, Heimaey and Elliðaey sites have different vegetation communites, which reflect the differences in seabird influence (Magnússon *et al*. 2014, Leblans *et al*. 2017). The Lyngfellisdalur and Nýjahraun sites on Heimaey are not likely to have ever hosted a seabird colonies due to their topographical characteristics, while Elliðaey has served as breeding ground for seabirds from early times. The most common seabird species on Elliðaey is Atlantic puffin (*Fratercula arctica*) but on Surtsey it is mainly seagulls of different species (*Larus* sp.) and northern fulmar (*Fulmarus glacialis*). Appendix 1 gives an overview of the researh activities that have taken place on the older islands.

Table 1. Explanation for the different site names used in this study.

Site name	Island	Yrs of origin	Seabird influence	No of plots
H-48-low	Heimaey	1973	low	4
S-58-low	Surtsey	1963-67	low	4
S-58-high	Surtsey	1963-67	high	4
H-5900-low	Heimaey	5900 BP	low	4
E-5900-high	Elliðaey	5900 BP	high	4

The study took place in four permanent 10x10 m study plots at each site that were established at Nýjahraun in 2021, Lyngfellisdalur and Elliðaey in 2013 and on Surtsey in 1990 (Table 1, Fig. 2). The vegetation in the high nutrient inputs sites at Elliðaey and Surtsey was a grassland dominated with *Festuca richardsonii* Kartesz, *Poa* sp. and *Stellaria media* (L.) Vill. In the Lyngfellisdalur "old site" the vegetation communty was dominated by *Anthoxantum odoratum* L., *Galium verum* L. and *Luzula multiflora* (Ehrh.) Lej., a herb rich heathland community representing lower fertility (Magnusson *et al*. 2014). The vegetation on Nýjahraun and outside the seabird colony on Surtsey was dominated by *Honckenya peploides* (L.) Ehrh. and *Leymus arenarius* (L.) Hochst, and also moss on Nýjahraun. Further information about the site conditions can be found in Sigurdsson & Leblans (2020), Leblans *et al.* (2017) and Magnusson *et al.* (2014).

GPP and environmental parameters

Measurements took place in middle of July 2020 on Surtsey and in 2021 on Heimaey and Elliðaey with an EGM-4 portable gas analyzer and a transparent CPY5 cuvette (PP-Systems, Amesbury, MA, USA) in the permanent plots. Four measurements were done at 1, 4, 8 and 11 m along a diagonal line across each plot. First the net CO_2 flux (Net Ecosystem Exchhange; NEE) was measured in light and thereafter the cuvette was covered and the measurement was repeated in darkness, yielding the ecosystem respiration rate (RE). Gross photosynthesis rate (GPP) was calculated as:

$$GPP = NEE + RE\,. \qquad (1)$$

Other measurements recorded together with the GPP measurements included soil temperature at 10 cm depth and photosynthetically active radiation (PAR) in μmol photons m^{-2} s^{-1}. Also we measured volumetric water content (VWC;%) in the 0-5 cm surface soil layer (Theta-probe, model ML3, Delta-T Devices Ltd, Cambridge, UK).

Remote sensed vegetation indices

Measurements were done in middle of July 2020 on Surtsey and 2021 on Heimaey and Elliðaey with multispectral sensors mounted on a 2 m long pole (Spectrosense 2+, model SKL910/4, Skye Instruments Ltd., Powys, UK). Each measurement covered 0.6 m^2 of surface. Five measurements were done above each plot, one in each corner and one in the middle. The instrument measures four spectral bands from which three vegetation indices were calculated:

$$NDVI = \frac{R800 - R630}{R800 + R630}\,, \qquad (2)$$

$$PRI = \frac{R532 - R570}{R532 + R570}\,, \qquad (3)$$

$$CCI = \frac{R532 - R630}{R532 + R630}\,, \qquad (4)$$

where R indicates reflectance at the specific wavelengths in nm.

Normalized difference vegetation index (NDVI) is calculated from visible and near-infrared wave bands and relates to the density of chlorophyll per unit area (Myneni *et al.*, 2002). It is more related to vegetation cover and structure than plant physiological activity

Figure 2: Six out of the 20 study plots used in this study. Two study plots on Nýjahraun on Heimaey (a-b). a) In the most sheltered parts of Nýjahraun moss is dominating, b) but in the largest and more exposed part on Nýjahraun vascular plants dominate. c) Plot outside and inside d) the seagull colony on Surtsey. Plots on 5900 year old bedrock in e) Lyngfellisdalur on Heimaey where sebird influence is at minimum and f) on Elliðaey where seabird nutrient inptus are high. Photos BDS.

such as photosynthetic rates (GPP). Photochemical reflectance index (PRI) is responsive to the carotenoid pigment composition in leaf tissues (Peñuelas *et al.*, 2011). Those pigments are involved in regulating photosynthetic processes. It shows the leaf light use efficiency per unit leaf surface, rather than the rate of photosynthesis per unit area (Peñuelas *et al.*, 1995); i.e. it needs to be scaled with both surface leaf area (vegetation cover) and photosynthetically active radiation (PAR) to give GPP. Chlorophyll/carotenoid index (CCI) is closely related to PRI, and is also related to the carotenoid pigment composition

(Gamon *et al.*, 2016). It is, however, also sensitive to the amount of chlorophyll pigments (Wong *et al.*, 2019). That means that it is more directly related to gross photosynthesis (GPP) than PRI is. Therefore it catches both physiological and structural features of plant canopies.

Vegetation cover

A measurement tabe was placed across the 10 x 10 m plots and the cover of both non-vascular and vascular plants was determined by line-intercept method (see Magnússon *et al*. 2014). Existing data was used from Surtsey (from 2018) and Lyngfellisdalur and Elliðaey (from 2010), whereas the measurements were done in July 2021 for Nýjahraun.

Data and statistical analyses

The site differences were tested with an one-way ANOVA. In case of significant ANOVA model, pairwise differences were tested by post hoc LSD tests, when the requirements of normality and homoscedasticity of the residuals were met. The latter was visually inspected. Linear regression was used to derive relationships between GPP and VPC and vegetaton indices.

RESULTS AND DISCUSSION

Soil water

Soil water content was significantly higher in the older soils of Elliðaey and Lyngfellisdalur, than in the younger Surtsey and Nýjahraun soils (Fig. 3a), but no difference was found between H-49-low and S-59-low. The seabird-affected soils on Surtsey contained intermediate amounts of water. The observed difference mirrored the differences in soil organic matter between the sites (Leblans *et al*. 2017) and is therefore indicative of improvements in water holding capacity as the soils develop.

Vegetation cover

Moss cover was highest on the old soils with low nutrient inputs in Lyngfellisdalur, but due to relatively high within-site variability, it was not significantly different across sites (Table 1). Vascular plant cover (VPC) was therefore a more sensitive parameter than total plant cover, both to age and to nutrient inputs (Fig. 3b and Table 2). It was noteworthy that the highest VPC was found within the 58 years old seagull colony on Surtsey (111% ±18%), even if it was not significantly different from the seabird-affected Elliðaey (92% ±3%). The old Lyngfellisdalur, with low seabird influence, had an intermediate vascular plant cover of 69%, but still the highest total plant cover, due to the high contribution of mosses there (Table 2). The difference in soil nitrogen (N) among four of the sites has the same pattern as the difference in VPC found here (Leblans *et al.* 2017).

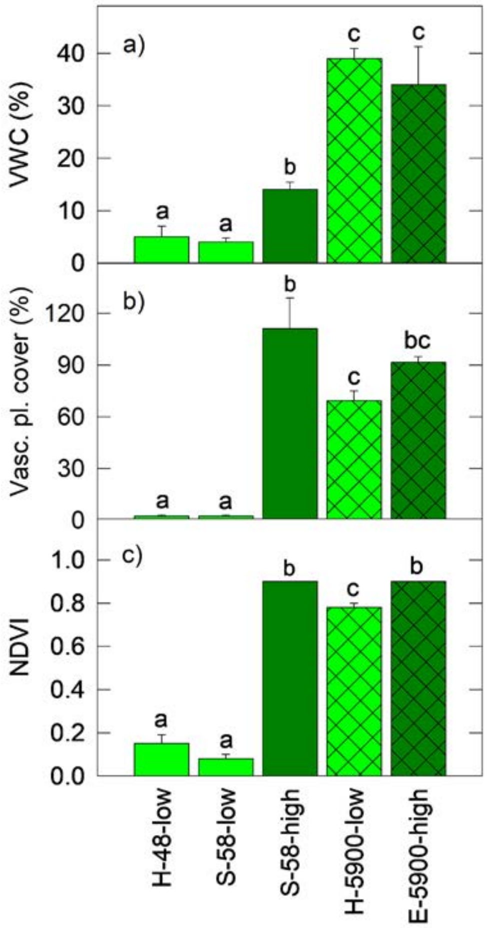

Figure 3. a) Volumetric water content (VWC), b) Vascular plant cover and c) Normalized Difference Vegetation Index (NDVI) on the 48 years old Nýjahraun on Heimaey (H-48-low), on the 58 year old Surtsey outside (S-58-low) and within a seabird affected area (S-58-high), in Lyngfellisdalur on Heimaey since 5900 BP without seabird influence (H-5900-low) and on Elliðaey (E-5900+high) where seabirds bring in nutrients from the sea. Vertical bars represent SE of n=4. Different letters above bars indicate significant differences (P<0.05) by post-hoc LSD tests.

That Surtsey (S-58-high) had already reached significantly higher VPC than was found in the 5900-year-old Lyngfellisdalur shows how the seabird nutrient inputs have greatly enhanced the plant succession rate, as has also been found by others (e.g. Magnusson *et al.* 2014). On the other young

Table 2. Moss cover and total plant cover, surface cover of vegetation in the cuvette used for GPP measurements, as well as mean soil temperature at 10 cm depth (Ts10), irradiance, net ecosystem exchange (NEE, µmol CO_2 m^{-2} s^{-1}; note negative values indicate net uptake) and ecosystem respiration (RE, µmol CO_2 m^{-2} s^{-1} on the 48 years old Nýjahraun on Heimaey (H-48-low), on the 58 years old Surtsey outside (S-58-low) and within a seabird affected area (S-58-high), in Lyngfellisdalur on Heimaey since 5900 BP without seagull influence (H-5900-low) and on Elliðaey (E-5900+high) where seabirds bring in nutrients. Different letters behind means indicate significant differences among sites (P<0.05) by post-hoc LSD tests.

Ecosystem	Moss cover	Total pl cover	Cuvette surface. cover	Ts10	PAR	NEE	RE
H-48-low	7%	9.2% a	23% a	16.7 a	349 a	-0.06	0.06 a
S-58-low	0%	2.3% a	8% a	13.9 b	285 a	-0.13	0.07 a
S-58-high	0%	111% c	94% b	12.5 c	765 b	-0.80	1.32 c
H-5900-low	73%	142% b	100% b	12.2 c	470 ab	-0.56	0.69 b
E-5900-high	0.3%	92% c	100% b	13.0 bc	620 b	+0.23	3.33 d
ANOVA P	n.d.	<0.001	<0.001	<0.001	0.03	0.08	<0.001

sites, where seabird nutrient inputs had not affected the succession, the VPC remained at only 2% after 48-58 years (Fig. 3b). The pattern in VPC more or less reflects the reported differences in accumulated soil nitrogen (N) stocks among the sites (Leblans et al. 2017).

NDVI and its relationship to vegetation cover

The site differences in measured NDVI had very similar relative differences as were seen in vascular plant cover (Fig. 3b and c). The two seabird-influenced sites on Surtsey and Elliðaey had significantly highest NDVIs of 0.90, while Lyngfellisdalur site had an intermediate NDVI of 0.78 and Nýjahraun and most of Surtsey, not affected by seabirds, lowest of 0.11 on average.

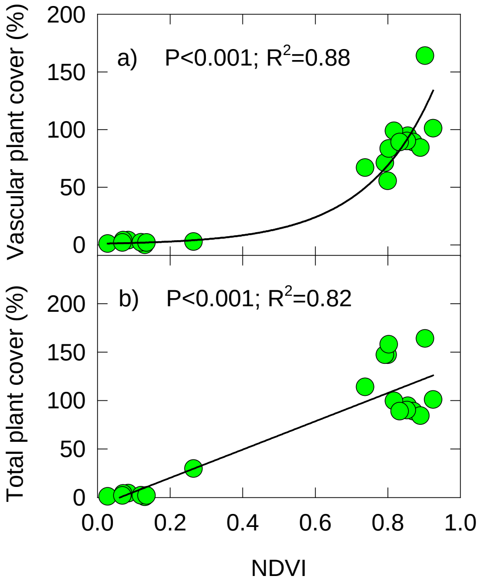

Figure 4. The relationship NDVI and (a) vascular plant cover (VPC) and (b) total plant cover (TPC) including mosses and lichens. The two calibration curves are shown in Eqs. 5 and 6.

Two other studies have reported NDVI of Surtsey, one based on high-resolution satellite data around the permanent study plots on Surtsey (Magnússon et al. 2020) and another using a coarser resolution but mapping the long-term annual changes in the NDVI across the whole island (Magnússon et al. 2022). The present close-to ground NDVI measurements of the permanent plots gave comparable NDVI values inside and outside the seabird-affected area as the Magnússon et al. (2020) study, but somewhat higher NDVI values inside the seabird-affected area than Magnússon et al. (2022) reported. The low spatial resolution used in that study will, however, include more exposed unvegetated lava surfaces within each pixel than measured within or just around the permanent plots, which likely explains this difference.

There was a highly significant exponential relationship between NDVI and vascular VPC across the sites in the present study, shown in Fig. 4a and with Eq. 5:

$$VPC = e^{5.2948 \times NDVI}, \quad (5)$$

where VPC is in % (summed cover of all vascular plant species) and NDVI is a unitless index of 0-1. Eq. 5 explained 88% of the observed variation in VPC among all plots on the three islands. This relationship is of the same form as has been reported between NDVI and aboveground vegetation biomass in Surtsey (Magnússon *et al.* 2020) (Table 2).

The relationship between NDVI and total plant cover (TPC) across the three islands, including moss cover, was however of different form, linear instead of exponential and somewhat weaker ($R^2 = 0.82$, Fig. 4b):

$$TPC = 145.91 \times NDVI - 8.86\,, \qquad (6)$$

This observed difference in the form of the relationship and its lower R^2 may indicate an issue when NDVI is used to estimate vegetation cover across variable plant communities or communities where moss is an important component. A vegetation community with a moss layer has more layering in the vegetation canopy. It may therefore not be so surprising that VPC was more strongly related to remote sensed NDVI. Further work is needed to develop robust methods to estimate moss biomass or cover from multispectral measurements for subarctic ecosystems.

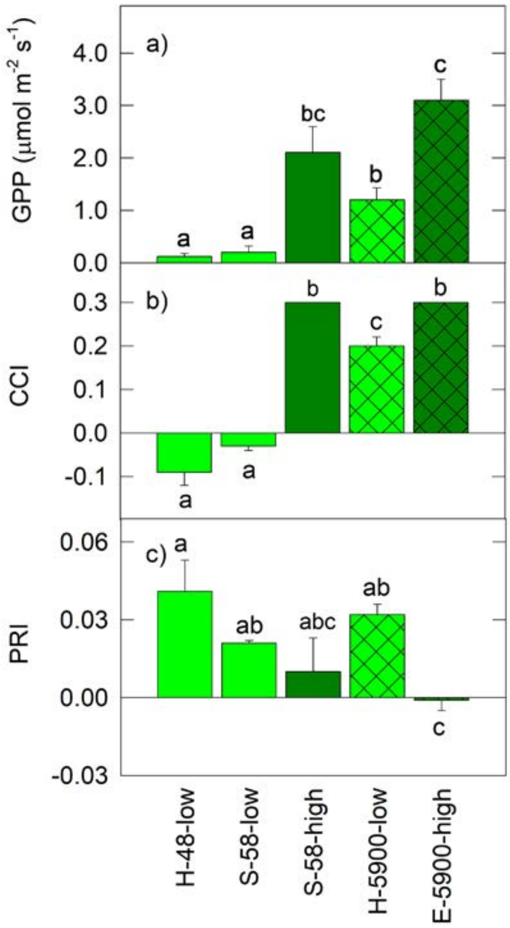

Figure 5. Gross Primary Production (GPP), chlorophyll/carotenoid index (CCI) and photochemical reflectance index (PRI) in the 48 years old Nýjahraun on Heimaey (H-48-low), on the 58 years old Surtsey outside (S-58-low) and within a seabird-affected area (S-58-high), Lyngfellisdalur since 5900 BP on Heimaey (H-5900-low) without seabird influence and Elliðaey (E-5900-high) where seabirds bring in nutrients from the sea. Vertical bars represent SE of n=4. Different letters above bars indicate significant differences (P= <0.05) by post-hoc LSD tests.

GPP, CCI and PRI

How much energy and carbon enter the ecosystem annually is mainly a function of three things: i) amount of leaf area, ii) photosynthetic activity of the plants and iii) length of the growing season (Chapin *et al.* 2002). In this study we have measurements of plant cover and remote sensed NDVI that both are closely related to i) and measurements of gross photosynthetic rate (GPP) and the remote sensed plant indices PRI and CCI that all are related to ii).

The measured GPP was significantly lowest in Nýjahraun on Heimaey and in areas outside the seabird colony on Surtsey (Fig. 5a), where the plant cover and NDVI was also lowest (Fig. 3). The significantly highest GPPs were measured in the seabird-affected sites, where the nutrient availability was highest (Leblans *et al.* 2017). This pattern of GPP was the same as was reported in an earlier study on Surtsey, Elliðaey, Álsey and Heimaey (Sigurdsson 2011). The GPP of Lyngfellisdalur was significantly lower than of the fertile grassland of Elliðaey (Fig. 5a), which was in line with significantly lower chloropyll per unit area (NDVI) there (Fig. 3c), even

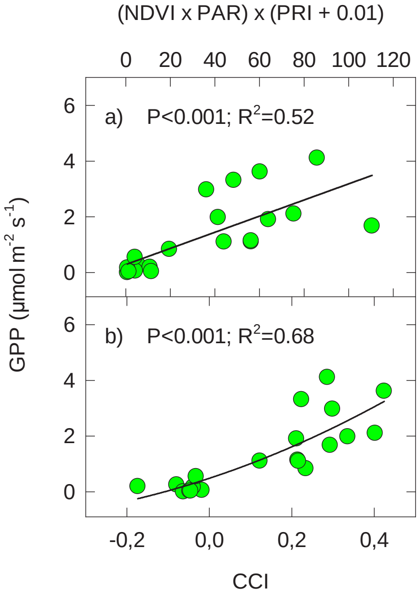

Figure 6. The relationship between (a) uncalibrated GPP (calculated from measured NDVI, PRI and PAR) and measured GPP and (b) between chlorophyll/carotenoid index (CCI) and measured GPP. The two calibration curves are shown in Eqs. 7 and 8.

if it had the highest total plant cover (Table 2)

PRI estimates light use efficiency of plants at the level of PAR that occurs when measurements are taken (Wong *et al.* 2019). PRI did not change significantly across the sites, except between the Nýjahraun and Elliðaey, where the PRI was significantly lower in the dense vegetation community of the latter (Fig. 5c). It should, however, be noted that the PAR was somewhat lower when the Nýjahraun and Surtsey seabird-colony plots were measured (Table 2), which makes a direct comparison of the PRI values across the sites problematic.

When we tried to use PRI to model the measured GPP across the islands, the best relationship also included information about NDVI and PAR (Fig. 6a):

$$GPP = 0.029 \times \left((NDVI \times PAR) \times (PRI + 0.1)\right) + 0.287, \quad (7)$$

where GPP is measured gross photosynthesis in μmol CO_2 m^{-2} s^{-1} and PAR is photosynthtically active radiation in μmol photons m^{-2} s^{-1} and NDVI and PRI are vegetation indices. This relationship is similar to what Wong *et al.* (2020) developed for forest ecosystems. Even if Eq. 7 significantly simulated the measured GPP, it only explained 52% of the observed variation in GPP (Fig. 6a). Therefore, a better model would be preferred for remote sensing of GPP.

The chlorophyll/carotenoid index (CCI) was developed later than NDVI and PRI indices (Gamon *et al.*, 2016) and it has been identified as more directly related to gross photosynthesis than PRI (Wong *et al*., 2019). Indeed, the measured differences in CCI more-or-less mirrored the relative differences in measured GPP (Fig. 5b). It sensed the two sites with high nutrient inputs with the significantly highest CCI values, the Lyngfellisdalur plant community with intermediate values and the Nýjahraun and Surtsey outside the seagull colony with the significantly lowest CCI values.

When we used CCI to estimate GPP across all the sites, the following curvilinear relationship was found (Fig. 6b):

$$GPP = 0.4867 + 4.8824 \times CCI + 3.8384 \times CCI^2 . \quad (8)$$

This relationship explained 68% of the observed variability in GPP, which is a promising finding. It is therefore clear that the use of the CCI index for estimating GPP is to be preferred method to the more traditional way of using both NDVI and PRI for such modelling. However, further measurements of GPP and CCI at contrasting PAR conditions should be done to better test how sensitive the CCI is to variations in light compared to GPP.

CONCLUSIONS

Nýjahraun versus Surtsey

This was the first study of primary succession on the Nýjahraun lavafield on Heimaey to our knowledge. We did not find any significant differences in the measured variables between the intact parts of Nýjahraun and the plots outside the seabird colony in Surtsey. As colonization of N-fixing plants has been found to be an important driver of primary succession on other volcanos and cause similar shifts as the seabirds on Surtsey (del Moral & Magnusson 2014), it would be interesting to add more plots to the Nýjahraun study to also include the areas covered by *Lupinus nooktatensis* there.

How far has Surtsey come compared to the older islands?

This study shows once again how the plant community and plant-derived process in the seabird-affected area in Surtsey have in less than 60 years reached similar levels as observed on a 5900-year-old island in the Vestmannaeyjar archipelago. However, when the areas outside the seagull colony of Surtsey were compared to Lyngfellisdalur the ecosystem development had only reached 3% (VPC) to 12-13% (GPP, VWC) in the first 48-58 years.

How important are seabirds for ecosystem development?

This study adds to the older existing studies from Surtsey in showing how the seabirds greatly speed up the ecosystem development with their nutrient inputs from the ocean to the terrestrial ecosystem. Especially the plant processes are maximized within decades, while soil development, here represented by VWC, responds more slowly.

Remote sensing and other planned research

The estimation of aboveground plant biomass for the whole area of Surtsey by Magnússon *et al.* (2020) was the first remote sensing application used in ecological research on the island. The present study adds to this work and is an important step towards using such tools to track vegetation development and GPP in space and time on the island.

REFERENCES

Baldursson, S. & Á. Ingadóttir (Eds.), 2007. Nomination of Surtsey for the UNESCO World Heritage List. Reykjavik: Icelandic Institute of Natural History.

Chapin III, F.S., P.A. Matson & H.A. Mooney, 2002. Principles of terrestrial ecosystem ecology. New York, Berlin, London: Springer.

del Moral, R. & B. Magnússon, 2014. Surtsey and Mount St. Helens: a comparison of early succession rates. Biogeosciences, 11(7), 2099-2111. https://doi.org/10.5194/bg-11-2099-2014

Gamon, J.A., K.F. Huemmrich, C.Y.S. Wong, I. Ensminger, S. Garrity, D.Y. Hollinger, Aþ Noormets & J. Peñuelas, 2016. A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers. Proceedings of the National Academy of Sciences, USA 113: 13087-13092.

Ingimundardóttir, G.V., N. Cronberg & B. Magnússon, 2022. Bryophytes of Surtsey, Iceland: Latest developments and a glimpse of the future. Surtsey Research, 15, 61-87. https://doi.org/10.33112/surtsey.15.6

Leblans, N.I.W., B.D. Sigurdsson, R. Aerts, S. Vicca, B. Magnússon & I.A. Janssens, 2017. Icelandic grasslands as long-term C sinks under elevated organic N inputs. Biogeochemistry, 134(3), 279-299. https://doi.org/10.1007/s10533-017-0362-5

Magnússon, B., S.H. Magnússon, E. Ólafsson & B.D. Sigurdsson, 2014. Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. Biogeosciences, 11(19), 5521-5537. https://doi.org/10.5194/bg-11-5521-2014

Magnússon, B., G.A. Gudmundsson, S. Metúsalemsson & S.M. Granquist, 2020. Seabirds and seals as drivers of plant succession on Surtsey. Surtsey Research, 14, 115-130. https://doi.org/10.33112/surtsey.14.10

Magnússon, B., P. Wasowicz & B. Magnússon, 2022. Vascular plant colonisation, distribution and vegetation development on Surtsey during 1965–2015. Surtsey Research, 15, 9-29. https://doi.org/10.33112/surtsey.15.2

Myneni R.B., S. Hoffman, Y. Knyazikhin, J.L. Privette, J. Glassy, Y. Tian, Y. Wang, X. Song, Y. Zhang, G.R. Smith, A. Lotsch, M. Friedl, J.T. Morisette, P. Votava, R.R. Nemani & S.W. Running, 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sens. Envir. 83: 214-231. https://doi.org/10.1016/S0034-4257(02)00074-3

Peñuelas, J., I. Filella & J.A. Gamon, 1995. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. New Phytol. 131: 291-296. https://doi.org/10.1111/j.1469-8137.1995.tb03064.x

Peñuelas J., M.F. Garbulsky, & I. Filella I., 2011. Photochemical reflectance index (PRI) and remote sensing of plant CO2 uptake. New Phytol. 191: 596-599. https://doi.org/10.1111/j.1469-8137.2011.03791.x

Ustin, S.L., A.A. Gitelson, S. Jacquemoud, M. Schaepman, G.P. Asner, J.A. Gamon & P. Zarco-Tejada, 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. Remote Sens. Envir. 113: S67-S77. https://doi.org/10.1016/j.rse.2008.10.019

Sigurðsson, B.D., 2011. Mælingar á virkni vistkerfa í Surtsey og nálægum eyjum Vestmannaeyja. Rit Fræðaþings landbúnaðarins, 8, 396-399.

Sigurdsson, B.D., & N.I.W. Leblans, 2020. Availability of plant nutrients and pollutants in the young soils of Surtsey compared to the older Heimaey and Elliðaey volcanic islands. Surtsey Research, 14, 91-98. https://doi.org/10.33112/surtsey.14.8

Wong, C.Y.S., P. D'Odorico, Y. Bhathena, M.A. Arain, & I. Ensminger, 2019. Carotenoid based vegetation indices for accurate monitoring of the phenology of photosynthesis at the leaf-scale in deciduous and evergreen trees. Remote Sens. Envir. 233: 111407. https://doi.org/10.1016/j.rse.2019.111407

Wong, C.Y.S., P. D'Odorico, M.A. Arain & I. Ensminger, 2020. Tracking the phenology of photosynthesis using carotenoid-sensitive and near-infrared reflectance vegetation indices in a temperate evergreen and mixed deciduous forest. New Phytol., 226(6), 1682-1695. https://doi.org/10.1111/nph.16479

APPENDICES

Appendix 1. Overview over research excursions to the older islands in the Vestmannaeyjar archipelago, who were primarily responsible for measurements and publications from this work so far.

Date	Who	Main research activities and publications
Álsey		
10 Jul 2010	BM, BDS, Erling Ólafsson, *et al.*	Vegetation and invertebrate survey, C-fluxes (Sigurðsson, 2011)
Elliðaey		
11 Jul 2010	BM, BDS, Erling Ólafsson, *et al.*	Vegetation and invertebrate survey, C-fluxes (Sigurðsson, 2011)
15-24 Jul 2013	BDS, Járngerður Grétarsdóttir, Hafdís Hanna Ægisdóttir, *et al.*	Permanent plots established, vegetation survey (Magnússon *et al.*, 2014)
15-24 Jul 2013	BDS, Niki Leblans, *et al.*	Soil sampling, vegetation harvest (Thuys, 2014; Leblans *et al.*, 2017) and PRS probes (Sigurdsson & Leblans, 2020).
19-20 Jul 2018	Gróa Valgerdur Ingimundardóttir, Nils Cronberg *et al.*	Bryophyte survey (Ingimundardóttir *et al.*, 2022)
28 Jul 2021	BDS, EMK	Soil fauna sampling, NDVI and C-fluxes on permanent plots
Lyngfellisdalur - Heimaey		
15-24 Jul 2013	BDS, Járngerður Grétarsdóttir, Hafdís Hanna Ægisdóttir, *et al.*	Permanent plots established, vegetation survey (Magnússon *et al.*, 2014)
15-24 Jul 2013	BDS, Niki Leblans, *et al.*	Soil sampling, vegetation harvest (Thuys, 2014; Leblans *et al.*, 2017) and PRS probes (Sigurdsson & Leblans, 2020).
29 Jul 2021	BDS, EMK	Soil fauna sampling, NDVI and C-fluxes on permanent plots
Nýjahraun - Heimaey		
29 Jul 2021	BDS, EMK	Soil fauna sampling, soil sampling, NDVI and C-fluxes on permanent plots

REFERENCES

Not found in the paper

Thuys, R., 2014. Hoe veranderen plant traits langsheen een bodemchronosequentie op IJslandse eilanden? (M.Sc. thesis). University of Antwerp, Antwerp, Belgium.

Sequence-based identification of soil fungi in different habitats on Surtsey

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ABSTRACT

Studies on primary succession and biological surveys in Surtsey have described the presence of different organisms including plants, soil fauna and fungi. However, since the last fungal census of 2008, based on visual observations, no further studies on fungal communities on the island have been published. In the present study, we aimed to expand the knowledge of the fungal communities of Surtsey using Internal Transcribed Spacer (ITS2) metabarcode sequencing to survey soil samples from 23 permanent plots, within and outside a gull colony. Additionally, we related fungal community composition to soil and ecosystem environmental variables that have been analyzed from these plots previously. We report at least 18 new genera and 44 new species for Iceland and 56 new species for Surtsey in this metabarcode survey, likely representing a combination of established organisms as well as those that may be present as dormant propagule bank. Our data indicate that fungal communities differ in areas with and without sea gulls as well as those that differ in soil substrate. Further, the community composition correlates with the number of gull nests, vegetation cover, ecosystem respiration, total N and exchangeable P. This survey provides new insights on the fungal community dynamics in relation to other biotic and abiotic factors. These findings complement what available data on soil biosphere on Surtsey and improve our understanding of primary succession.

INTRODUCTION

After Surtsey was formed between 1963 and 1967 primary succession has taken place and plants and sea birds have established in some areas contributing to soil formation and facilitating the arrival of other colonizers (Magnússon *et al.,* 2009). Several studies on primary succession and a variety of biological surveys have reported the presence of different taxonomic groups including lichens, vascular plants, soil microfauna and fungi (Magnússon *et al.,* 2009; Eyjólfsdóttir. 2008; Ilieva-Makulec *et al.*, 2015). For example, the funga on the island have been described by collecting sporocarps (Baldursson & Ingadöttir. 2007; Eyjólfsdóttir. 2008) and fungal spores (Greipsson & El-Mayas, 2000). In those studies, species representing different fungal phyla and occupying different ecological niches were observed. For example, ectomycorrhizal and arbuscular mycorrhizal fungi, which have an important role for plant colonization in the newly formed habitats, have been reported (Magnússon *et al.,* 2009). However, since the last fungal census in 2008 no additional studies on fungal communities have been published even though the research on colonization and expansion by flora and fauna has continued (Magnússon *et al.,* 2020).

Metabarcode sequencing provides means to study soil fungal communities in greater depth and resolution (Baalid *et al.,* 2012; Geml *et al.,* 2014) and has been a valuable in studying fungal primary succession (Baalid *et al.,* 2012; Brown and Jumpponen, 2014). In the present study, we

https://doi.org/10.33112/surtsey.15.4

used metabarcode sequencing to analyze soil fungal communities in 23 permanent plots within and outside the gull colony in the southern part of Surtsey. We aimed to expand the knowledge of the species present on the island. Additionally, our goal was to correlate the fungal community structure with the environmental variables that have been measured in these plots over the years.

MATERIALS AND METHODS

The surveyed fungal communities in soils sampled from the 23 permanent plots established in 1990. These plots chosen to cover different substrate types and elucidate the influence of seagulls. The plots were located within and beyond the seagull colony. The two areas were then further subdivided into plots representing two substrates (Fig. 1): 1. Plots with no or shallow (≤10 cm) soils formed by windborne tephra sands that had covered the basaltic lava surfaces (Lava substrate) and 2. plots with deep soils (> 30 cm soil) in areas where the tephra sands had been deposited during the eruption (Sand substrate) (see Leblans *et al.*, 2014 for further details) (Table 1). Distinct plant communities have established within and beyond the seagull colony depending on the difference in the soil substrates (Table 1; Magnússon *et al*., 1996; Leblans *et al*., 2014).

In July 2014, we collected ten soil samples within each permanent plot along a 10 m. transect. The soil samples were pooled to one per plot. From this pool approx. 30 grams of soil was preserved in 25ml of 2X CTAB buffer and transported to the laboratory at Lund University where the material was freeze dried, ball-milled and the DNA was extracted using CTAB (hexadecyltrimethylammonium bromide) and EDTA (Ethylenediaminetetraacetic acid). The nucleic acids were purified from the cellular debris by chloroform and precipitated using isopropanol/ethanol. The precipitated extracts were further purified using the NucleoSpin Soil DNA extraction kit (Macherey-Nagel. Düren. Germany).

Aliquots of the extracted DNAs were shipped to Kansas State University and stored at -20°C until processed further. The DNA concentration

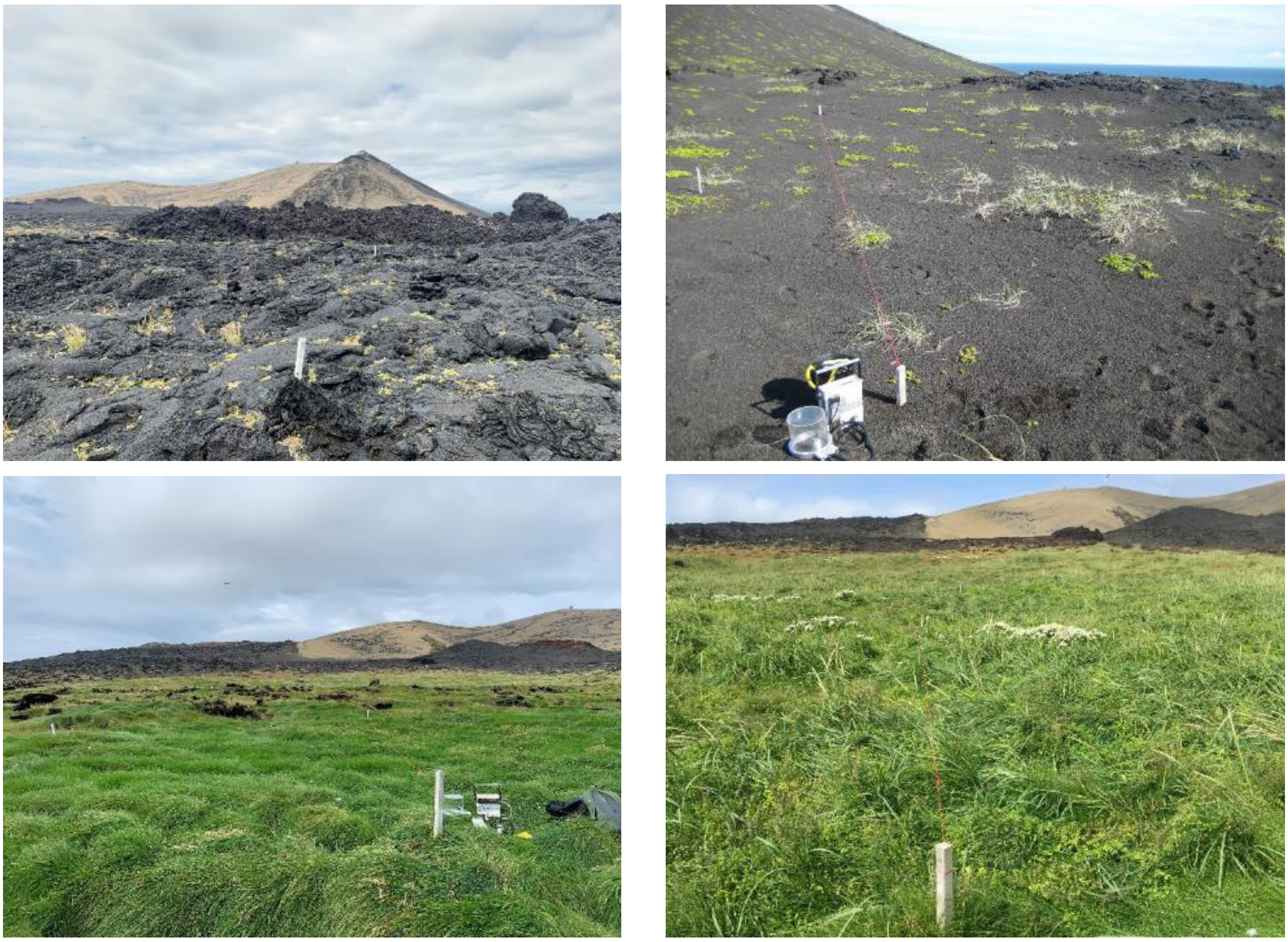

Figure 1. Photographs of the permanent plots formed on a lava substrate (to left) and sand substrate (to right) outside (top two) and inside (bottom two) the gull colony. Photos BDS.

Table 1. Characteristics of the permanent survey plots on Surtsey. Number of seabird nests during 2003-2015 within 1000 m^2, vascular plant and moss cover (%) in 2016, aboveground plant biomass (g m^{-2}) in 2018, Normalized Difference Vegetation Index (NDVI, unitless) 2016-2020, soil pH in 2004 and soil organic C and N concentration (%) in the 0-10 cm stratum in 2014, exchangeable total mineral N, P, Cu and Cd (μg of element 10 cm^{-2} 5 days^{-1}) in 2013 and ecosystem respiration (μmol CO$_2$ m^{-2} sec^{-1}) measured annually during 2015-2020.

	Inside the gull colony		Outside the gull colony	
Substrate	Shallow = lava	Deep = sand	Shallow = lava	Deep = sand
Seabird nests[1]	3.8	3.1	0.0	0.0
Flora				
Dominant vascular plant spp[1,2]	*Festuca rubra > Poa pratensis > Poa annua > Sagina procumbens*	*Poa pratensis > Stellaria media > Leymus arenarius*	*Sagina procumbens > Puccinellia distans > Cerastium fontanum > Silene uniflora*	*Honckenia peploides > Leymus arinarius > Rumex acitocella > Siline uniflora*
Vasc. pl. cover[1]	68%	177%	2%	5%
Moss cover[1]	1%	0%	5%	0%
Veg. biomass[1]	234	576	4	9
NDVI[5]	0.73	0.89	0.14	0.10
Soil				
pH[3]	6.5	6.8	7.2	7.8
Soil C[3]	8.9	1.4	0.24	0.04
Soil N[3]	0.52	0.11	0.02	0.01
Exch.able N[4]	21.3	111.2	6.6	5.3
Exch.able P[4]	20.2	20.5	0.5	0.4
Exch.able Cu[4]	0.06	0.08	0.24	0.13
Exch.able Cd[4]	0.01	0.01	0.06	0.04
Processes				
Ecos. Resp.[3,5]	1.65	2.24	0.08	0.10

1) Magnússon *et al.*, 2020. 2) Magnússon *et al.*, 2014. 3) Sigurdsson & Magnusson, 2010. 4) Sigurdsson & Leblans, 2020, 5) Sigurdsson *et al.*, 2022

was measured using a Nanodrop ND2000 spectrophotometer (Thermo Scientific, Wilmington, Delaware, USA) and normalized to 5 ng/μL. For positive control, we constructed the fungal mock community from nine fungal pure cultures that broadly represent fungal taxa (Ascomycota: *Aspergillus niger*, *Chaetomium globosum*, *Penicilium griseoroseum*), *Saccharomyces cerevisiae*, *Sordaria fimicola*; Basidiomycota: *Coprinopsis cinerea;* Chytridiomycota: *Phlyctochytrium acuminatum* (synonym *Spizellomyces acuminatus*); Mucoromycota: *Phycomyces blakesleeanus*, *Rhizopus stolonifera*). Molecular grade RNA- and DNA-free H$_2$O was used as a negative control.

We targeted Internal Transcribed Spacer 2 (ITS2) using forward fITS7 (Ihrmark et al. 2012) and reverse ITS4 (White et al. 1990) primers with 12bp barcodes as described in Narayanan et al. (2021). All PCR reactions were performed in triplicate 50μL reactions. Each PCR reaction included 10μL or 20ng of the template, 200 μM of each deoxynucleotide, 1μmol of forward and reverse primers, 10 μL of 5X Green HF PCR buffer (Thermo Scientific,Wilmington, Delaware, USA), 14.75 μL of molecular grade water and 0.5 units of the proofreading Phusion Green Hot Start II High-Fidelity DNA polymerase (Thermo Scientific, Wilmington, Delaware, USA). PCR amplification was performed using Eppendorf MasterCyclers (Eppendorf, Hamburg, Germany). The PCR reactions began with an initial denaturing step for 30 s (98°C) and were followed by 35 cycles of 10 s of denaturing (98°C); 30 s of annealing (54°C); 1 min of extension (72°C); and concluding with a 10 min final extension (72°C). Positive and negative controls were included in every PCR amplification.

The PCR products were visualized by agarose gel (1.5%) electrophoresis to ensure the successful amplification and correct amplicon sizes. The triplicate amplicons were combined into one per experimental unit and cleaned using Omega Mag-bind® RXNPure Plus system following a modified manufacturer protocol using 1:1 ration of magnetic beads to the

PCR volume and two rinse steps with 80% ethanol. The cleaned product was quantified using Nanodrop ND2000 spectrophotometer (Thermo Scientific, Wilmington, Delaware, USA) and 250ng of amplicons from each experimental unit pooled separately for sequencing. Illumina-specific primers and adapters were added in four PCR cycles with KAPA Hyper Prep Kit (Roche, Pleasenton, CA USA) and 0.5µg starting DNA. Libraries were sequenced (2 x 300 cycles) using Illumina MiSeq Personal Sequencing System at the Integrated Genomic Facility at Kansas State University. Sequence data are available at the Sequence Read Archive (BioProject PRJNA815675).

Sequence data processing

We processed 941,027 (37,641 ± 12,933) raw sequences using the mothur pipeline (v. 1.38.0; Schloss et al. 2009) as per the MiSeq standard operation protocol (Kozich et al. 2013) where possible. Sequences were extracted from paired-end .fastq files, reverse and forward reads contiged and any sequences with ambiguous bases, sequences with more than 1base pair (bp) mismatch with primer and any mismatches to the sample-specific 12 bp molecular identifiers (MIDs), or homopolymers longer than 9 bp were omitted. The >99% similar sequences were pre-clustered (Huse et al. 2008), screened for chimeras using UCHIME algorithm (Edgar et al. 2011), and putative chimeras removed. The remaining sequences were assigned to taxa using the UNITE reference data base (Abarenkov et al. 2020) and clustered to Operational Taxonomic Units (OTUs) at 97% similarity using vsearch (Rognes et al. 2016). This resulted in a total of 159,948 high quality target sequences (6,898 ± 3,434 sequences per sample). Rare OTUs (fewer than 10 in the dataset) and those that were detected in the negative controls were removed from the further analysis.

We iteratively (100 iterations) estimated bacterial and fungal richness and diversity for each sample using mothur (v. 1.38.0; Schloss et al. 2009). To minimize biases resulting from differences in sequencing depths among the libraries (Gihring et al. 2011), we rarefied the fungal data to 1,000 sequences per sample. We estimated observed (S_{Obs}) and extrapolated (Chao1) OTU richness, Shannon's diversity (H'), and evenness (E_H).

The statistical analyses for the fungal communities were performed using the VEGAN package (Oksanen *et al*., 2013) in R (R Core Team. 2013). Fungal communities were visualized with three-dimensional ordination using non-parametric multidimensional scaling (NMDS). To test for correlations between environmental variables previously measured in the permanent plots (i.e. sum of gull nests, soil nutrient amounts, vegetal cover) and the fungal community ordinations, the Envfit analysis was performed.

To detect if the fungal communities were significantly influenced by substrate type and the presence of gulls, permutational multivariate analysis of variance was done (PERMANOVA; Anderson, 2014). Differences between plots were tested by using the pairwise Adonis test with Bonferroni correction. To test if the abundance of a given fungal species is significantly associated with substrate type or the presence of gulls, the Indicator Species Analysis was performed (Cáceres *et al.*, 2012).

RESULTS

Of the 50 most abundant OTUs present in the permanent plots (Figure 2), 13 are may represent new reports for Iceland, 30 new fungal species for Iceland and 45 new species for Surtsey (compare to Hallgrímsson & Eyjólfsdóttir, 2022). We used indicator taxon analyses to highlight those that were disproportionately more abundant in one habitat type than in the others. In these analyses, 19 OTUs were disproportionately more abundant in the gull plots with lava substrate; 15 in the gull plots with sand substrate; 3 in plots beyond the gull colony and with lava substrate; and, 3 in plots beyond the gull colony with sand substrate (Table 2).

The substrate type and the presence of gull colonies affected the fungal communities (PERMANOVA: $p<0.0001$; $F=1.9$; $R^2=0.2$) (Figure 3). The pairwise comparisons indicated that plots inside the gull colonies differed from those outside the gull colonies. The two substrates (lava and sand) also differed within the gull colonies (pairwise Adonis, $p < 0.05$; $F =1.7$, $R^2=0.2$) but not outside them.

Several environmental variables previously measured in these permanent plots significantly correlated with the soil fungal community composition: the average and the sum of gull nests; the vegetation cover (sum of vascular and non-vascular plant cover) and vegetation biomass; NDVI; ecosystem respiration; soil pH; P exchangeable; Cu exchangeable; Cd exchangeable; total C and total N were significantly correlated with the NMDS ordinations (Figure 3).

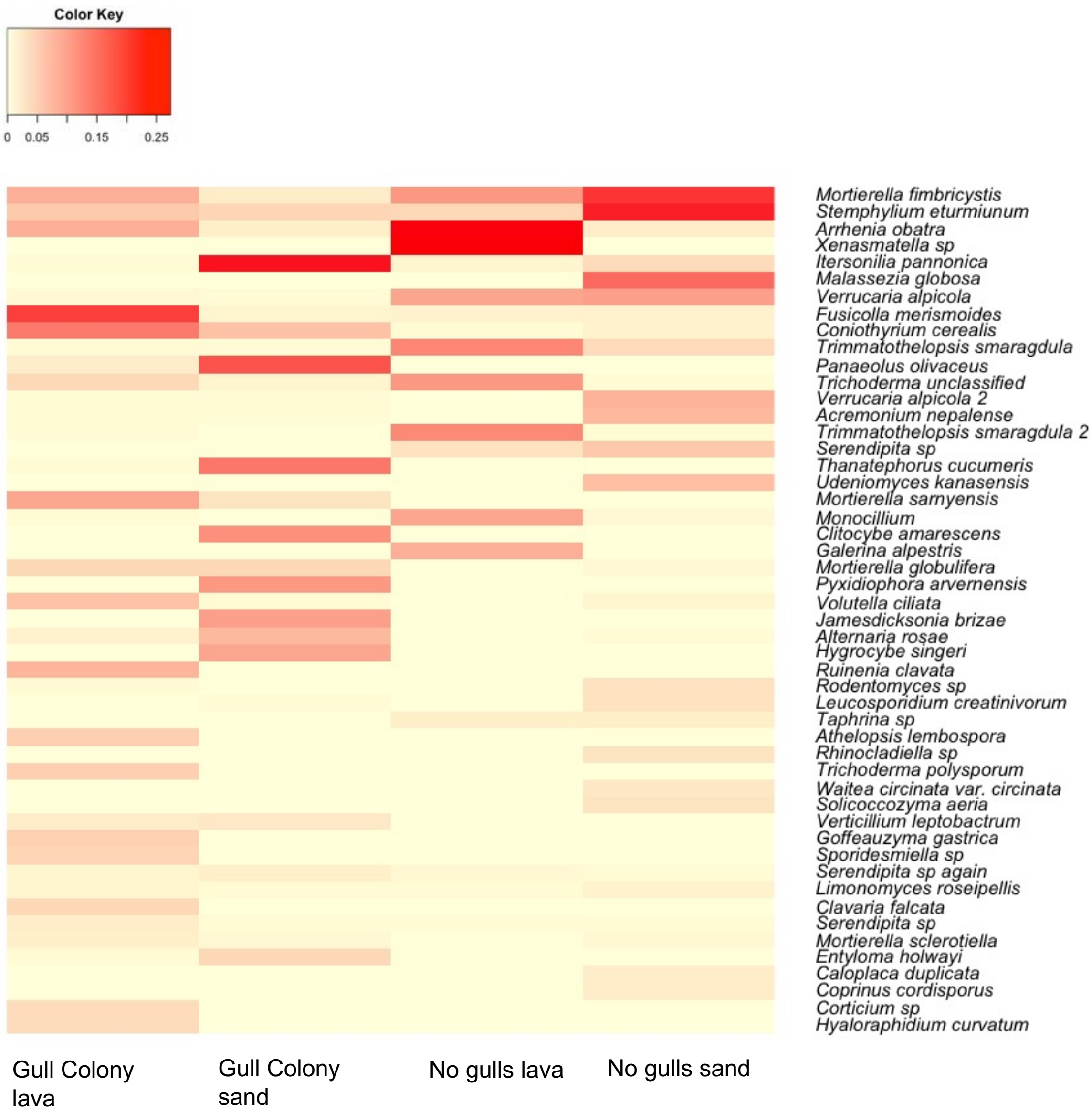

Figure 2. Heat map of the 50 more abundant fungal species in the permanent plots. The values in the color key correspond to the average relative abundance of the species for each treatment plot.

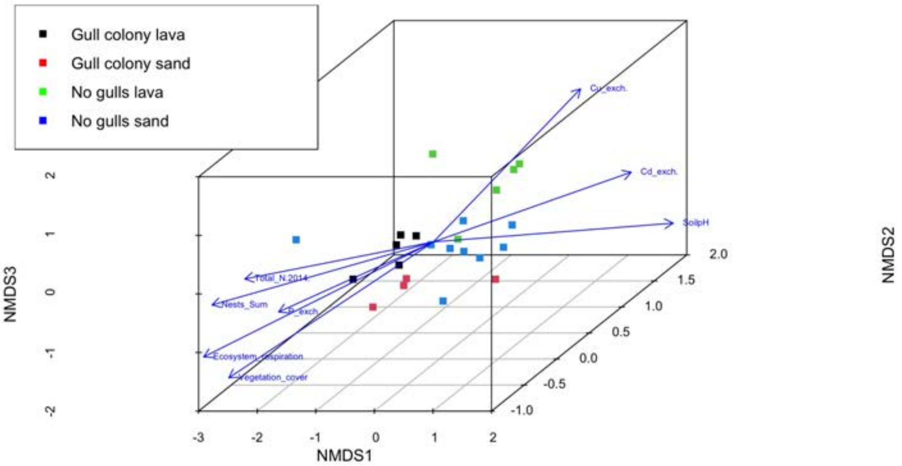

Figure 3. Three-dimensional NMDS ordination of the fungal communities from the permanent plots. The blue arrows represent the environmental variables that were significantly correlated with the ordination axis. The vector corresponding to the amount of total C overlapped with the vector corresponding to Total N. The vegetation biomass and NDVI (not showed in this graph) formed vectors with similar directions as the vegetation cover and the ecosystem respiration respectively.

Table 2. List of OTUs significantly associated with substrate type or the presence of gulls. Fidelity index = 1 means that the species occurs only in that group. Sensitivity index=1 means that the species is present in all replicates from that group.

Taxonomic assignment	Fidelity index	Sensitivity index	Stat	p value
Gull colony with lava substrate				
Goffeauzyma gastrica	0.99	1.00	0.99	0.005
Fusicolla merismoides	0.84	1.00	0.92	0.005
Ruinenia clavata	0.98	0.80	0.89	0.015
Neoascochyta tardicrescens	0.75	1.00	0.86	0.015
Kurtzmanomyces sp.	0.91	0.80	0.86	0.02
Rhinocladiella sp.	0.86	0.80	0.83	0.05
*Brachyphori*s sp.	0.84	0.80	0.82	0.01
Serendipita sp.	0.61	1.00	0.78	0.015
Parastagonospora avenae	0.76	0.80	0.78	0.015
Flagelloscypha sp.	1.00	0.60	0.78	0.02
Alfaria terrestris	1.00	0.60	0.78	0.025
Beauveria bassiana	0.96	0.60	0.76	0.035
Acaulospora nivalis	0.72	0.80	0.76	0.03
Schizothecium glutinans	0.71	0.80	0.75	0.045
Serendipita sp.	0.68	0.80	0.74	0.045
Dominikia sp.	0.87	0.60	0.72	0.03
Apiotrichum	0.86	0.60	0.72	0.045
Cladophialophora sp.	0.52	1.00	0.72	0.035
Drechslera sp.	0.41	1.00	0.64	0.045
Gull colony with sand substrate				
Jamesdicksonia brizae	0.97	1.00	0.98	0.005
Entyloma dahliae	0.87	1.00	0.94	0.01
Clitocybe amarescens	0.99	0.75	0.86	0.01
Pyxidiophora arvernensis	0.99	0.75	0.86	0.015
Sarocladium summerbellii	0.85	0.75	0.80	0.035
Cortinarius fulvescens	0.75	0.75	0.75	0.02
Parastagonospora novozelandica	0.73	0.75	0.74	0.045
Dominikia aurea	1.00	0.50	0.71	0.015
Papiliotrema frias	1.00	0.50	0.71	0.025
Lepista sordida	1.00	0.50	0.71	0.015
Filobasidium wieringae	1.00	0.50	0.71	0.025
Pyxidiophora arvernensis	1.00	0.50	0.71	0.015
Drechslera poae	0.98	0.50	0.70	0.04
Rhizoctonia alpina	0.88	0.50	0.66	0.025
Pseudoseptoria obscura	0.78	0.50	0.63	0.045
No gulls lava substrate				
Trimmatothelopsis smaragdula	0.74	1.00	0.86	0.02
Serendipita sp.	0.82	0.80	0.81	0.015
Cotylidia undulata	0.96	0.60	0.76	0.025
No gulls sand substrate				
Hirsutella rhossiliensis	0.85	0.67	0.75	0.02
Powellomyces sp.	0.71	0.78	0.74	0.03
Powellomyces sp.	0.98	0.56	0.74	0.05

DISCUSSION

In the current survey new genera and species for Surtsey (and even for Iceland) are reported. From the 50 more abundant OTUs up to 45 species were new registers for the island. However, this does not necessarily mean all those species are actively growing. The DNA detected for some of them could belong to dormant structures like spores from propagule banks. From the species that were significantly more abundant in the gull colonies plots with lava as substrate, only two arbuscular mycorrhizal fungal (AMF) species were found *Acaulospora nivalis* and *Dominikia* sp. In the gull colony plots with sand as substrate *Dominikia aurea* was significantly more abundant. No more AMF species were significantly represented in the gull plots and the rest of significantly abundant species belonged to yeasts, saprotrophic, phytopathogenic and entomopathogenic fungi (*Beauveria bassiana*). *Serendipita* sp. was found to be significantly abundant in the lava substrates from both inside and outside the gull colonies. *Serendipita* is a genus of root endophyte associated with AMF plants and whose species have been reported to be beneficial to its plant host in terms of nutrition and drought tolerance (Hallasgo *et al.,* 2020 ; Zhang *et al.,* 2017). It could be relevant to further study the effect of this endophyte and AMF species on the plant communities' adaptation to the different substrates and nutrient regimes in the permanent plots. In this context it should be pointed out that Delavaux *et al.* (2021) recently showed that AMF plant species have more limited dispersal ability than other mycorrhizal and non-mycorrhizal plant species and decrease relatively more on islands and with distance to continents.

In 2000 Greipsson & El-Mayas collected AMF spores belonging to the species *Glomus hoi* and *Scutellospora calospora* in dunes colonized by *Leymus arenarius* in Surtsey. In the survey of the present study *G. hoi* and *S. calospora* were not detected but the genera *Glomus*, *Paraglomus*, *Claroideoglomus* and *Rhyzoglomus* were found. However, they were not significantly influenced by the habitat types (according to the Species indicator analysis) and their abundance was low (less that 1 % of the species relative abundance). A higher abundance of AMF species (especially the *Glomus* spp.) should be expected in the gull colony plots where *Leymus arenarius* is co-dominating the plant community. The more abundant species registered in this study were saprotrophic fungi and plant pathogens. Since saprotrophic species produce more biomass per soil volume than the AMF species (as reported by Jiang *et al.*, 2020) it is possible that they earlier contributed with more DNA and diluted the signal of the AMF species. The use of ingrowth meshbags that select for extramatrical mycorrhizal growth (Wallander *et al.*, 2001) could be useful to increase the resolution of AMF signal and to study the differences in AMF composition in the permanent plots.

Ectomycorrhizal species were also registered in the present survey. For example *Cortinarius fulvescens* was significantly associated with the plots inside the gull colonies with sand substrate. This fungus is probably forming association with Salix plants that have established here; *Salix herbacea*. Eyjolfsdottir 2009 found an unidentified *Cortinairus* species which probably was *C. fulvescens*, and also several other ectomycorrhizal genera in her survey of sporocarps, namely *Hebeloma*, *Inocybe* and *Laccaria*. From these genera only *Hebeloma* was found in the present study, but at low numbers (less that 1 % of the species relative abundance).

Fungal communities in the plots within the seagull colony differed from those beyond it. Moreover, the number of seagull nests, vegetation cover, ecosystem respiration, total nitrogen and exchangeable P exchangeable were correlated with the ordination of the fungal communities from the Gull plots. Taken together, this indicates that the N and P inputs from the seagull deposits that have led to greater C accumulation, vegetation cover and plant biomass (Leblans *et al,*. 2014; Magnússon *et al.*, 2020) may also drive fungal community dynamics. Our data confirm that the presence of the seagulls is the key factor in shaping the soil biosphere on the island as has been reported for other soil organisms including microfauna (Magnússon *et al.*, 2014 ; Ilieva-Makulec *et al.*,2015) and bacteria (Marteinsson *et al.*, 2015).

The substrate (lava or sand) also affected the fungal communities but only within the seagull colony. The sand plots (>30 cm of tephra sand) contain deeper soil than the lava plots. Under these conditions there is a lesser desiccation risk when soil temperatures fluctuate providing thus better environmental conditions for plant roots and soil microorganisms (e.g. Sigurdsson 2009; Sigurdsson & Stefansdottir, 2015). These different substrates could have shaped the composition of fungal communities as they also differ in the plant cover, plant biomass and plant community composition between the plots (Magnússon *et al.*, 2020). For plots outside the gull colony on the other hand, the two different substrates were not enough to cause differences in the fungal communities indicating that both vegetal cover and plant species composition are the more important factors influencing fungal communities. This is consistent with other studies showing that the soil fungal community varies along with changes in the plant community (Zinger *et al.*, 2011; De Bellis *et al.*, 2007).

By using next generation sequencing the aim of the present study was to expand the knowledge of the funga of Surtsey. Indeed, we have provided new species registers (including AMF) that were not described before with other survey methods. Moreover, we found that the fungal community structure is strongly influenced by the nutrients brought from the sea by marine birds as has been described for other soil organisms. Since soil fungi play a key role for plant nutrition and carbon sequestration these results are key to understand primary succession. Further studies on the effect of fungal endophytes on plant colonization to the new habitats are advised.

REFERENCES

Abarenkov, K., A. Zirk, T. Piirmann, R. Pöhönen, F. Ivanov, R.H. Nilsson & U. Kõljalg, 2020. UNITE mothur release for eukaryotes. Version 04.02.2020. UNITE Community. https://doi.org/10.15156/BIO/786382

Anderson, M. J., 2014. Permutational multivariate analysis of variance (PERMANOVA). *Wiley statsref: statistics reference online*, 1-15.

Baldursson, S. & A. Ingadóttir, (eds.), 2007. Nomination of Surtsey for the UNESCO World Heritage List. Icelandic Institute of Natural History. Reykjavik, 123 pp.

Blaalid, R., T. O. R. Carlsen, S. Kumar, R. Halvorsen, K. I. Ugland, G. Fontana & H. Kauserud, 2012. Changes in the root-associated fungal communities along a primary succession gradient analysed by 454 pyrosequencing. Mol. Ecol. 21(8), 1897-1908. https://doi.org/10.1111/j.1365-294X.2011.05214.x

Brown, S. P. & A. Jumpponen, 2014. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. Mol. Ecol. 23(2), 481-497. https://doi.org/10.1111/mec.12487. Epub

De Bellis, T., G. Kernaghan & P. Widden, 2007. Plant community influences on soil microfungal assemblages in boreal mixed-wood forests. Mycologia 99(3), 356-367. https://doi.org/10.1080/15572536.2007.11832560

De Cáceres, M., P. Legendre, S. K. Wiser & L. Brotons, 2012. Using species combinations in indicator value analyses. Methods Ecol. Evol. 3(6), 973-982. https://doi.org/10.1111/j.2041-210X.2012.00246.x

Delavaux, C. S., P. Weigelt, W. Dawson, F. Essl, M. van Kleunen, C. König,. . . J. D. Bever, 2021. Mycorrhizal types influence island biogeography of plants. Communications Biol. 4(1), 1128. https://doi.org/10.1038/s42003-021-02649-2

Edgar, R.C., B.J. Haas J.C. Clemente, C. Quince & R. Knight, 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinform. 27, 2194-2200. https://doi.org/10.1093/bioinformatics/btr381

Eyjólfsdóttir, G. G., 2009. Investigation of the funga of Surtsey 2008. Surtsey Res. 12, 105-111.

Geml, J., B. Gravendeel, K. J. van der Gaag, M. Neilen, Y. Lammers, N. Raes, ... & M. E. Noordeloos, 2014. The contribution of DNA metabarcoding to fungal conservation: diversity assessment, habitat partitioning and mapping red-listed fungi in protected coastal *Salix repens* communities in the Netherlands. PloS One 9(6), e99852. https://doi.org/10.1371/journal.pone.0099852

Gihring, T.M., S.J. Green & C.W. Schadt, 2011. Massively parallel rRNA gene sequencing exacerbates the potential for biased community diversity comparisons due to variable library sizes. Environm.Microbiol. 14, 285-290. https://doi.org/10.1111/j.1462-2920.2011.02550.x.

Greipsson, S. & H. El-Mayas, 2000. Arbuscular mycorrhizae of Leymus arenarius on coastal sands and reclamation sites in Iceland and response to inoculation. Restor. Ecol. 8, 144-150. https://doi.org/10.1046/j.1526-100x.2000.80021.x

Hallasgo, A. M., B. Spangl, S. Steinkellner & K. Hage-Ahmed, 2020. The fungal endophyte Serendipita williamsii does not affect phosphorus status but carbon and nitrogen dynamics in arbuscular mycorrhizal tomato plants. J. Fungi 6(4), 233. https://doi.org/10.3390/jof6040233

Hallgrímsson, H. & G.G. Eyjólfsdóttir, 2023. Íslenskt sveppatal. (Checklist of Icelandic fungi) (No. 5X). Icelandic Institute of Natural History, Reykjavik, 214 pp (In press).

Huse, S.M., L. Dethlefsen, J.A. Huber, M.D. Welch, D.A. Relman & M.L. Sogin, 2008. Exploring microbial diversity and taxonomy using SSU rRNA hypervariable tag sequencing. PLoS Genet. 4, 1000255. https://doi.org/10.1371/journal.pgen.1000255

Ihrmark, K., I.T.M. Bodeker, K. Cruz-Martinez, H. Friberg, A. Kubartova, J. Schenck, Y. Strid, J. Stenlid, M. Brandstrom-Durling, K.E. Clemmensen & B.D. Lindahl, 2012. New primers to amplify the fungal ITS2 region - evaluation by 454-sequencing of artificial and natural communities. FEMS Microbiol. Ecol. 82, 666-677. https://doi.org/10.1111/j.1574-6941.2012.01437.x

Ilieva-Makulec, K., B. Bjarnadóttir, & B. D. Sigurdsson, 2015. Soil nematode communities on Surtsey, 50 years after the formation of the volcanic island. Icel. Agric. Sci. 28, 43-58. https://doi.org/10.16886/IAS.2015.05

Jiang, Y., L. Luan, K. Hu, M. Liu, Z. Chen, S. Geisen, ... & B. Sun, 2020. Trophic interactions as determinants of the arbuscular mycorrhizal fungal community with cascading plant-promoting consequences. Microbiome 8(1), 1-14. https://doi.org/10.1186/s40168-020-00918-6

Kozich, J.J., S.L. Westcott, N.T. Baxter, S.K. Highlander & P.D. Schloss, 2013. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. Appl. Environm. Microbiol. 79, 5112-5120. https://doi.org/10.1128/AEM.01043-13

Leblans, N., B.D. Sigurdsson, P. Roefs, R. Thuys, B. Magnússon & I. A. Janssens, 2014. Effects of seabird nitrogen input on biomass and carbon accumulation after 50 years of primary succession on a young volcanic island, Surtsey. Biogeosci. 11, 6237–6250. https://doi.org/10.5194/bg-11-6237-2014

Magnússon, B., G. A. Gudmundsson, S. Metúsalemsson & S. M. Granquist, 2020. Seabirds and seals as drivers of plant succession on Surtsey. Surtsey Res. 14, 115-130. https://doi.org/10.33112/surtsey.14.10

Magnússon, B., S. H. Magnússon & S. Fridriksson, 2009. Developments in plant colonization and succession on Surtsey during 1999–2008. Surtsey Res. 12, 57-76.

Magnússon, B., S.H. Magnússon, & J. Gudmundsson, 1996. Gróðurframvinda í Surtsey. Icel. Agric. Sci. 10, 253-272.

Magnússon, B., S. H. Magnússon, & S. Fridriksson, 2009. Developments in plant colonization and succession on Surtsey during 1999–2008. Surtsey Res. 12, 57-76.

Magnússon, B., S.H. Magnússon, E. Ólafsson & B.D. Sigurdsson, 2014. Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. Biogeosci.,11(19), 5521-5537. https://doi.org/10.5194/bg-11-5521-2014

Marteinsson V., A. Klonowski, E. Reynisson, P. Vannier, B. D. Sigurdsson & M. Ólafsson, 2015. Microbial colonisation in diverse surface soil types in Surtsey and diversity analysis of its subsurface microbiota. Biogeosci. 12, 1191-1203. https://doi.org/10.5194/bg-12-1191-2015

Narayanan, A., K.J .Ismert, M. Smith & A. Jumpponen, 2021. Soil fungal communities are compositionally resistant to drought manipulations – evidence from culture-dependent and culture-independent analyses. Fungal Ecol. 51, 101062. https://doi.org/10.1016/j.funeco.2021.101062

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'hara, ... & H. Wagner, 2013. Community ecology package. R package version, 2(0).

Rognes, T., T. Flouri, B. Nichols, C. Quince & F. Mahé, 2016. VSEARCH: a versatile open source tool for metagenomics. PeerJ 4, e2584. https://doi.org/10.7717/peerj.2584

Schloss, P.D., S.L. Westcott, T. Ryabin, J.R. Hall, M. Hartmann, E.B. Hollister, R.A. Lesneiwski, B.B. Oakley, D.H. Parks, C.J. Robinson, J.W. Sahl, B. Stres, G.C. Thallinger, D.J. Van Horn & C.F. Weber, 2009. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Appl. Environ. Microbiol. 75, 7537-7541. https://doi.org/10.1128/AEM.01541-09

Sigurdsson, B.D., 2009. Ecosystem carbon fluxes of *Leymus arenarius* and *Honckenya pebloides* on Surtsey in relation to water availability: a pilot study. Surtsey Res. 12, 77-80.

Sigurdsson, B. D. & B. Magnusson, 2010. Ecosystem respiration, vegetation development and soil nitrogen in relation to breeding density of seagulls on a pristine volcanic island, Surtsey, Iceland. Biogeosci. 7, 883-891. https://doi.org/10.5194/bg-7-883-2010

Sigurdsson, B. D. & G. Stefánsdóttir, 2015. Ecosystem CO2 flux rates in relation to vegetation type and age of *Leymus arenarius* dunes on Surtsey. Surtsey Res. 13, 9-15.

Sigurdsson, B. D. & N. I. W. Leblans, 2020. Availability of plant nutrients and pollutants in the young soils of Surtsey compared to the older Heimaey and Elliðaey volcanic islands. Surtsey Res. 14, 91-98. https://doi.org/10.33112/surtsey.14.8

Sigurdsson, B. D., E. M. Kapinga & B. Magnusson, 2022. Vegetation cover, gross photosynthesis and remotely sensed vegetation indices in different aged sub-arctic volcanic islands in the Vestmannaeyjar archipelago. Surtsey Res. 15, (in print). https://doi.org/10.33112/surtsey.15.3

Wallander, H., L. Nilsson, D. Hagerberg & E. Bååth, 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. New Phytol. 151, 753e760. https://doi.org/10.1046/j.0028-646x.2001.00199.x

White T.J., T. Bruns, S. Lee & J.W. Taylor, 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH Sninsky JJ, (Eds.), PCR Protocols: A Guide to Methods and Applications. Academic Press, New York, 315-322.

Zhang, W., J. Wang, L. Xu, A. Wang, L. Huang, H. Du,... & R. Oelmüller, 2018. Drought stress responses in maize are diminished by *Piriformospora indica.* Plant Signal Behav. 13(1), e1414121. https://doi.org/10.1080/15592324.2017.1414121

Zinger, L., D. P. Lejon, F. Baptist, A. Bouasria, S. Aubert, R. A. Geremia & P. Choler, 2011. Contrasting diversity patterns

of crenarchaeal, bacterial and fungal soil communities in an alpine landscape. PLoS One 6(5), e19950.
https://doi.org/10.1371/journal.pone.0019950

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

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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

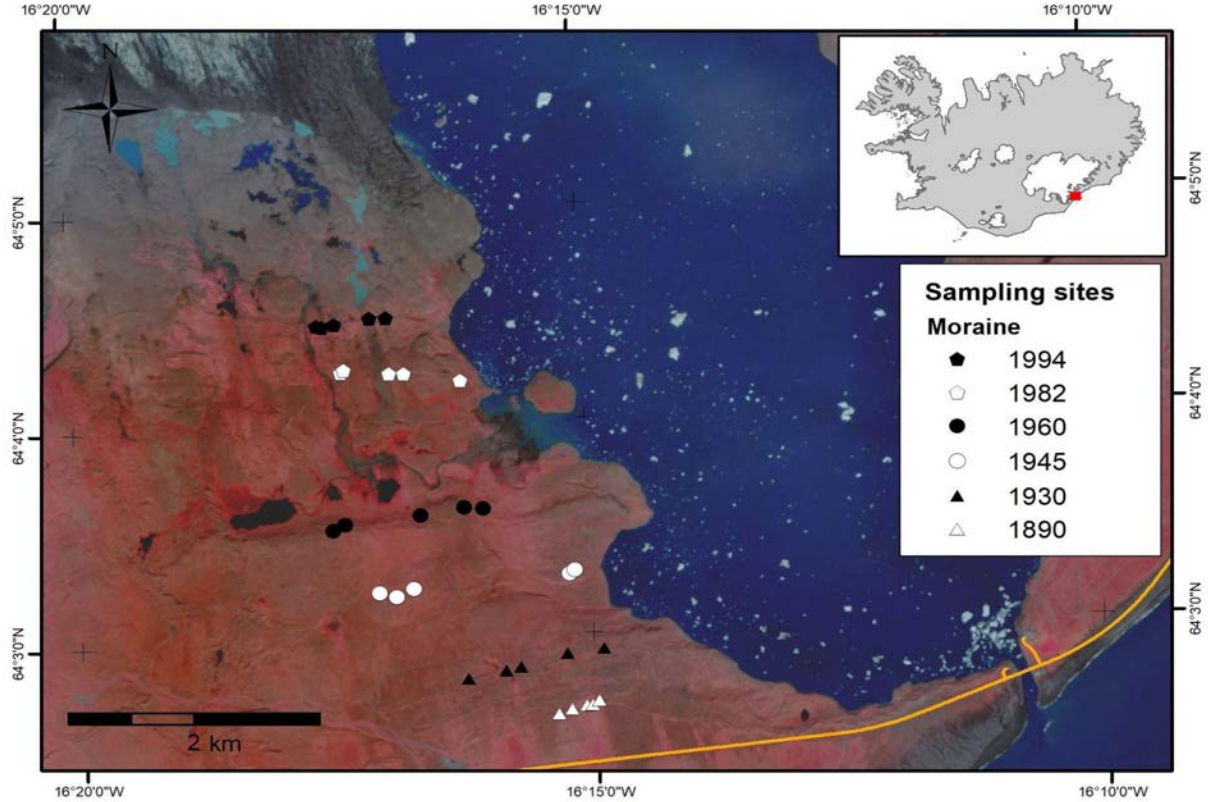

Figure 1. Sampling sites from July 2018 within the glacial fore-field of Breiðamerkurjökull, shown on an infrared Sentinel-2 satellite image from 22 August 2018. The sites are located along the estimated position of the glacier terminus at a given point in time (see e.g. S. Guðmundsson 2014 and S. Guðmundsson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

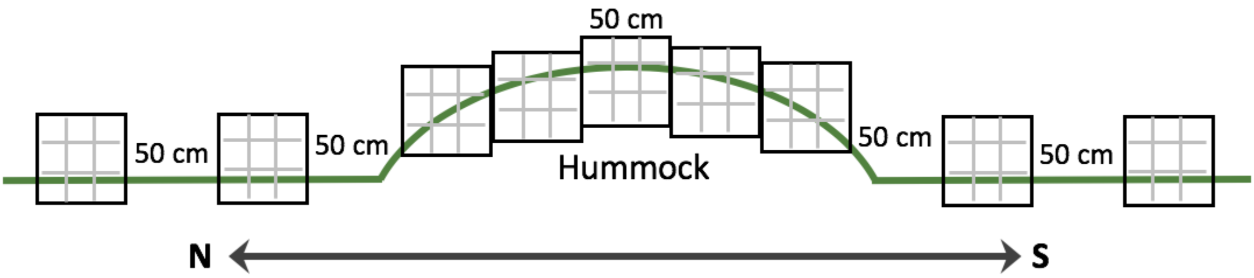

Figure 2. The setup of nine 50 x 50 cm quadrats placed on each bird hummock. One quadrant was placed on the hummock's center while the other eight were lined up to the north and the south up to 3 m distance from the center.

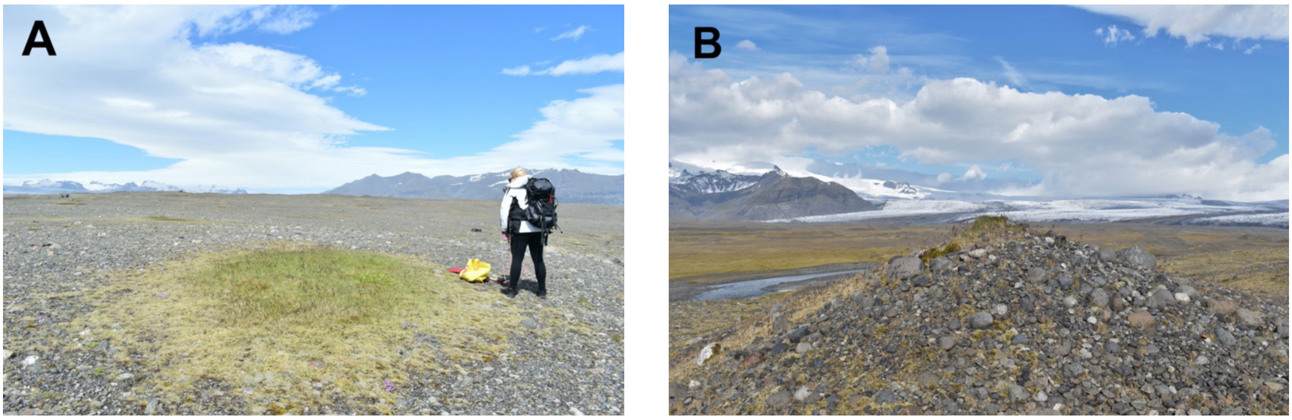

Figure 3. Bird hummocks on moraines of different age within the Breiðamerkurjökull fore-field in SE-Iceland. A. Moraine from the year 1945. B. Moraine from the year 1982. Photos SS, July 2018.

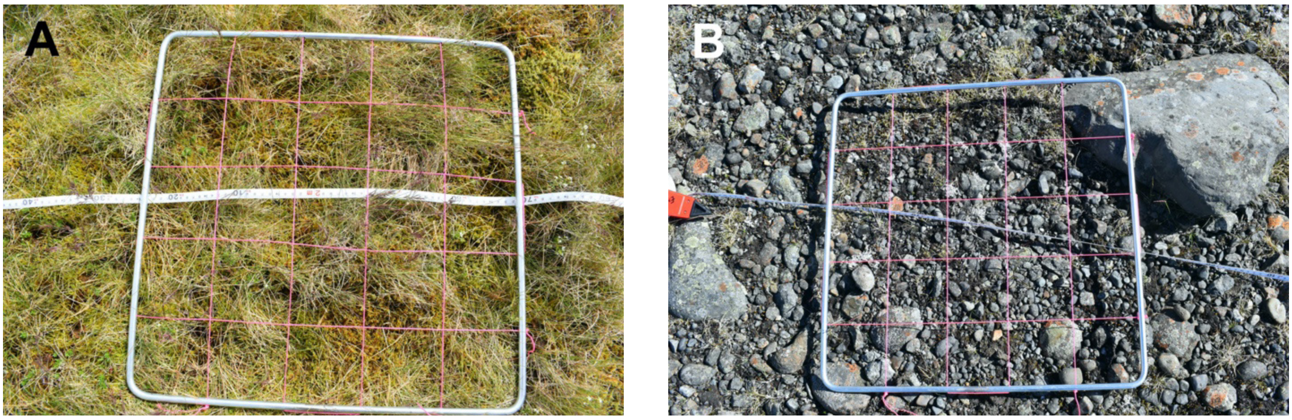

Figure 4. Examples of vegetation quadrats from a sampling site on moraine formed in 1890, within the Breiðamerkurjökull fore-field in SE- Iceland. A. The center of a bird hummock. B. Three meters north of the hummock's center. Photos SS, July 2018.

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

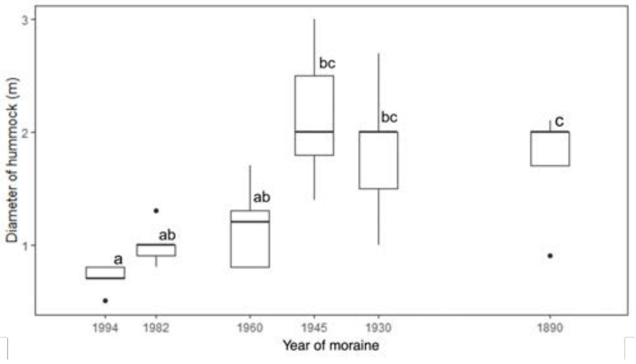

Figure 5. A boxplot comparing the diameter of bird hummocks at different aged moraines within the Breiðamerkurjökull fore-field in SE-Iceland. The letters a, b, and c indicate significant differences between the moraines.

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

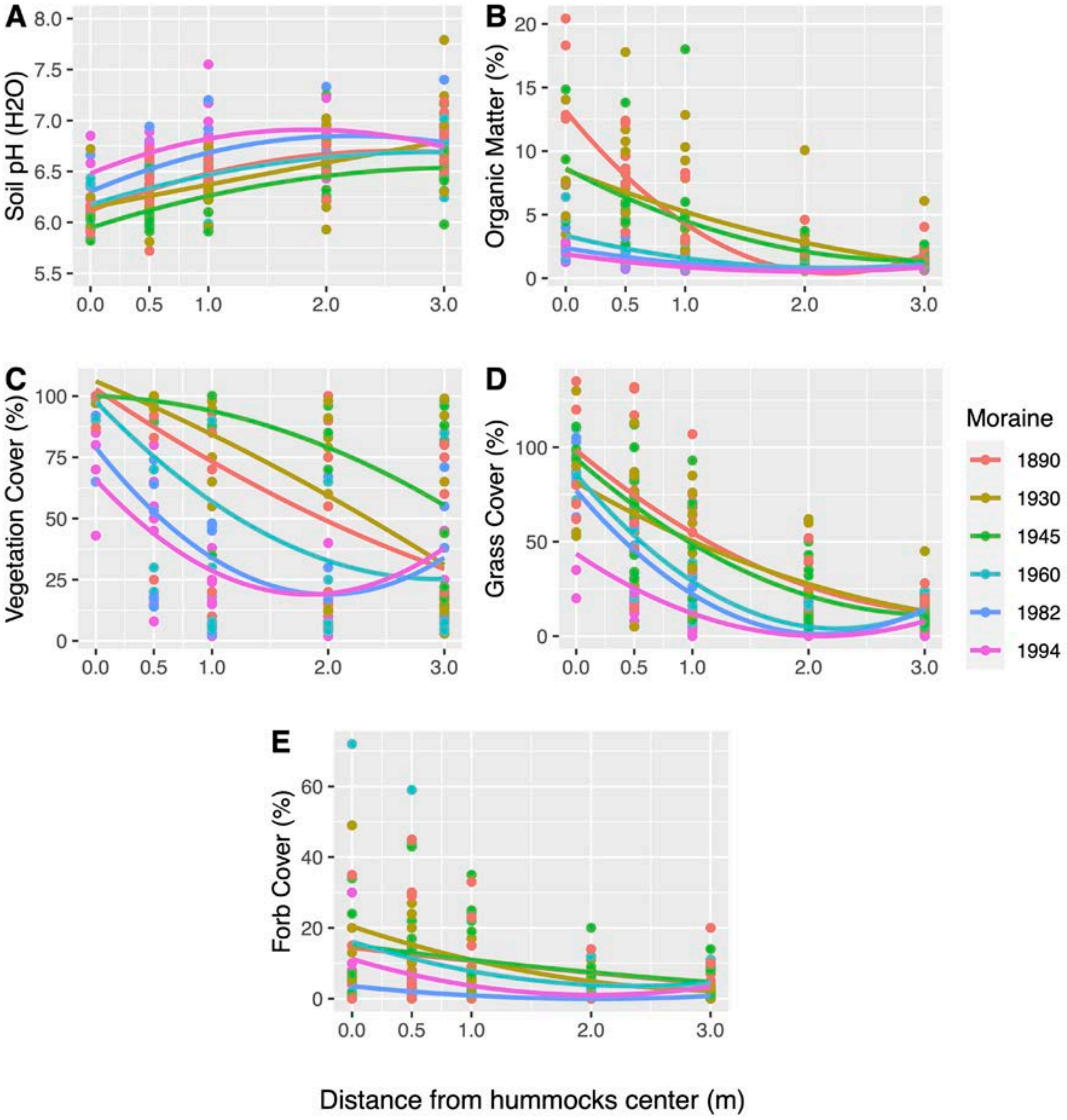

Figure 6. The relationship between measured variables and distance from hummock center at the Breiðamerkurjökull fore-field in SE- Iceland. A) pH (H2O), B) percentage of organic matter, C) vegetation cover (%), D) grass cover, and E) forb cover. The lines are quadratic fits.

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

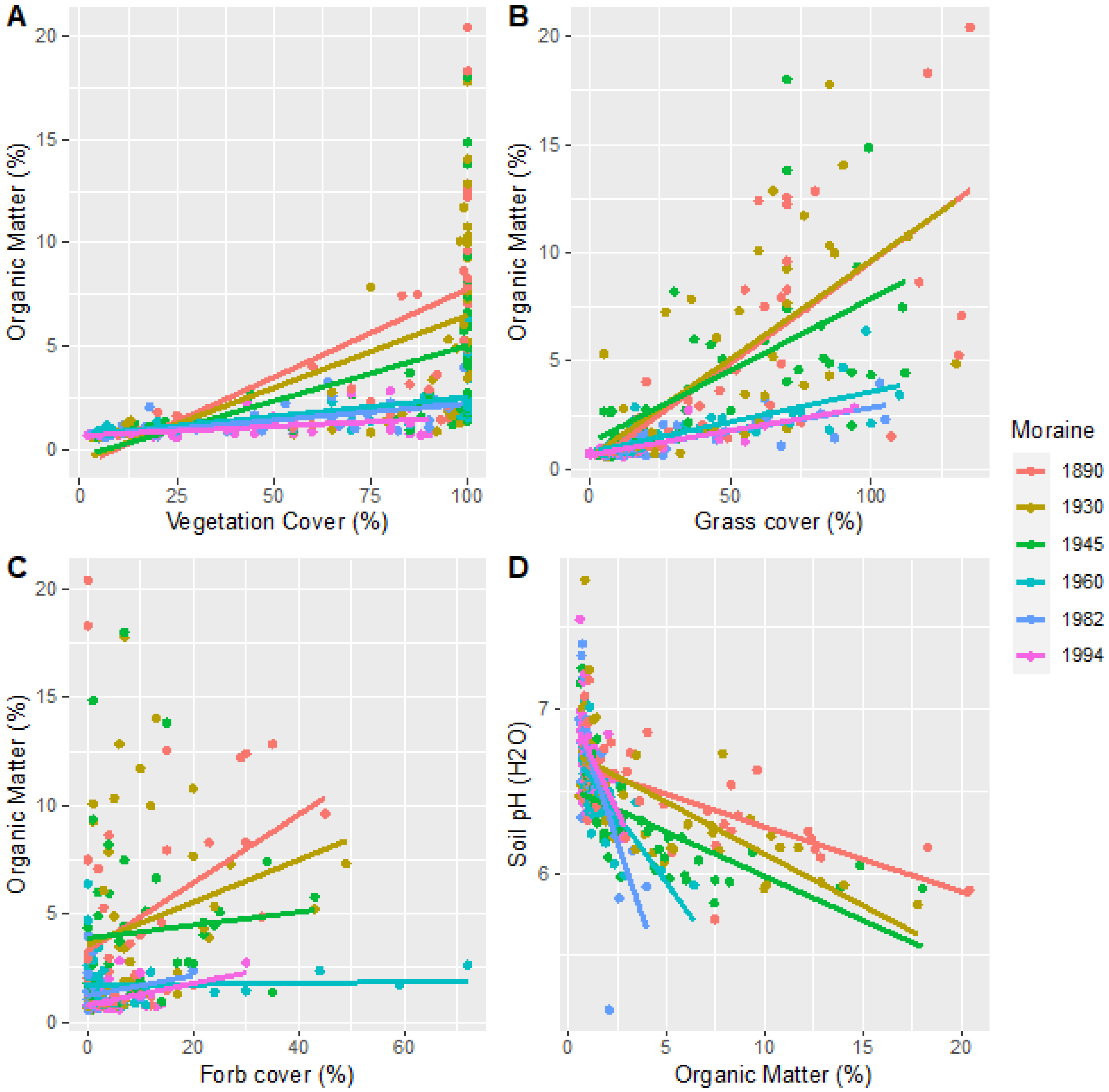

Figure 7. Graphs showing relationships between measured variables and OM concentration within the Breiðamerkurjökull fore-field, SE- Iceland. A) Vegetation cover, B) grass cover, C) forb cover, and D) soil pH $_{H2O}$. The lines are linear regressions.

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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REFERENCES

Barton K., 2022. MuMIn: Multi-Model Inference. R package. version 1.46.0. https://CRAN.R-project.org/package=MuMIn

Bates, D., M. Maechler, B. Bolker & S. Walker 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bernasconi, S. M., A. Bauder, B. Bourdon, I. Brunner, E. Bünemann, I. Chris, N. Derungs, P. Edwards, D. Farinotti, B. Frey, E. Frossard, G. Furrer, M. Gierga, H. Göransson, K. Gülland, F. Hagedorn, I. Hajdas, R. Hindshaw, S. Ivy-Ochs, . . . A. Zumsteg, 2011. Chemical and biological gradients along the Damma glacier soil chronosequence, Switzerland. *Vadose Zone Journal*, *10*(3), 867-883.

Braun-Blanquet, J. 1932. Plant sociology. The study of plant communities. Plant sociology. The study of plant communities. First ed.

De La Peña-Lastra, S. 2021. Seabird droppings: Effects on a global and local level. Science of The Total Environment, 754, 142148. https://doi.org/10.1016/j.scitotenv.2020.142148

Dias, M. P., R. Martin, E.J. Pearmain, I.J. Burfield, C. Small, R.A. Phillips, ... & J.P. Croxall, 2019. Threats to seabirds: a global assessment. Biological Conservation, 237, 525-537. https://doi.org/10.1016/j.biocon.2019.06.033

Doughty, C. E., J. Roman, S. Faurby, A. Wolf, A. Haque, E.S Bakker, ... & J.C. Svenning, 2016. Global nutrient transport in a world of giants. Proceedings of the National Academy of Sciences, 113(4), 868-873. https://doi.org/10.1073/pnas.1502549112

Einarsson, M.A., 1984. Climate of Iceland. World survey of climatology, 15, pp.673-697.

Graves, S., H.P. Piepho, & L. Selzer, with help from Sundar Dorai-Raj 2019. multcompView: Visualizations of Paired Comparisons. R package version 0.1-8. https://CRAN.R-project.org/package=multcompView

Guðmundsson, S. 2014. Reconstruction of late 19th century geometry of Kotárjökull and Breiðamerkurjökull in SE-Iceland and comparison with the present. (Doctoral dissertation).

Guðmundsson, S., H. Björnsson & F. Pálsson, 2017. Changes of Breiðamerkurjökull glacier,SE-Iceland, from its late nineteenth century maximum to the present. Geografiska Annaler:

Series A, Physical Geography 99(4): 338–352. https://doi.org/10.1080/04353676.2017.1355216

Jóhannesdóttir, L. & K. Hermannsdóttir, 2019. Kortlagning skúmshreiðra á Breiðamerkursandi 2018. Náttúrustofa Suðausturlands, Höfn í Hornafirði, mars 2019. 14 bls.

Kristinsson, H. 2010. Íslenska plöntuhandbókin. Blómplöntur og byrkningar. 3. útg. aukin og endurbætt. Reykjavík: Mál og menning.

Leblans, N.I.W., B.D. Sigurdsson, R. Aerts, S. Vicca, B. Magnússon & I.A. Janssens, 2017. Icelandic grasslands as long-term C sinks under elevated organic N inputs. Biogeochemistry 134, 279–299. https://doi.org/10.1007/s10533-017-0362-5.

Lund-Hansen, L.C. & P. Lange, 1991. The numbers and distribution of the Great Skua Stercorarius skua breeding in Iceland 1984-1985., Acta Naturalia Islandica no. 34, Icelandic Museum of Natural History.

Magnússon, B., S.H. Magnússon, E. Ólafsson, & B.D. Sigurdsson, 2014. Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. Biogeosciences, 11(19), 5521-5537. https://doi.org/10.5194/bg-11-5521-2014.

Magnússon, B., Guðmundsson. G.A., Metúsalemsson S., & Granquist S.M. 2020. Seabirds and seals as drivers of plant succession on Surtsey. Surtsey Research 14: 115-130. https://doi.org/1033112/surtsey.14.10

Nelson, D.W. & L.E. Sommers. 1996. Total carbon, organic carbon, and organic matter. In: Methods of Soil Analysis, Part 2, 2nd ed., A.L. Page et al., Ed. Agronomy. 9:961-1010. Am. Soc. of Agron., Inc. Madison, WI. https://doi.org/10.2136/sssabookser5.3.c34.

Olsen, K. M. 2013. Skuas and jaegers. A&C Black.

Ólafsson, E. & L. Ásbjörnsdóttir, 2014. Surtsey í sjónmáli. Edda Publishing

R Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Sigurdsson, B.D. & B. Magnusson, 2010. Ecosystem respiration, vegetation development and soil nitrogen in relation to breeding density of seagulls on a pristine volcanic island, Surtsey, Iceland. Biogeosci. 7, 883-891. https://doi.org/10.5194/bg-7-883-2010

Sigurðsson, B.D., S. Heiðmarsson, H. Björnsson & E. Einarsson, 2020. Gróðurframvinda á jökulskerjum í Breiðamerkurjökli í 80 ár. Náttúrufræðingurinn 90(4–5), 225–240.

Skarphéðinsson, K.H., B. Katrínardóttir, G.A Guðmundsson & S.N.V Auhage, 2016. Mikilvæg fuglasvæði á Íslandi. Fjölrit Náttúrufræðistofnunar Nr. 55. 295 s.

Turner-Meservy, C., O.K. Vilmundardóttir, R. Lal, & G. Gísladóttir, 2022. Soil chemical properties in glacial moraines across a chronosequence influenced by avifauna and volcanic materials: Breiðamerkurjökull, Iceland. CATENA, 209, 105836. https://doi.org/10.1016/j.catena.2021.105836.

Vigfusdottir, F. 2012 Drivers of productivity in a subarctic seabird: Arctic Terns in Iceland (Doctoral dissertation, University of East Anglia).

Vigfusdottir, F. 2021. Seabirds. (In: Gudmundur J. Oskarsson (edt.). State of Icelandic marine environment and ecosystems and future outlook. Report by Icelandic Marine and Freshwater Research Institute 2021. Haf- og vatnarannsóknir, HV 2021-14.)

Vilmundardóttir, O., G. Gísladóttir, & R. Lal, 2015. Between ice and ocean; soil development along an age chronosequence formed by the retreating Breiðamerkurjökull glacier, SE-Iceland.Geoderma, 259, 310-320. https://doi.org/10.1016/j.geoderma.2015.06.016.

Watts, W. 1962. Norður yfir Vatnajökul. Icelandic transl. Jón Eyþórsson. Bókfellsútgáfan, Reykjavík, 208.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York

Wickham H., R. François, L. Henry, & K. Müller, 2022. dplyr: A Grammar of Data Manipulation. R package version 1.0.8. https://CRAN.R-project.org/package=dplyr

Bryophytes of Surtsey, Iceland: Latest developments and a glimpse of the future

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ABSTRACT

Surtsey island was formed in a volcanic eruption south of Iceland in 1963 – 1967 and has since then been protected and monitored by scientists. It is the youngest island in the Vestmannaeyjar archipelago. The archipelago is of volcanic origin, but the other islands are ca. 5 000 to 40 000 yrs old. The first two moss species were found on Surtsey as early as 1967 and several new bryophyte species were discovered every year until 1973 when regular sampling ended. Systematic bryophyte inventories in a grid of 100 m × 100 m quadrats were made in 1970 – 1972 and 2008. Here we report results from an inventory in 2018, when the same quadrats of the grid system as in 2008 were searched for bryophytes. In addition, we surveyed the bryophyte flora of Elliðaey – a ca. 5 000 yrs old island at the more sheltered north-eastern end of the archipelago.

On Surtsey, distributional expansion and contraction of earlier colonists was revealed as well as presence of new colonists. Total number of taxa increased from 43 to 59 between 2008 and 2018. The average species richness increased from 4.5 taxa/quadrat in 2008 to 6.6 taxa/quadrat in 2018 (empty quadrats omitted): 32 quadrats showed an increase in species richness; three quadrats showed no change; ten quadrats showed a slight decrease of 1 – 2 taxa, while one quadrat showed a considerable decrease of 7 taxa – that quadrat was within the lush grassland of the gull colony where bryophytes were outcompeted by the graminoids. Quadrats with the strongest increase in species richness were also within areas affected by seabirds but had not been as overgrown with grassland. On Elliðaey, the predominant habitat was grassland, like the one at the centre of the gull colony on Surtsey. On the island, we registered 22 taxa; 13 were also found on Surtsey in 2018, 4 have been found on Surtsey in earlier surveys and 4 species have never been found on Surtsey.

We predict the species richness on Surtsey will continue to grow but level off before starting to decrease as the lava fields disappear and grassland becomes more dominant. Continued monitoring, without long breaks, is essential to evaluate how fast the bryophyte vegetation develops in the years to come.

INTRODUCTION

The island Surtsey (63° N, 20° W), was formed in an undersea volcanic eruption, of a kind later known as a Surtseyan eruption. The eruption started in November 1963 (Thorarinsson 1965) and lasted till June 1967. Surtsey belongs to the Vestmannaeyjar archipelago, 7 – 33 km off the south coast of Iceland (Fig. 1) (Magnússon *et al*. 2009). The archipelago is of a volcanic origin but up until the Surtsey eruption, it had been dormant for about 5 000 years (Sigurðsson & Jakobsson 2009). Surtsey therefore provides a unique opportunity to document the primary succession of an island in this archipelago, while the older islands in the system provide a comparison, separated in time. They give an indication of what will become of Surtsey, and its biota, in the distant future. While Heimaey (13.4 km^2) is the largest island in the archipelago, and the only inhabited one, Surtsey is at the present the second largest at 1.2 km^2 in 2019 (Óskarsson *et al.* 2020) and Elliðaey the third largest at 0.5 km^2 (Magnússon *et al.* 2014).

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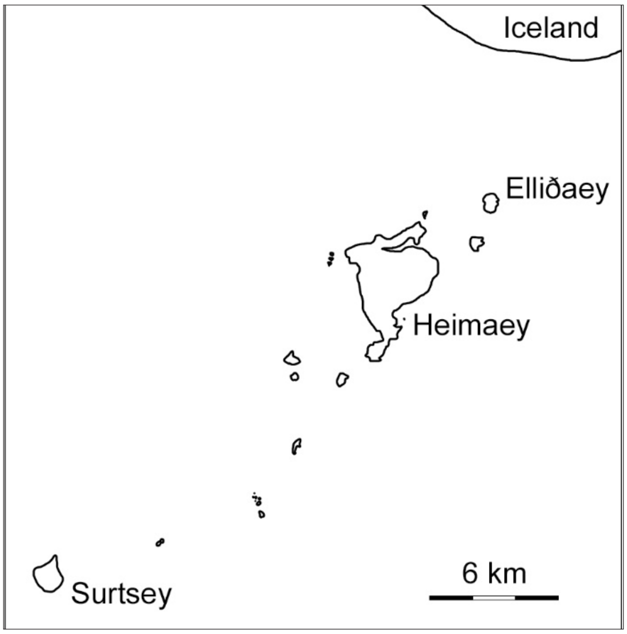

Figure 1. An overview of the Vestmannaeyjar archipelago, off the south coast of Iceland. The archipelago stretches about 38 km, with Surtsey at the south-western end and Elliðaey at the north-eastern end. Map: GVI, based on a satellite image from Google Maps (accessed on April 15, 2022).

Surtsey reached an area of 2.65 km^2 by the end of the eruption in 1967 (Jakobsson *et al.* 2000) but the southern lava fields, that still make up the bulk of the island's area, are easily eroded by the crushing impact of high energy ocean waves. The palagonite tuff hills to the north of the craters are, on the other hand, considerably more durable and less exposed. By 1974, 0.5 km^2 of the lava fields had already disappeared, but through the years, erosion has gradually become slower (Óskarsson *et al.* 2020). Jakobsson and Guðmundsson (2003) predicted that only 0.5 km^2 of the island would remain by 2100 and only a 0.4 km^2 palagonite tuff crag would survive for centuries to come, such as can be seen with Surtsey's older sister islands in the archipelago. According to Óskarsson *et al.* (2020), the erosion predictions still hold.

Elliðaey is at the opposite end of the 38 km long volcanic system of Vestmannaeyjar archipelago (Fig. 1) and estimated to be 5 000 – 6 000 years older than Surtsey. The system had been seemingly dormant since the birth of Elliðaey and other nearby islands, or up until the Surtsey eruption in 1963 – 1967, and the Heimaey eruption in 1973. Elliðaey is dominated by fertile grassland, grazed by sheep throughout the year and has large colonies of Atlantic puffins and other seabirds (Sigurðsson & Jakobsson 2009).

It can be argued that Elliðaey can give us an insight into the future and reveal how Surtsey's plant communities may develop. The vegetation of Elliðaey is rather well known regarding vascular plants, but less so for mosses and liverworts. In 2013, four 10 m × 10 m permanent plots were set up and studied on Elliðaey, but such plots had been set up on Surtsey in 1990 and the following years. In 2018 there were 29 plots in operation on Surtsey (Magnússon *et al.* 2020). These have been monitored biannually for plant cover, including moss cover, but had not been systematically screened for bryophyte species. However, in 2003, bryophytes were sampled in permanent plots in operation on the island at the time, and later identified to taxa. The study of vascular plants and land-invertebrates within the plots on Surtsey has, on the other hand, been both detailed and regular (e.g., Magnússon *et al.* 2020; Magnússon *et al.* 2009; Ólafsson & Ingimarsdóttir 2009). Regular monitoring of bryophytes within the permanent plots would provide valuable information on the succession of bryophyte communities on Surtsey in comparison to vascular plant communities. In a review of bryophyte island biogeography, Patiño and Vanderpoorten (2021) point out the surveys on Surtsey as a unique assessment of bryophyte colonization dynamics with high future potential.

BRYOPHYTE COLONIZATION ON SURTSEY

The geology of Surtsey received well deserved attention and has been monitored since the island emerged from the ocean. Since spring 2009, an automated weather station and a web-camera have been operated by the Icelandic Meteorological Office and the Surtsey Research Society, which greatly enhances the opportunities to interpret changes in environment and habitats in Surtsey through time. The colonization of both plants and animals on Surtsey has been closely monitored since the island's early days, as well as the establishment and development of organismal communities. However, as mentioned before, not all organism groups have received equal attention.

While vascular plants have been monitored continuously and systematically (e.g., B. Magnússon *et al.* 2014), there was no thorough inventory of bryophytes for a time span of 35 years. Up until 1973, bryophyte colonization had indeed been monitored (Bjarnason & Friðriksson 1972; Einarsson 1968; Friðriksson *et al.* 1972; Jóhannsson 1968;

Magnússon & Friðriksson 1974), and in 1967 a grid system of 100 m × 100 m quadrats was implemented for that purpose (Friðriksson & Johnsen 1968). The grid system was used in the moss inventories made in 1969 – 1972 (full inventories) and 2008 (partial inventory covering every other quadrat). Between 1972 and 2008, the collection of bryophytes was sporadic and registered findings are based on specimens in the AMNH and ICEL herbaria databases (Ingimundardóttir *et al.* 2014).

The inventory of bryophytes in 2008 revealed distributional contraction of some early colonists as well as expansion of others. Some of the species that were abundant in 1972 had declined considerably: *Racomitrium ericoides* (Brid.) Brid. (as *R. canescens* (Hedw.) Brid. prior to 1984), *Leptobryum pyriforme* (Hedw.) Wilson, *Schistidium apocarpum* coll., *Funaria hygrometrica* Hedw., *Philonotis* spp., *Pohlia* spp., *Bartramia ithyphylla* Brid., and *Schistidium strictum* (Turner) Loeske ex Mårtensson; while others had continued to flourish, for example: *Schistidium maritimum* (Sm. ex R.Scott) Bruch & Schimp., *Racomitrium lanuginosum* (Hedw.) Brid., *R. fasciculare* (Hedw.) Brid. and *Bryum argenteum* Hedw. (Ingimundardóttir *et al.* 2014).

New colonists were discovered as well, eight of which had never been reported from Surtsey before: *Bryum elegans* Nees, *Ceratodon* cf. *heterophyllus* Kindb., *Didymodon rigidulus* Hedw., *Kindbergia praelonga* (Hedw.) Ochyra, *Schistidium confertum* (Funck) Bruch & Schimp., *S. papillosum* Culm., *Tortula hoppeana* (Schultz) Ochyra and *T. muralis* Hedw. (Ingimundardóttir *et al.* 2014).

It is important to keep in mind the profound changes that took place on Surtsey between the years 1972 and 2008, one being the sheer loss of area, amounting to at least 0.9 km^2. In addition, the habitats underwent drastic changes. Areas affected by geothermal activity and moisture were extensive in the earlier years and favoured by certain bryophytes (Magnússon & Friðriksson 1974), whereas such areas were scarce in 2008 and lithophytic bryophytes were by far the most prominent group. The development of a gull colony after 1985 and subsequently a grassland (13 ha in 2018) fed by nutrients accumulated by the birds, are recent elements contributing to the successional development of plant communities (Magnússon *et al.* 2020). Thirteen of the bryophyte species discovered in 2008 were confined to the gull colony or its close proximity, and most were secondary colonists (Ingimundardóttir *et al.* 2014), known to favour soil with organic content (Dierssen 2001).

In the summer of 2018, ten full years had passed since the island was last studied with regard to

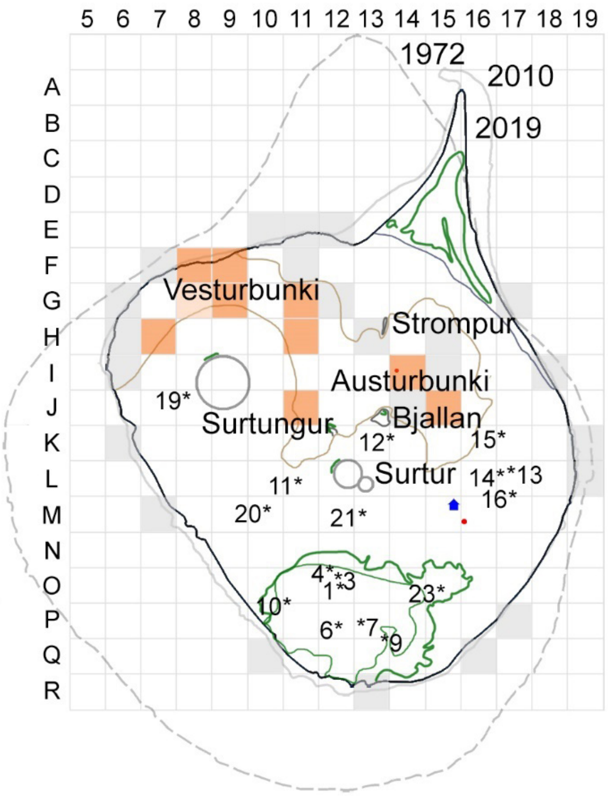

Figure 2. The figure shows the 100 m × 100 m grid system used to monitor the distribution of bryophytes, as well as the main habitat types on Surtsey and examples of past shorelines. The northern spit of the island, roughly denoted by blue contour, is made up of coastal sediments. The area denoted by beige colour approximately represents the palagonite tuff cone, named Vesturbunki and Austurbunki. Protruding lava formations on the palagonite tuff are marked with grey colour, Strompur and Bjallan are tallest. Quadrats filled with orange colour had noticeable heat emission in 2018, the pale orange quadrat had steam emission noted in 2008 but none in 2018. Quadrats filled with grey were deemed unsafe to access in 2008. Black circles indicate the main craters, Surtungur and Surtur. Green polygons show where there was dense vegetation and a colony of seagulls or fulmars: light green is adjusted from Magnússon *et al.* (2009) and solid green from Magnússon *et al.* (2020). The blue house indicates the location of the research facilities, Pálsbær, and close by, the helicopter platform (concrete) is marked in red (M16). The red marking in the palagonite tuff Austurbunki marks lighthouse ruins (concrete), standing at the islands highest point (154 m a.s.l.). Permanent plots used in our study are marked with asterisks and numbers. Map: GVI and The Icelandic Institute of Natural History.

bryophytes, and to the best of our knowledge, it was the third visit of a professional bryologist to the island. The previous ones having been in August 1967, when Bergþór Jóhannsson visited the island after students had discovered moss on the island, and by him again in May 1970 (Friðriksson *et al.* 1972; Jóhannsson 1968). Apart from these three occasions, bryophytes have been identified by specialists while sampled by biologists with botanical interests. Another difference between 2008 and 2018 was that the work was carried out by a single person in 2008 (GVI) and two people in 2018 (GVI and NC), thus increasing the fieldwork intensity. The field trip in 2018 also encompassed an inventory of bryophytes on Elliðaey.

Our aim in 2018 was to keep the monitoring of bryophytes on Surtsey on track by revisiting the 100 m × 100 m quadrats that were surveyed in 2008. We also wanted to study the bryophyte communities on Elliðaey for a comparison with Surtsey, in order to better predict how the succession on Surtsey may unroll.

MATERIALS AND METHODS

Our methods on Surtsey in 2018 followed that of the methods used in 2008 by Ingimundardóttir *et al.* (2014), though any deviations were noted: Surtsey (Fig. 2) was visited for bryophyte collection during July 16 – 19, and Elliðaey (Fig. 3) July 19 – 20, 2018 by GVI and NC together. For sampling, the same 100 m × 100 m grid (Friðriksson & Johnsen 1968) was used as in the earlier surveys of bryophyte distribution on Surtsey in 1970 – 1972 and 2008 (Friðriksson *et al.* 1972; Ingimundardóttir *et al.* 2014; S. Magnússon & Friðriksson 1974). Every other 100 m × 100 m quadrat of the island, the same as in 2008, was searched and sampled as long as it was safe to access – we left out at least a 2 m wide border next to the edge of the cliffs. A few additional quadrats were sampled to complete the inventory in cases where a certain quadrat seemed likely to reveal additional species not found elsewhere: 9 on the palagonite tuff ridge, mainly because this time, we ventured closer to the edge of the cliffs than in 2008; 1 quadrat was added on the sandy lava field east of the palagonite tuff. General notes about the habitat of each quadrat were made as well as an estimation of total bryophyte cover: no cover; low cover (<1%, e.g., Fig. 4 centre images); moderate cover (1 – 20%, e.g., Fig. 5 left); – high cover was never observed. We will also present some previously unpublished data from the fieldwork in 2008.

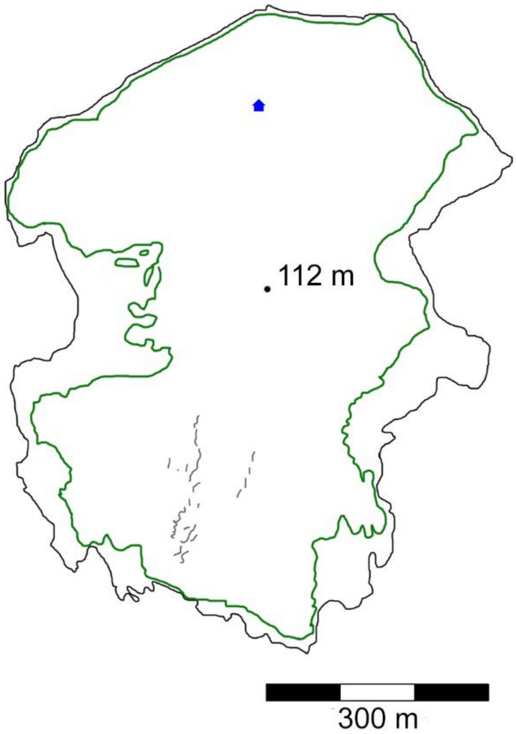

Figure 3. The contours of Elliðaey. The area within the green contour is covered with a lush grassland in a sloping landscape (see Fig. 15), except for an occasional protruding lava formation (grey lines indicate where they are mostly to be found). The shoreline and the core are made up of palagonite tuff, with only the occasional lava. The blue house marks the Elliðaey lodge. The shore is partly made up of bird cliffs whereas the grassland is a breeding ground for Atlantic Puffins and Leach's Storm-Petrels. Map: GVI, based on a satellite image from Google Maps (accessed on March 19, 2022) and data from National Land Survey of Iceland.

To establish the position of each quadrat on Surtsey, a handheld Garmin GPS was used with an accuracy of about ±10 m. An effort was made to avoid samples with dubious assignment to quadrats, that is, sampling at the border between quadrats was avoided, unless a particular species was absent from inside a quadrat and only present along the borders. However, with the following exception: At first, we worked with the erroneous assumption that the GPS points of each quadrat showed the centre point, when in fact they indicated the lower left corner of each quadrat. This affected the following seventeen quadrats: E14, E16, F8 – F10, G7 – G9, G11, H7 – H8, K14, K16 – K18, L15 and L17. On Elliðaey (Fig. 3), every habitat type was sampled, and an attempt was made to give a complete inventory.

Figure 4. Habitat types on Surtsey. Top left: Standing on Austurbunki (palagonite tuff), looking over the northern spit (see Fig.1), made up of coastal sediment. Top right: The east slope of the palagonite tuff, the beige-coloured top is the palagonite tuff whereas the darker coloured material is loose tephra, susceptible to movement, especially in winter weathers. On and under the lower rim of the palagonite tuff a green lustre from bryophyte colonies can be seen, the same pattern ran along the cone to the northern side. Centre left: ʻAʻā lava in the south-eastern part of Surtsey, mostly free from sand. Centre right: Sandy lava fields cover large areas of Surtsey, both south of the palagonite tuff cone and east of it (where this photo was taken). Lyme grass can be seen in the foreground and at the back. Bottom left: Looking east from the palagonite tuff ridge Vesturbunki, the crater Surtungur is to the right, surrounded with a sandy lava field, and the lighthouse ruins are visible at the top of Austurbunki in the distance (154 m a.s.l.). Bottom right: Looking to northwest, towards the palagonite tuff ridge, with cushions of *Schistidium* spp. growing on the palagonite tuff in the foreground. Photographs: GVI 2018.

In addition, a selection of 15 out of the 29 10 m × 10 m permanent plots on Surtsey (Magnússon *et al.* 2020) were surveyed for bryophyte species composition. The plots that were deemed likely to survive the erosion of Surtsey's shoreline in the next few decades were prioritized. Also, plots in proximity to similar plots already sampled were given a lower priority. Identifications in these plots were made in the field. We also present data on bryophytes in the permanent plots, collected by plant ecologist Sigurður H. Magnússon in 2003 and determined by Bergþór Jóhannsson.

Figure 5. The lava at the edges of the gull colony was to some extent covered with moss (left image), whereas areas in the colony's centre were covered with lush grassland (right image). The photo also shows members of the expedition systematically searching for seabird nests. Photographs: GVI and NC 2018.

On both islands, samples of all species in each quadrat (Surtsey) or habitat (Elliðaey) were put in plastic bags which were placed in a freezer upon returning to the lab. The material was subsequently thawed and sorted by species under a dissecting microscope and placed into separate paper bags. Care was taken to remove only the smallest amount necessary for identification and never to obliterate the populations. The samples from 2018 were preserved at Lund University, Biology Department; and samples from 2008 have been at the Icelandic Institute of Natural History since 2014 (Ingimundardóttir *et al.* 2014).

During work with species determination under microscope, numerous photos were taken, especially for critical groups. These photos may prove to be useful for future inventories when determinations may need to be compared and perhaps re-assessed, and because the voucher specimens in some cases include only few shoots.

All bryophyte samples prior to 2008 were identified by bryologist Bergþór Jóhannsson (1933 – 2006). Samples from 2008 were identified by bryologist Henrik Weibull and from this investigation by Nils Cronberg (NC). Gróa Valgerdur Ingimundardóttir (GVI) assisted in the determinations on both occasions. Nomenclature follows the latest checklist for European mosses (Hodgetts *et al.* 2020), except for *Ceratodon heterophyllus* where we follow Frey *et al.* (2006); for details on the nomenclature followed, see the annotated checklist in Appendix A, where we listed all bryophyte species that have been found on Surtsey up until April 2022. Information from specimens in the herbaria (ICEL and AMNH) of the Icelandic Institute of Natural History was also compiled here (Appendix A & B). We are not aware of bryophyte samples from Surtsey being preserved elsewhere.

RESULTS AND DISCUSSION

Bryophyte distribution

In total, 57 quadrats were surveyed on Surtsey in 2018, most of which had also been surveyed in 2008 when 70 quadrats were visited (Fig. 6). Due to erosion, a couple of quadrats had disappeared or were now located too close to the sea to be safely visited (K6 and R13; Fig. 2). The erosion is fastest at the southern and southwestern edges of the lava aprons, which are most exposed to the strong westerly winds of the Icelandic Low (a semi-permanent low-pressure system between Iceland and southern Greenland) (Britannica 2012), and subsequent high energy wave action, grinding the lava.

The overlap between the surveys in 2008 and 2018 was 47 quadrats, two of which were devoid of bryophytes in 2008 but in 2018 had some moss growing in the moisture at the roots of the semi-loose tephra that makes up the northeast slopes of the palagonite tuff cone (Fig. 6: quadrat E14 & H17). In the same area, higher up in the slope, we saw potential moss colonies on the palagonite tuff as green lustre in inaccessible areas (Fig. 2 & 4 top right). Our general impression was that moss cover had increased considerably between 2008 and 2018, especially on the palagonite tuff, which was noticeably void of moss cover in 2008, except in cracks and by fumaroles.

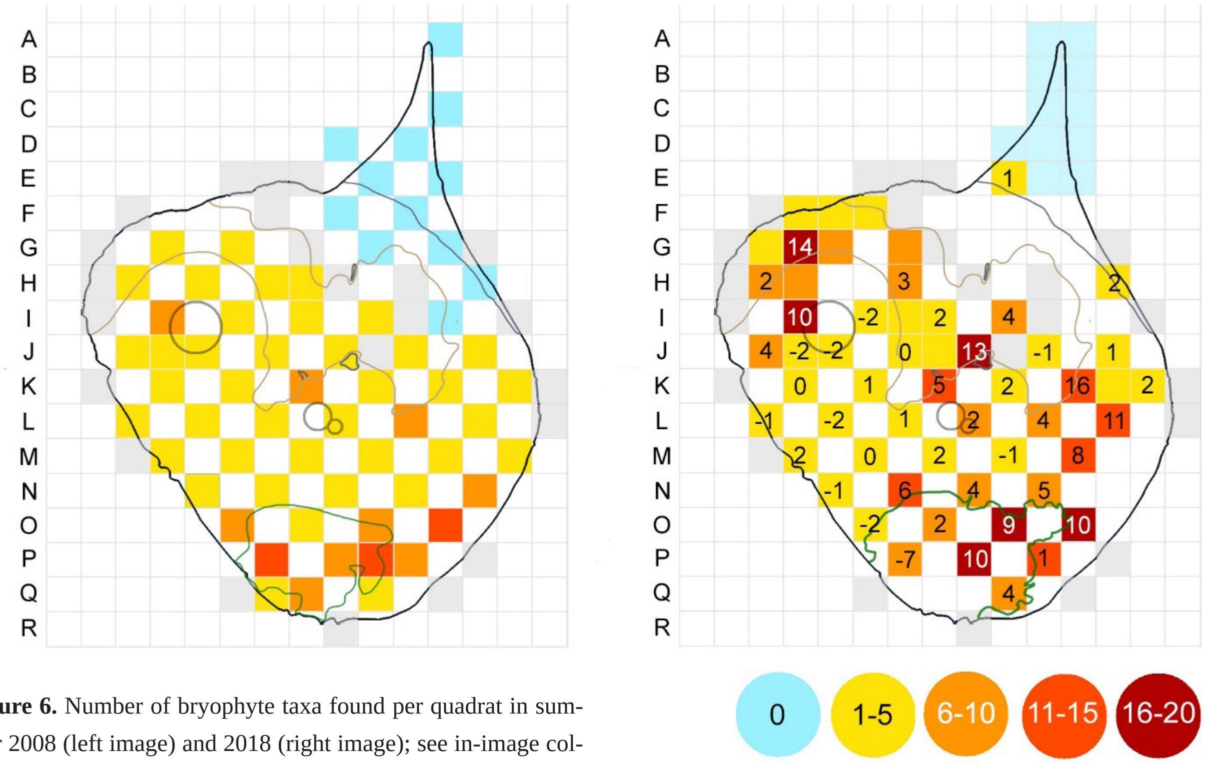

Figure 6. Number of bryophyte taxa found per quadrat in summer 2008 (left image) and 2018 (right image); see in-image colour legend. Trends in species numbers per quadrat between 2008 and 2018 are marked with numbers in the right image, where available. Quadrats filled with grey were deemed unsafe to access in 2008. Circles indicate the craters, Surtungur and Surtur. The area denoted by beige colour approximately represents the palagonite tuff cone, named Vesturbunki and Austurbunki. Protruding lava formations on the palagonite tuff are marked with grey colour. Green polygons show where there was dense vegetation and a colony of seagulls: contour on left images is from Magnússon *et al.* (2009), and the one on the right image is from B. Magnússon *et al.* (2020). Maps: GVI and The Icelandic Institute of Natural History

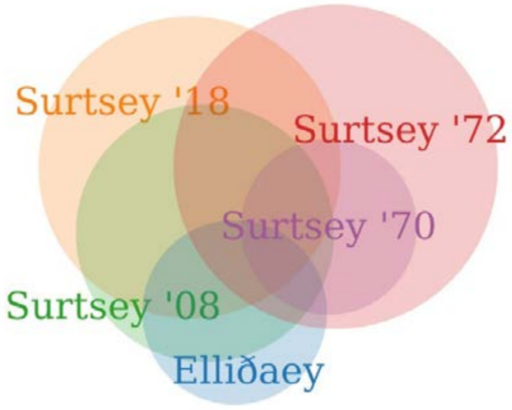

Figure 7. Area proportional Venn diagram for the total number of taxa (Appendix B) found on Surtsey in the surveys in 1970, 1972, 2008 and 2018. Each circle represents a total species number for a given year: 1970 = 17, 1972 = 72, 2008 = 39, 2018 = 59; the intersections indicate the species in common.

Species richness

In total, 123 bryophyte taxa have been registered on Surtsey (Appendix A & B). Comparing the two surveys of 2008 and 2018, 59 taxa were encountered in 2018 inventory, compared to 43 taxa in 2008; 31 taxa were found in both inventories (Fig. 7). Nine species were only observed in 2008, whereas 24 species were only found in 2018, however, ten of these had been encountered during earlier inventories. It is often difficult to confirm if species are gained or lost, because most of the pertinent species are small and inconspicuous, occurring in small populations and in few quadrats. Some species or subspecies might also belong to critical groups that have historically been subject to alternative taxonomical treatments, for example several of the most common genera on Surtsey: *Bryum*, *Schistidium*, *Racomitrium* and *Didymodon*. Furthermore, specimens may lack critical characteristics, so it is only possible to determine them to genus level. Thus, some of the species identified in the 2018 survey might be hidden as undetermined species of various genera in previous surveys.

The bryophyte species richness of Surtsey rose sharply after the eruption ended in 1967, climbing from 2 species in 1967 to 73 species in 1972 (Fig. 8). Compared to other groups, only about ten lichen and vascular plant species, respectively, had colonized

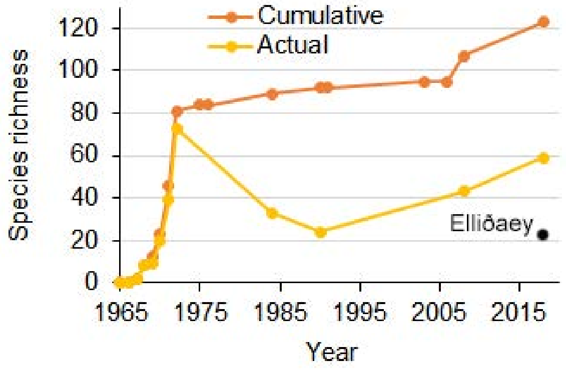

Figure 8. Bryophyte species richness on Surtsey, both actual and cumulative. The species richness on Elliðaey in 2018 is also shown.

the island during the same time period (Kristinsson & Heiðmarsson 2009; Magnússon *et al.* 2009). However, despite the sparsity of data for bryophytes, it seems evident that they have not followed the same pattern as vascular plants, which colonized Surtsey quickly but entered a lag period after 1975, with roughly 10 species, whereas species richness of bryophytes took a dive after 1972. The lag period for vascular plants ended after 1985 as gulls started forming a breeding colony and new niches for vascular plants formed. Vascular plant succession on Surtsey has proved quite dependent upon vertebrate activity, from both birds and seals (Magnússon *et al.* 2020). Lichens also benefitted from colonizing birds (Kristinsson & Heiðmarsson 2009), but it cannot be confirmed whether bryophyte richness started increasing after 1985 as well, although our data is coherent with such a development.

The mean number of species per selected quadrat on Surtsey was 4.5 in 2008 and had risen to 6.6 in 2018 (empty quadrats omitted). Thirty-two quadrats showed an increase in species richness; three quadrats showed no change; ten quadrats showed a slight decrease of 1 – 2 taxa while one quadrat showed a considerable decrease of 7 taxa (Fig. 6).

Species richness in 2008 was higher in areas colonized by seabirds (Fig. 6) as opposed to areas without breeding seabirds. This effect was even more evident in 2018, with 9.7 species/quadrat with breeding seabirds (Fig. 6) compared to 4.9 species/quadrat outside these areas. Of the 59 taxa found on Surtsey 2018, 45 (76%) were found in these areas. Outside areas with breeding seagulls (conservatively in M16, N – R 10 – 15) of Lesser Black-Backed Gulls (*Larus fuscus* L.), Herring gulls (*L. argentatus* Pontopp.) and Greater Black-Backed Gulls (*L. marinus* L.), Arctic Fulmar (*Fulmarus glacialis* (L.)) seemed to play a key role. The fulmars frequented and or bred in the following areas: the NNW edge of Vesturbunki, Surtungur, Surtur, Bjallan and small lava crater west of Bjallan (F8 – 10, G7 – 8, H7, I8, J13, K12 and L13; Fig. 2, own observations, but

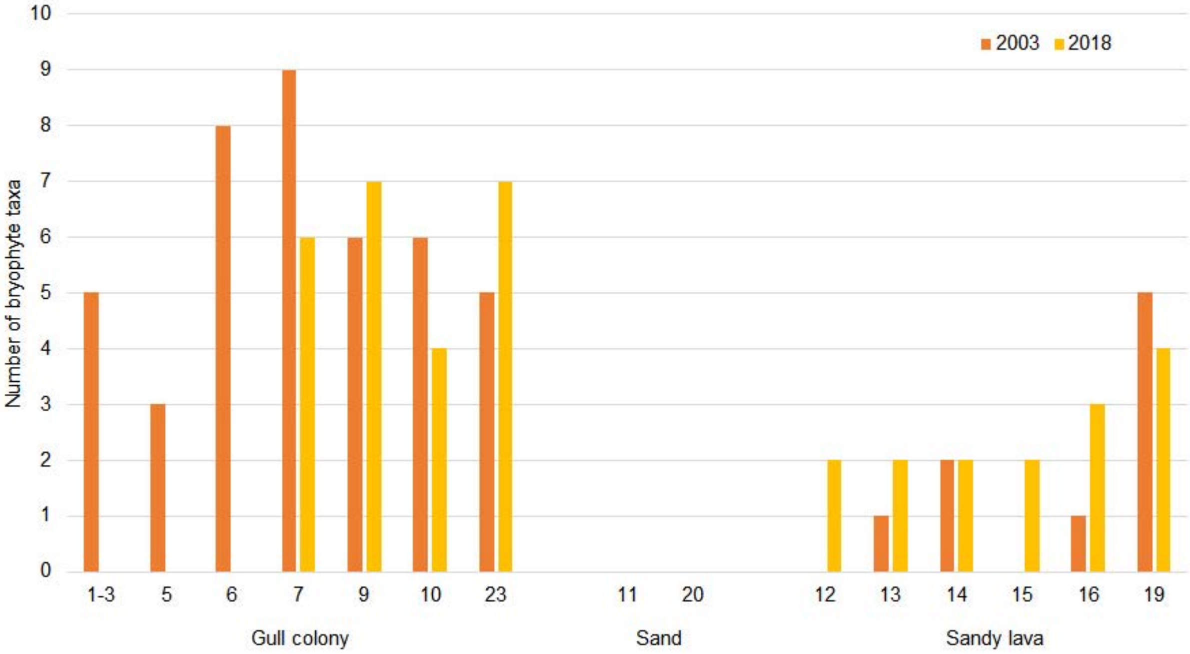

Figure 9. Number of bryophyte taxa found in permanent plots on Surtsey, investigated in both 2003 and 2018 (numbers on X-axis). See figure 1 for the plots' location on Surtsey.

for details see Petersen (2009)). In addition, birds frequent the helicopter platform, and a few gull-nests were found nearby (quadrat M16). The most species rich quadrats were within the previously mentioned areas (Fig. 6) as well as most of the quadrats that showed the greatest increase of species. Interestingly, the only quadrat with a marked decrease in richness (P11, Fig. 6) was also within a bird colony. In that quadrat, the grassland was dense and extensive, and so were the cushions of *Schistidium* on the protruding lava. Presumably, species less adapted to high nutrient conditions were outcompeted and/or shaded out by the dense grasses.

Missing species

Eight of the bryophyte taxa found in 2008 were not rediscovered in 2018 (Appendix B). Seven of those had only been found in a single quadrat: the liverwort *Reboulia hemisphaerica*, and the mosses *Trichostomum brachydontium, Philonotis fontana, Hymenoloma crispulum, Ceratodon heterophyllus, Rhytidiadelphus squarrosus* and *Ptychostomum capillare*. The eighth taxon, the liverwort *Cephaloziella* cf. *divaricata*, was found in nine quadrats in 2008 and may be present in the five unconclusive samples of *Cephaloziella* in 2018, four of which coincided with previous findings' locations (O14, O16, P13 and Q14). The unrecorded taxa include several small and inconspicuous species which are likely to go undetected without focussed searching, but also relatively large and visible species, such as *Rhytidiadelphus squarrosus* and *Philonotis fontana*, were not encountered. However, it is important to keep in mind that only about every other quadrat on Surtsey was searched and even so, parts of the island are difficult to cover in limited time, especially lava fields with cave-like depressions and hollows.

The following four species seem to have the prospects for reappearing in future surveys, due to occurrence of suitable habitats on Surtsey and potential source populations on neighbouring islands and/or mainland Iceland. The liverwort *Reboulia hemisphaerica* is found growing on palagonite tuff in several locations in south Iceland and two islands in the Vestmannaeyjar archipelago (Jóhannsson 2002). *Trichostomum brachydontium* is found in south Iceland, including the Vestmannaeyjar archipelago, mostly close to the seashore, growing on soil, rocks, and lava (Jóhannsson 1992a). The exact location of the 2008 samples is uncertain. *Hymenoloma crispulum* was found with sporophytes in N12 in 1972 (Magnússon & Friðriksson 1974), rediscovered in 1984 (Appendix B) and in quadrat H9 in 2008. H9 was not visited in 2018 and so it is possible the colony was still present. *H. crispulum* is widespread in Iceland and is also found on Heimaey in the Vestmannaeyjar archipelago. It most frequently occurs with sporophytes and is found on rocks, lava and sand, from the coast and up to the central highlands (Jóhannsson 1991). *Ptychostomum capillare* is found both in south Iceland and the Vestmannaeyjar archipelago, growing mostly on lava but also on soil. In 1969, it was widespread, growing in small, sand-filled hollows in the lava field area (quadrats MN 13 – OPQ 12 – 14), and sometimes on the lava itself. At that time, there were some heat and steam emissions in that area, but the species was not limited to them (Bjarnason & Friðriksson 1972). In 2008, it was only found in Q12, the same area as in 1969.

Ceratodon cf. *heterophyllus* was found for the first time on Surtsey in 2008 and was not rediscovered in 2018. The species has not been found elsewhere in Iceland, and it is to be noted that *C. heterophyllus* Kindb. is a controversial taxon, endemic to arctic North America (Ireland 1980). The species was registered in 2008 with some doubt. *Ceratodon heterophyllus* is not included in the European checklist for bryophytes (Hodgetts *et al.* 2020), but is mentioned in *The Liverworts, Mosses and Ferns of Europe* as having been described from Spitsbergen (Frey *et al.* 2006). Morphological variation in the common *C. purpureus* is large (e.g. Frey *et al.* 2006; Ireland 1980) and the morphotypes encountered on Surtsey during 2018 were quite diverse and often reddish in colouration.

Philonotis fontana is often found with sporophytes, growing in freshwater wetlands or on moist cliffs. It is common around Iceland but is not found in the Vestmannaeyjar archipelago (Jóhannsson 1995). In 1971 – 1972, *Philonotis* spp. (according to the authors, likely to be immature specimens of *P. fontana*) was widespread on Surtsey, found in 51 quadrats in 1972 and in abundance in some quadrats (Magnússon & Friðriksson 1974). In 2008, *Philonotis* cf. *fontana* was found in quadrat O14 at 63°17'53.3"N and 20°35'59.5"W, but no *Philonotis* species was found in that quadrat in 2018. *P. tomentella* was only found in 1990 and *P. capillaris* was found in three quadrats in 2018. The fact that the distribution of *Philonotis* cf.

fontana has declined is perhaps less surprising than how frequent it was in the early days. In 1972, most of the samples of *Philonotis* came from moist, sandy hollows. In 2008 and 2018, none of the habitats were moist to the extent to favour *P. fontana*. According to Elmarsdóttir & Vilmundardóttir (2009), *Philonotis* seems to be common in geothermal areas in Iceland as it was found in 19 of 28 high-temperature geothermal areas studied (with temperatures over 15°C).

Rhytidiadelphus squarrosus was found in a single quadrat in 1972 (Magnússon & Friðriksson 1974) and in 2008 only in P11. In 2018, that quadrat was located well within the gull colony. It was characterized by rough lava, mostly covered with *Poa* and *Festuca* grassland and with a lot of *Schistidium* on the lava outcrops. *R. squarrosus* is common in lawns, grasslands, heaths, and lava fields in Iceland (including Heimaey) (Jóhannsson 1996). Considering that it is conspicuous and easy to determine, a vigorous population would be hard to miss – except of course in omitted quadrats. Even though the species is common in grasslands it favours nutrient poor habitats, as opposed to the nutrient rich grassland of the Surtsey gull colony.

New species

In 2018, 16 new taxa were listed (Appendix B). However, some of these might not represent an actual change in species composition since several of the genera that expanded in 2018 were represented by inconclusive samples in 2008 (denoted as "sp.") e.g., *Brachythecium* (1 quadrat), *Didymodon* (2 quadrats), *Pohlia* (1 quadrat), *Schistidium* (20 quadrats) as well as *Bryum* (26 quadrats; including species now referred to the segregate genus *Ptychostomum*). No samples of these genera were left inconclusive in 2018.

Specimens of the genus *Bryum* and *Ptychostomum* are often difficult to determine, especially when sporophytes are missing and in the survey from 2008 a total of 26 were not determined to species (registered as *Bryum* spp.). Undetermined *Bryum*/*Ptychostomum* specimens have been recorded ever since bryophytes were first found on Surtsey in 1968. This makes the comparison of presence/absence data for this genus somewhat difficult to evaluate. In the present survey, specimens without sporophytes but having frequent multicellular gemmae were determined to *Bryum dichotomum*. The specimens were rather variable in size but characterized by reddish leaf base and pointed leaf apex with shortly excurrent nerve. Whereas this taxon was only recorded once in 2008, we found it in 33 quadrats in 2018. Although some specimens from 2008 may be hidden among the undetermined samples (stored at the Icelandic Institute of Natural History), it seems likely that this taxon has spread rapidly, presumably by vegetative dispersal. It was found on loose material in somewhat protected microsites, but also around fumaroles.

We also registered somewhat larger specimens which carried both archegonia and antheridia in the same inflorescence, i.e., being synoicous, which separate them from most *Bryum*/*Ptychostomum* species. These specimens were similar, characterized by a conspicuously bright red leaf base and rather long leaves, so it seemed possible that they all belong to the same species. Even when sporophytes were present, peristomes were most often in poor shape, and it was only possible to narrow down the determination to a species complex consisting of *Ptychostomum arcticum*/*compactum*/*inclinatum* or possibly *P. salinum*. All these species have earlier been identified from Surtsey (as *Bryum arcticum*, *B. algovicum*, *B. archangelicum* and *B. salinum*), but not in the 2008 survey, where they may be concealed among the *Bryum* sp. specimens. A comparative study employing molecular markers would be desirable to reveal the true diversity and phylogenetic relationship of *Bryum/Ptychomitrium* on Surtsey.

A more spectacular change on Surtsey is that six liverworts were encountered for the first time in 2018: *Aneura pinguis*, *Cephaloziella* cf. *varians*, *Lophozia longidens, L. sudetica*, *Nardia scalaris* and *Tritomaria scitula*. The liverwort genus *Cephaloziella* is often difficult to determine to species. It is therefore with some hesitation that several specimens found were tentatively specified as *Cephaloziella* cf. *varians*. In 2008, liverworts were very rare and hard to find, whereas it was somewhat easier in 2018. These liverworts were all found on grass-covered soil in protected cavities in the lava formations in the outskirts of the gull colony area. It is probable that accumulation of soil in protected patches have paved the way for their colonization, and perhaps the exceptionally rainy summer of 2018 (Icelandic Met Office 2019) also favoured these delicate, moisture dependant species.

Most of the newcomers were found in only a single quadrat: *Aneura pinguis*, *Didymodon tophaceus*, *Lophozia longidens*, *Nardia scalaris*, *Sphenolobus minutus*, *Tortula mucronifolia*, *Tortula* *subulata* and *Tritomaria scitula.* Four were found in two quadrats: *Lophozia sudetica, Ptychostomum pseudotriquetrum, Schistidium frigidum* var. *havaasi* and *S. pruinosum.* One was found in three quadrats: *Schistidium maritimum* subsp. *piliferum*; and one in four quadrats: *Cephaloziella* cf. *varians*.

Habitats

The spit

In both surveys, no bryophytes were found on the northern spit (Fig. 2), which is made up of coastal sediment and boulders. Despite the unstable nature of the habitat, where waves wash over in winter, there was a cover of vascular plants in 2008, that had grown considerably denser in 2018. Both seals and seabirds breed on the spit and have fuelled the buildup of vascular plant communities (Magnússon *et al.* 2020) but that has, as of yet, not favoured bryophytes.

The palagonite tuff and fumaroles

As mentioned earlier, our impression was that the bryophyte cover had increased considerably on the palagonite tuff in 2018, which ten years earlier, was practically naked, only fostering small colonies of bryophytes growing in cracks and near fumaroles. In 2018, tufts of moss on the palagonite tuff could be seen from a distance (Fig. 11 low right). On the other hand, bryophytes were noticeably missing closest to the hot rims of fumaroles, a pattern not noted in 2008. Close to the edge of the sea cliffs on Vesturbunki were protrusions and brims, providing microhabitats suitable for bryophytes. There were also nesting fulmars, providing a nutrient source.

Two species were found in quadrats with fumaroles and not elsewhere. The former, *Dicranella crispa*, was first found in 1968, and then again in over 10 quadrats in 1971 and 1972 and has been encountered on Surtsey a few times since then. It is widespread in Iceland and grows on moist or rather dry, naked to half-naked soil (Jóhannsson 1992a). The latter, *Didymodon tophaceus*, is a calciphile known from southern Europe to southern Scandinavia, and Iceland where it is known to be without sporophytes and grow in geothermal areas, by hot springs and streams, and on moist sandstone (palagonite tuff). It has only been found in seven locations in Iceland, in addition to Surtsey (Frey *et al.* 2006; Jóhannsson 1991) where it was first discovered in 2018.

The skirt of the palagonite cone

The northern and north-western sides of the palagonite tuff cone Austurbunki were skirted with semi-loose tephra (Fig. 4 top right) and were both hard to access and unlikely to provide valuable information on bryophytes due to substrate instability. Bryophyte growth was absent in 2008 and minuscule in 2018. The southern edges of the cone were skirted with loose and dry tephra, devoid of bryophytes (see the approximate contour of the exposed palagonite tuff in Fig. 2 and the habitat in Fig. 4 bottom).

Surtungur

Of the four quadrats intersecting the large crater Surtungur (Fig. 2), we visited three and found in those a total of 19 taxa. Three of which only had that single occurrence on Surtsey: *Distichum capillaceum, Tortula mucronifolia* and *T. subulata* var. *graeffii*. The total number of taxa was probably an underestimate because the crater is partially difficult to access. The sheltered inside of Surtungur is the only area on Surtsey where thick carpets of *Racomitrium lanuginosum* have formed, but the cushions were in a rather poor condition in 2018 and there had been an accumulation of sand (Fig. 10).

Sandy lava-fields

Many quadrats had only one to three species with low coverage, these quadrats were often dominated by loose tephra interspersed with occasional lava outcrop. The most common species were *Bryum dichotomum* Hedw., *Schistidium maritimum, S. flexipile* (Lindb. ex Broth.) G.Roth and *Racomitrium lanuginosum*, mostly growing in cracks in the lava. Permanent plots R12 to R17, R19 and R21 were located within sandy lava fields and had very little bryophyte cover (Table 1, Fig. 9). Permanent plots

Figure 10. *Racomitrium lanuginosum* cushions in Surtungur crater displayed a lot of dead moss in 2018 (cropped image, NC), compared to 2008 (background image, GVI). The photos show the amount of sand had also increased (see below the red rock).

R11 (Fig. 11) and R20 were covered in tephra and had no bryophytes, neither in 2003 nor 2018 (Fig. 2).

'A'ā lava

The 'a'ā lava field east of the gull colony did not have a sandy surface and was almost devoid of vegetation (Fig. 4 centre left). The *Racomitrium lanuginosum* cushions in this area showed considerable signs of degradation. Quadrats O16 and P15 were in the 'a'ā lava and the northern edge of the field stretched into M16 (Fig. 2).

Gull colony

In the centre of the colony, there was a dense and lush grassland with a few outcrops of lava. In quadrat O12, where permanent plots R1, R3 and R4 were located (Fig. 2), we were unable to discern which of the permanent plots we had located in the thick grass and so they were joined into "R1/3/4" (Table 1).

The outcrops became gradually more frequent towards the outer fringe of the colony and the grass cover progressively thinner. There, mosses had greater cover than vascular plants (Fig. 5 left) and higher species richness (Fig. 9). Permanent plots R1 through R10, and R23 were all within the gull colony: plot R1/3/4 and R6 were dominated by a thick cover of mainly *Poa* and *Festuca* grasses and in those we found no bryophytes (Fig. 5 right); R7 through R10, and R23 had a considerable grass cover but also crevices and protruding lava formations, where bryophytes could be found at considerable density.

Plot R6 is located where the first breeding pairs of gulls were found in 1986. Inside the gull colony the vegetation quickly grew denser and species richer with respect to vascular plants. When the first permanent plots were established in 1990, the effects of the gull colony were already apparent, with a considerable increase in vegetation. The plots inside the colony in 1990 had around 30% cover (high compared to the rest of the island); only 8 years later, the cover had, in places, reached 100%. Plots outside the colony (Magnússon & Magnússon 2000) showed negligible increase in species richness and cover (Magnússon *et al.* 2009; Magnússon & Magnússon 2000). R6 showed marked increase in moss cover in 2000 – 2006, by which time the cover started to decrease (Magnússon *et al.* 2009) and in 2018 we found no bryophytes within that plot. This pattern of slow increase of cover and species richness without impact by the breeding birds is apparent for bryophytes as well. The initial response to nesting or resting birds is an increase in both cover and richness,

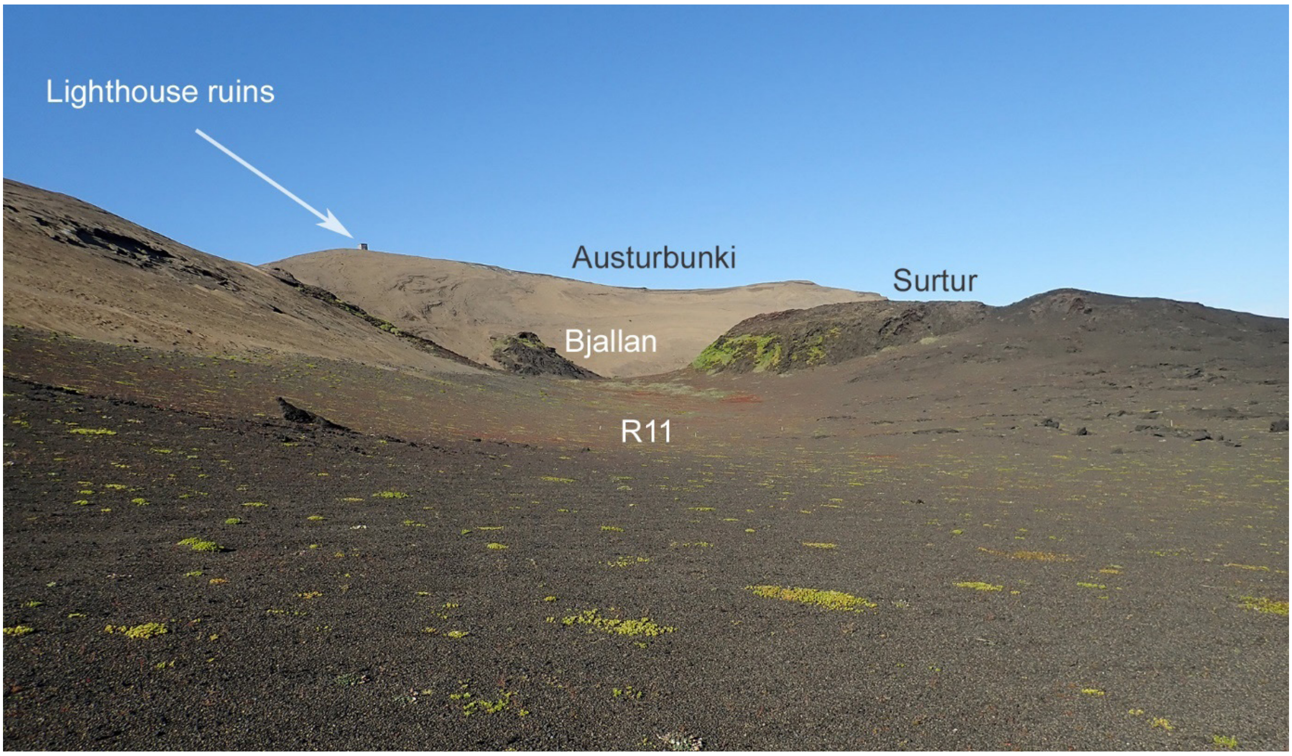

Figure 11. Standing roughly in quadrat M10, looking northeast, with permanent plot R11 in the centre, characterized by the red colour of *Rumex acetosella* L. The small crater Bjallan is seen to the centre of the palagonite tuff cone Austurbunki and the main crater Surtur. See figure 1 for perspective. Photograph: NC 2018.

but the bryophytes are then outcompeted by vascular plants as the grassland develops (Fig. 6 & 9).

Distributional changes of selected species

The distribution of several bryophyte species on Surtsey had increased markedly on Surtsey between 2008 and 2018 (Appendix B, Fig. 6). Fifteen species increased their area of occupancy by five quadrats or more between 2008 and 2018, whereas only two species showed a decrease to a similar degree.

Bryoerythrophyllum recurvirostrum was found in seven quadrats in 2008 but thirteen in 2018 (Fig. 12). The distribution indicates it may benefit from the traffic of seabirds but perhaps be sensitive to competition and/or nutrient rich habitats.

The cosmopolitan generalist species *Ceratodon purpureus* was first found on Surtsey in 1968, then growing with *Bryum* on lava. Already in 1970 it was found with spore capsules and therefore able to reproduce on Surtsey (Friðriksson *et al.* 1972). In 1971, it was found in 32 quadrats and the year after in 69 quadrats, this was coupled with a great increase in frequency within each quadrat: 88 % of the quadrats in 1971 had a single occurrence, compared to 33% in 1972, when most quadrats had 2 – 9 occurrences and three had 10 or more (Magnússon & Friðriksson 1974). Many of the quadrats where the species was found have now eroded away. The greatest colonization was around Surtungur and south of Surtur, or in the same areas as the species was found in 2018 (Fig. 12 right). The distribution increased from 10 to 19 quadrats between 2008 and 2018. It grew in and around the gull colony area, often together with *Plenogemma phyllantha*. *C. purpureus* is the only species of the genus found in Iceland. It is both common and widespread and found in a wide range of habitats, including beach-sand, concrete, palagonite tuff, and soil. Although it is dioicous, sporophytes are frequent in Icelandic material (Jóhannsson 1992b) and the same is true for Surtsey, which probably has enhanced its expansion. Whether the dip in distribution after 1972 was actual or not is hard to say based on our data.

The genus *Didymodon* Hedw. is sometimes considered to be difficult to identify, especially when growing in dry and wind exposed conditions where they are prone to become diminutive (Bjarnason 2018). The species found on Surtsey did not pose any

Table 1. Bryophyte species found in permanent plots on Surtsey (Fig. 2) in 2018. A note was also made on the amount, but no direct measurements. An example of *moderate bryophyte cover* can be seen in Fig. 5 (left). These photographs are just examples of habitats, not plots. All other photographs in this paper would be examples of *little bryophyte cover* (<1%) or *none*.

Bryophytes	**R1/3/4**	**R6**	**R7**	**R9**	**R10**	**R11**	**R12**	**R13**	**R14**	**R15**	**R16**	**R19**	**R20**	**R21**	**R23**
No bryophytes found	x	x				x							x		
Very little moss cover							x	x	x	x	x	x		x	
Moderate moss cover			x	x	x										x
Brachythecium albicans			x	x											x
Bryum cf. *capillare / elegans*			x	x	x										
Bryum dichotomum							x	x	x	x	x				x
Bryum spp.			x	x	x					x				x	
Cephaloziella spp.				x											x
Ceratodon purpureus											x				x
Pohlia sp.				x											
Racomitrium canescens coll.							x					x			x
Racomitrium fasciculare												x			
Racomitrium lanuginosum												x			x
Sanionia uncinata			x												
Schistidium maritimum			x	x				x	x		x	x		x	x
Schistidium spp.					x										
Plenogemma phyllantha			x	x	x										
Total number of taxa:	0	0	6	7	4	0	2	2	2	2	3	4	0	2	7

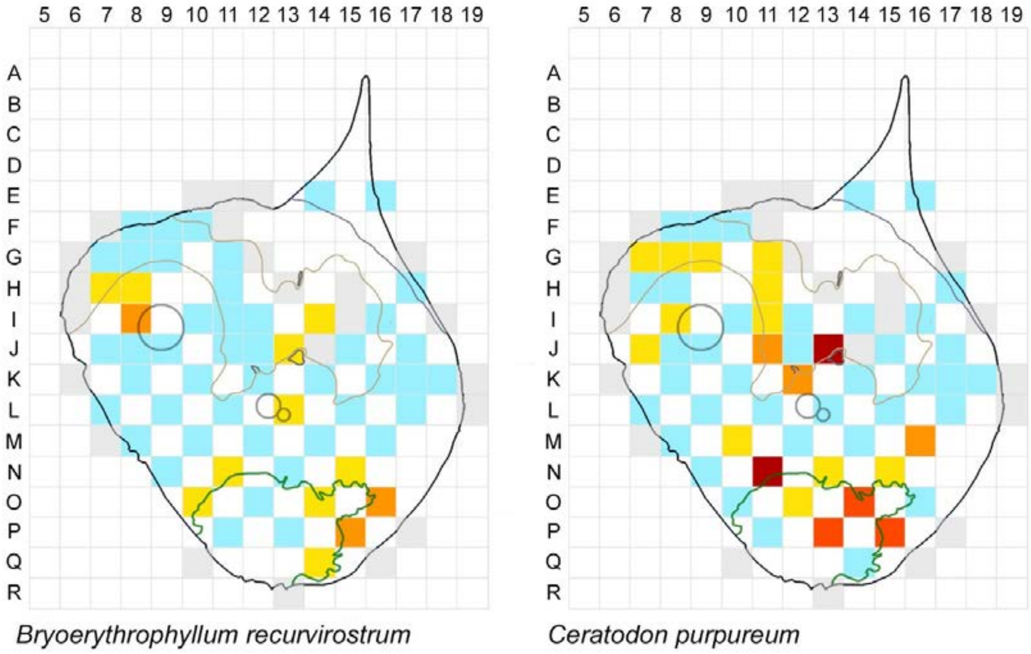

Figure 12. Distribution maps for *Bryoerythrophyllum recurvirostrum* and *Ceratodon purpureum*, two of the bryophyte species that showed greatest changes in distribution between 2008 and 2018. Only data from quadrats investigated in 1971, 1972, 2008 and 2018, are included. Legend: Pale blue = species not found in 2018; yellow = species found in 2018 but not in 2008; orange = species found in 2018 and 2008 but not in 1972; tomato red = species found in 2018, 2008 and 1972 but not in 1971; dark red = species found in all four surveys (2018, 2008, 1972 and 1971). Maps: GVI, The Icelandic Institute of Natural History.

serious determination problem under the microscope. The main challenge during our field work was that the species are rather small and occur in small populations, often mixed with other species. The genus was represented by five species in 2018: one was new (*D. tophaceus*), two showed the same area of occupancy as in 2008 (*D. fallax* and *D. rigidulus*), and two had expanded markedly (*D. brachyphyllus* from 2 quadrats in 2008 to 11 quadrats in 2018, and *D. icmadophilus* which was without records in 2008 but had seven occurrences in 2018). No sporophytes were found, but some of the species are known to have frequent vegetative dispersal agents (*D. tophaceus*, *D. rigidulus* and *D. brachyphyllus*).

Didymodon brachyphyllus (Fig. 13 left, Appendix B) was found in only 2 quadrats in 2008 (H12 and J11), while undetermined samples of the genus were found in two additional quadrats that year (G8 and L15). In 2018, the species was rediscovered in J11 (H12 was not revisited), additionally it was found in G8 and L15, as well as 12 other quadrats. This species is very small, with shoots up to one cm high, leaves only about 1.0 mm long and is distinguished from *D. vinealis* (Brid.) R.H.Zander mainly by the presence of gemmae in the leaf axils. It can often be spotted at a distance by orange colouration (personal observations (NC)). In Europe, *D. brachyphyllus* is only found in Iceland and in the 20th century it was hidden in ICEL herbarium among material of *D. vinealis* (then *Barbula vinealis* Brid.), confirmed from only 24 localities, among them Heimaey in the Vestmannaeyjar archipelago (Frey *et al.* 2006; Jóhannsson 1992a, 2003). *D. brachyphyllus* is epilithic and often found near the coast (Bjarnason 2018) and we found it in cracks in the palagonite together with *Tortula muralis*.

With exception for *Schistidium maritimum*, all species of *Schistidium* expanded their range from 2008 to 2018 (Appendix B). *S. flexipile* with as much as 30 quadrats (from five quadrats in 2008 to 35 quadrats in 2018), the other species by 6 – 8 quadrats. All species of *Schistidium* are monoicous and frequently fruiting. Presence of sporophyte is often necessary for identification and a lack of a well-developed sporophyte might explain a fairly high incidence of undetermined specimens (from 20 quadrats) in the 2008 survey. This also means that the difference in area of occupancy between the

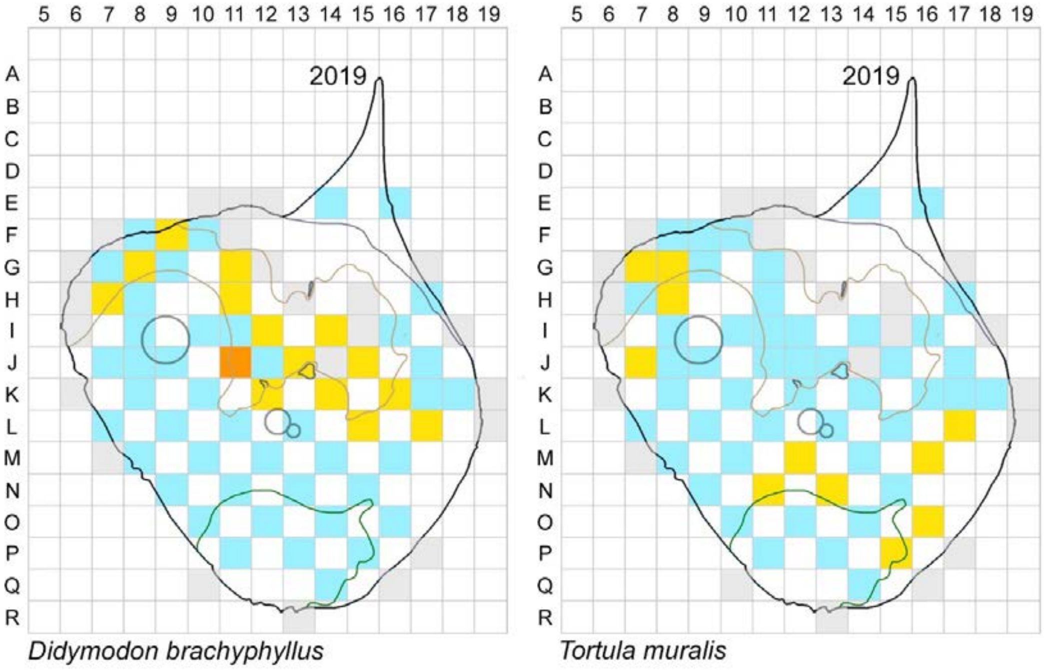

Figure 13. Distribution maps for *Didymodon brachyphyllus* and *Tortula muralis*, two of the bryophyte species that showed the greatest changes in distribution between 2008 and 2018. *D. brachyphyllus* was found in only 2 quadrats in 2008 and *T. muralis* was found in a single quadrat in 2008 (Table 1). Only data from quadrats investigated in 1971, 1972, 2008 and 2018, are included. Legend: Pale blue = species not found in 2018; yellow = species found in 2018 but not in 2008; orange = species found in 2018 and 2008 but not in 1972; tomato red = species found in 2018, 2008 and 1972; dark red = species found in all surveys (2018, 2008, 1972 and 1971). Maps: GVI, The Icelandic Institute of Natural History.

surveys may be somewhat inflated. Nevertheless, most *Schistidium* species are doubtlessly expanding, assumedly by locally generated spores. The genus is also the most speciose on Surtsey. We found a new species, *S. pruinosum*, in quadrats I14 and J11. The species is difficult to recognize in the field but when viewed under a microscope, it is characterized by densely papillose cells and double cell layers in the upper part of the leaves (see Supplement S1). Previously the species was only found in one location in Iceland, growing on concrete. It is notable that unopened spore capsules were sometimes found to be devoid of spores and that individuals sometimes displayed mixed characters, observations suggesting that hybridization may sporadically occur between *Schistidium* species.

A few other species with specific habitat demands increased their range on the island from 2008 to 2018, such as *Dichodontium pellucidum* in places with percolating water, *Tortula muralis* (Fig. 13) in cracks in the palagonite, and *Brachythecium albicans* on nutrient rich and sun exposed soil, aggregated in crevices in the lava fields to the south.

Declining species

Rather few species displayed declining area of occupancy, amongst those was *Schistidium maritimum*, dropping from 31 to 20 quadrats, *Racomitrium fasciculare* from 13 to 7 quadrats and *R. lanuginosum* from 26 to 21 quadrats.

The drop of *S. maritimum* can partially be explained by loss of some quadrats due to erosion at the south-western coast of the island. Competition with *S. flexipile* could also play a role, as these species appear to grow in the same habitat, often in mixed populations. Some specimens were determined to *S. maritimum* subsp. *piliferum*, which differ by having a short, thin, and sharp hairpoint, but these were often co-occurring with normal-looking *S. maritimum* (= subsp. *maritimum*), without a hairpoint, so this does not explain any change in area of occupancy.

In 2018, we observed that old and well-established mats of *Racomitrium lanuginosum* were dying, especially on volcanic rocks in the larger crater Surtungur, confirmed when photos from both surveys were compared (Fig. 10), but also on the

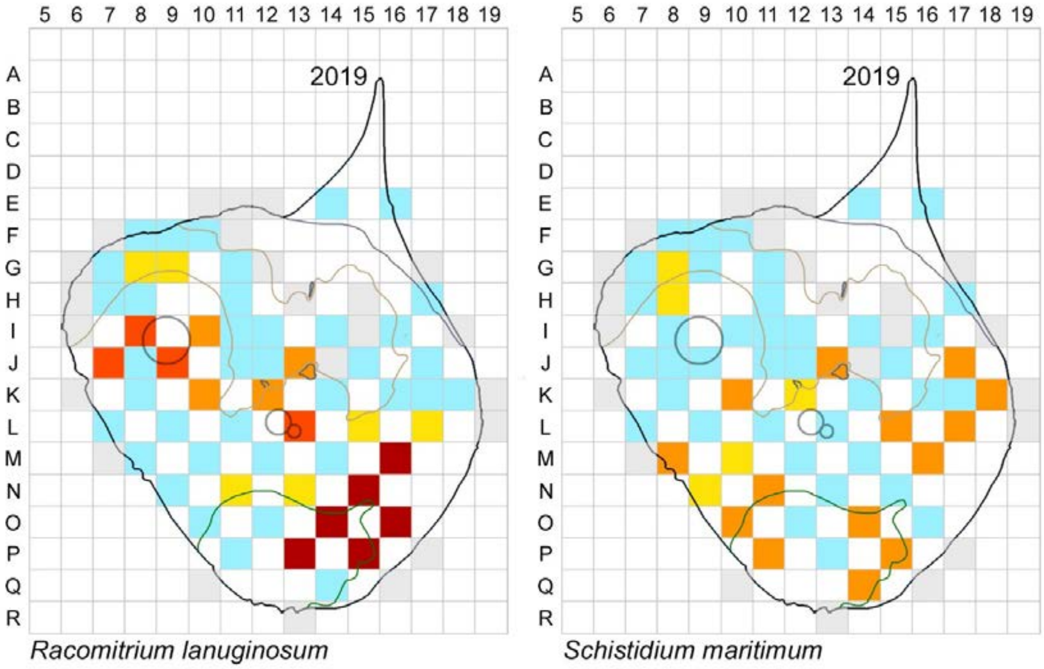

Figure 14. Distribution maps for *Racomitrium lanuginosum* and *Schistidium maritimum*, two of the bryophyte species that showed the greatest changes in distribution between 2008 and 2018. Only data from quadrats investigated in 1971, 1972, 2008 and 2018, are included. Legend: Pale blue = species not found in 2018; yellow = species found in 2018 but not in 2008; orange = species found in 2018 and 2008 but not in 1972; tomato red = species found in 2018, 2008 and 1972; dark red = species found in all surveys (2018, 2008, 1972 and 1971). Maps: GVI, The Icelandic Institute of Natural History.

'A'ā lava. The conspicuous species was found in 26 quadrats in 2008 but only in 20 quadrats in 2018 (Fig. 14, Appendix B). We saw no evident reason for the decline on Surtsey, but it might be symptomatic of a declining trend for this species similar to the close relative *R. fasciculare*. The *R. ericoides/canescens* complex has earlier shown a clear declining trend, but not between 2008 and 2018, when the area of occupancy increased somewhat.

These damages and decrease in distribution of *R. lanuginosum* were quite possibly due to the effect of increased sea spray and/or sand drift (see accumulation of sand in Fig. 14). The species is sensitive to nitrogen deposition and an increased nitrogen pollution seems to have had a damaging effect on *Racomitrium* heaths in the UK (Pearce *et al.* 2003). In Iceland however, nitrogen pollution is not a pressing issue as in mainland Europe (OSPAR 2007). Despite that fact, rather extensive damages emerged in the *Racomitrium* carpets in the highlands of southwestern Iceland, a little over a decade ago and many suspected sulphur-dioxide pollution from the geothermal power stations in the area – but results were inconclusive and damages to moss carpets were also found in areas unaffected by the geothermal power stations and drillholes (Efla 2009).

Several of the species that experienced a pronounced decline before 2008, such as *Funaria hygrometrica*, *Pohlia* spp. and *Sanionia uncinata*, were still present in the same number of quadrats as in 2008 (in 1, 1, and 3 quadrats, respectively).

Elliðaey and comparison to Surtsey

On Elliðaey, we found 22 bryophyte taxa (Table 2). The island was almost completely covered in a lush grassland (Fig. 15), like the grassland found at the centre of the gull colony on Surtsey. On the island there were also the occasional lava outcrops and exposed palagonite tuff, especially close to the shore and at the peak of the island – comparable to Surtsey, except much less extensive (Fig. 2 & 3). We found bryophytes in the following habitat types on Elliðaey: wetland, soil, lava, soil by lava, palagonite tuff, palagonite tuff away from the shoreline, and concrete. We found no bryophytes in the grassland.

The wetland was a small patch, no more than quarter of a hectare and not particularly wet despite heavy rain both during the summer and during our

Figure 15. Elliðaey was almost completely covered in a lush grassland, grazed by sheep, and occupied by puffins. On the photograph to the left, neighbouring islands of the same volcanic origin can be seen in the background. The photo to the right shows where the palagonite tuff was partly exposed, note the characteristic striations of the palagonite tuff. Photograps: NC 2018.

Table 2. Total of 22 bryophyte taxa were discovered on Elliðaey in seven different habitat types. None were found in the dominant grassland habitat of the island except if the wetland is there included. Four of the species have not been found on Surtsey, here given with the appropriate authors of the names; for author names of other species we refer to the checklist.

Bryophytes	Palagonite tuff	Palagonite by shore	On lava	On soil in lava	Wetland	Soil	Concrete
Amblystegium serpens		x					
Brachytheciastrum velutinum		x	x			x	
Brachythecium albicans		x		x			
Bryum argenteum	x	x					
Bryum dichotomum	x	x				x	
Ceratodon purpureus					x	x	
Chionoloma tenuirostre (Hook. & Taylor) M.Alonso		x					
Didymodon insulanus				x			
Drepanocladus aduncus					x		
Homalothecium sericeum (Hedw.) Schimp.	x						x
Kindbergia spp.	x	x					
Lophocolea bidentata (L.) Dumort.		x					
Plenogemma phyllantha	x	x	x	x			x
Ptychostomum elegans		x	x	x	x		
Ptychostomum pseudotriquetrum						x	
Sanionia uncinata		x					
Schistidium flexipile	x						
Schistidium maritimum		x	x				
Scuiro-hypnum plumosum (Hedw.) Ignatov & Huttunen				x		x	
Tortula hoppeana	x	x	x				
Tortula muralis	x						
Trichodon cylindricus		x					
Total number of taxa:	8	14	5	6	3	5	2

visit. Three bryophyte species were uncovered in this habitat, including *Drepanocladus aduncus* which is characteristic for wetlands, where it often grows submerged (Jóhannsson 1998). It was absent in other parts of Elliðaey. Wetland habitat was not found on Surtsey, but all the other habitats on Elliðaey had counterparts on Surtsey, although in lower geographic extent on Elliðaey (Fig. 2 & 3).

Thirteen of the taxa on Elliðaey were also present on Surtsey in 2018, four had been found on Surtsey in previous surveys and four species had never been found on Surtsey: *Chionoloma tenuirostre* (Hook. & Taylor) M.Alonso, *Homalothecium sericeum* (Hedw.) Schimp., *Lophocolea bidentata* (L.) Dumort. and *Scuiro-hypnum plumosum* (Hedw.) Ignatov & Huttunen. Each of these four species are potential future occupant of Surtsey, seeing as both source populations and habitats are present. *L. bidentata* prefers moist grassland and crevices in lava fields (Jóhannsson 1999), *C. tenuirostre* grows in crevices in lava fields and was registered before at two locations near Reykjavík in Iceland (Jóhannsson 1992a) and now Elliðaey; *H. sericeum* is common in Iceland, in cliffs and lava (Jóhannsson 1997); *S. plumosum* grows on stones and cliffs and is usually with sporophytes (Jóhannsson 1997).

CONCLUSION

Succession in Icelandic lava fields with a maritime climate typical for Surtsey (Petersen & Jónsson 2020), generally results in vast and thick carpets dominated by *Racomitrium lanuginosum*, or *Icelandic lava field moss heaths* (Ottósson *et al.* 2016). Such moss carpets formed early on, in the sheltered environment in the crater Surtungur, but seem unlikely to form to any extent elsewhere on Surtsey, given the expansion rate of the gull colony and the declining trend of *R. lanuginosum* on the island. This decline may be driven by sand drift and sea-spray. The lava fields of Surtsey are predicted to disappear by 2100, but well before this they will be under the strong influence of breeding seabirds. Lava fields on mainland Iceland have, to the best of our knowledge, not become seabird breeding grounds. Most are situated a considerable distance from the shore and are therefore spared both sea spray exposure as well as nutrient influx from birds. In coastal northern Norway, carpets of *R. lanuginosum* have been suggested as one of the stages of post-glacial succession in habitats without *Betula* L., while Edvarsen *et al*. (1988) proposed that sea spray kept *Betula* in check but not *R. lanuginosum*. With Surtsey decreasing in size, the effects of sea spray are likely to intensify. Some of the moss species on Surtsey have tolerance for salinity, such as *Plenogemma phyllantha* and *Schistidium maritimum*, but the tolerance level is unknown for many of the other species.

We can only but concur with our colleagues, Magnússon *et al*. (2014), that a lush, species-poor grassland will eventually develop on Surtsey. Most bryophytes are likely to lose in the competition with the tall grass species but continue to survive on protruding palagonite tuff and lava formations. On Surtsey, we deem palagonite protrusions likely to survive for centuries, at the edge of the northern cliffs of Vesturbunki. Similarly, lava protrusions, such as Strompur and Bjallan found on Austurbunki, seem likely to survive well into the distant future and foster bryophyte communities (Fig. 11).

Patiño and Vanderpoorten (2021) emphasize the potential of the data set from Surtsey for research on bryophyte immigration/extinction rates over time, studies that otherwise only have been possible by comparison of fossil material. According to the theory of island biogeography (MacArthur & Wilson 1967), islands will eventually reach an equilibrium between immigration and extinction. We see that such a situation has not been reached at Surtsey, but possibly at Elliðaey. We predict that the bryophyte species richness and moss cover will continue to gradually increase in the next few decades, to then taper off as the lava fields disappear and grassland proliferates. We predict that the species numbers will then start to decline towards the numbers found on Elliðaey. However, more continued monitoring is needed to make reliable predictions about the future developments on Surtsey and by no means do we see Elliðaey as a given end point of the island's succession. Notably, the islands are on the opposite ends of the archipelago, with Surtsey being completely exposed to the winds and ocean waves while Elliðaey is sheltered by Heimaey and other islands. Future observations will reveal how fast and to what extent the palagonite tuff will become vegetated. It is of a great importance not to let the gap between inventories of the bryophytes on Surtsey become too long while the island is still developing at such a fast rate.

Patiño and Vanderpoorten (2021) listed 50 fundamental questions in island biogeography, stressing that many questions remain unanswered in a bryological context. Given the existing data base for Surtsey, many of these questions could be addressed by forthcoming research. Future monitoring would benefit from sampling material for genomic studies, for ascertaining species determinations in critical genera such as *Bryum/Ptychostomum*, *Didymodon* and *Schistidium*, but also for monitoring infraspecific variation to understand effects of bottlenecks during colonization (founder events) as well as local differentiation and niche exploitation.

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SUPPLEMENTAL INFORMATION

Photographs of *Schistidium pruinosum* collected on Surtsey 2018. The photographs are taken through a microscope using a mobile-phone camera. The first 9 images (page 1-4) are from quadrat J11 and the last 9 images (page 5-7) are from quadrat I14. Photos are available in Supplement S1. Photos: NC 2020.

REFERENCES

Bjarnason, Á.H., 2018. Mosar á Íslandi, 367. Ágúst H. Bjarnason.

Bjarnason, Á.H. & S. Friðriksson, 1972. Moss on Surtsey, summer 1969. Surtsey Res. Prog. Rep. VI, 9-10.

Blom, H.H., 1998. *Schistidium*. *In* E. Nyholm (ed), Illustrated flora of Nordic mosses, pp. 287-330. Nordic Bryological Society.

Dierssen, K., 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. J. Cramer.

Edvardsen, H., Elvebakk, A., Øvstedal, D.O., Prøsch-Danielsen, L., Schwenke, J.T. & T. Sveistrup, 1988. A peat-producing *Empetrum* heath in coastal north Norway. Arct. Alp. Res. 20(3), 299-309. https://www.jstor.org/stable/1551262

Efla, 2009. Rannsóknir á mosa við jarðvarmavirkjun orkuveitu Reykjavíkur á Hellisheiði. Report from Efla Verkfræðistofa Inc., 33.

Einarsson, E., 1968. Comparative ecology of colonizing species of vascular plants. Surtsey Res. Prog. Rep. 4, 7-21.

Elmarsdóttir, Á. & O.K. Vilmundardóttir, 2009. Flokkun gróðurs og landgerða á háhitasvæðum Íslands – Unnið fyrir Orkustofnun. NÍ-09013. Icelandic Institute of Natural History.

Frey, W., Frahm, J.-P., Fischer, E., & W. Lobin, 2006. The liverworts, mosses and ferns of Europe. 139.

Friðriksson, S., 1970. The colonization of vascular plants on Surtsey in 1968. Surtsey Res. Prog. Rep. V, 10-14.

Friðriksson, S. & B. Johnsen, 1968. The colonization of vascular plants on Surtsey in 1967. Surtsey Res. Prog. Rep. IV, 31-39.

Friðriksson, S., Sveinbjörnsson, B. & S. Magnússon, 1972. Vegetation on Surtsey - summer 1970. Surtsey Res. Prog. Rep. VI, 54-59.

Frisvoll, A.A., 1983. A taxonomic revision of the *Racomitrium canescens* group (Bryophyta, Grimmiales). Gunneria, 41, 181.

Hodgetts, N.G., Söderström, L., Blockeel, T.L., Caspari, S., Ignatov, M.S., Konstantinova, N.A., Lockhart, N., Papp, B., Schröck, C., Sim-Sim, M., Bell, D., Bell, N.E., Blom, H.H., Bruggeman-Nannenga, M.A., Brugués, M., Enroth, J., Flatberg, K.I., Garilleti, R., Hedenäs, L. & R.D. Porley, 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. J. Bryol. 42(1), 1-116. https://doi.org/10.1080/03736687.2019.1694329

Holyoak, D.T., 2021. European Bryaceae. Pisces publications.

Ingimundardóttir, G.V., Weibull, H. & N. Cronberg, 2014. Bryophyte colonization history of the virgin volcanic island Surtsey, Iceland. Biogeosciences, 11(16), 4415-4427. https://doi.org/10.5194/bg-11-4415-2014

Ireland, R.R., 1980. The taxonomic status of *Ceratodon heterophyllus*. Bryologist, 83(2), 234-237. https://doi.org/10.2307/3242141

Jakobsson, S.P. & G. Guðmundsson, 2003. Rof Surtseyjar: Mælingar 1967-2002 og framtíðarspá. Náttúrufræðingurinn, 71, 138-144.

Jakobsson, S.P., Guðmundsson, G. & J.G. Moore, 2000. Geological monitoring of Surtsey, Iceland, 1967-1998. Surtsey Res. Prog. Rep. XI, 99-108.

Jóhannsson, B., 1968. Bryological observation on Surtsey. Surtsey Res. Prog. Rep. IV, 6.

Jóhannsson, B., 1991. Íslenskir mosar - Brúskmosaætt. Fjölrit Náttúrufræðistofnunar, 19, 139.

Jóhannsson, B., 1992a. Íslenskir mosar - Grýtumosaætt. Fjölrit Náttúrufræðistofnunar, 21, 120.

Jóhannsson, B., 1992b. Íslenskir mosar - Vendilmosaætt, sverðmosaætt, fjöðurmosaæt og bikarmosaætt. Fjölrit Náttúrufræðistofnunar, 20, 76.

Jóhannsson, B., 1993. Íslenskir mosar - Skeggmosaætt. Fjölrit Náttúrufræðistofnunar, 24, 116.

Jóhannsson, B., 1995. Íslenskir mosar - Skænumosaætt, kollmosaætt, snoppumosaætt, perlumosaætt, hnappmosaætt og toppmosaætt. Fjölrit Náttúrufræðistofnunar, 26, 129.

Jóhannsson, B., 1996. Íslenskir mosar - Röðulmosaætt, tildurmosaætt, glitmosaætt, faxmosaætt, breytingar og tegundaskrá. Fjölrit Náttúrufræðistofnunar, 29, 127.

Jóhannsson, B., 1997. Íslenskir mosar - Lokkmosaætt. Fjölrit Náttúrufræðistofnunar, 33, 83.

Jóhannsson, B., 1998. Íslenskir mosar - Rytjumosaætt. Fjölrit Náttúrufræðistofnunar, 34, 126.

Jóhannsson, B., 1999. Hornmosar og 14 ættir soppmosa. Fjölrit Náttúrufræðistofnunar, 38, 108.

Jóhannsson, B., 2002. Íslenskir mosar - Refilmosabálkur og stjörnumosabálkur. Fjölrit Náttúrufræðistofnunar, 43, 70.

Jóhannsson, B., 2003. Íslenskir mosar - Skrár og viðbætur. Fjölrit Náttúrufræðistofnunar, 44, 135.

Kristinsson, H. & S. Heiðmarsson, 2009. Colonization of lichens on Surtsey 1970-2006. Surtsey Res. Prog. Rep. 12, 81-104.

MacArthur, R.H. & E.O. Wilson, 1963. An equilibrium theory of insular zoogeography. Evolution, 17, 373–387. https://doi.org/10.1111/j.1558-5646.1963.tb03295.x

Magnússon, B., Guðmundsson, G.A., Metúsalemsson, S. & S.M. Granquist, 2020. Seabirds and seals as drivers of plant succession on Surtsey. Surtsey Res. 14, 115-130. https://doi.org/10.33112/surtsey.14.10

Magnússon, B. & S.H. Magnússon, 2000. Vegetation succession on Surtsey, Iceland, during 1990-1998 under the influence of breeding gulls. Surtsey Res. 11, 9-20.

Magnússon, B., Magnússon, S.H. & S. Friðriksson, 2009. Developments in plant colonization and succession on Surtsey during 1999-2008. Surtsey Res. XII(January 2009), 57-76.

Magnússon, B., Magnússon, S.H., Ólafsson, E. & B.D. Sigurdsson, 2014. Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. Biogeosciences, 11(19), 5521-5537. https://doi.org/10.5194/bg-11-5521-2014

Magnússon, S. & S. Friðriksson, 1974. Moss vegetation on Surtsey in 1971 and 1972. Surtsey Res. Prog. Rep. VII, 45-57.

Nyholm, E., 1975. Moss flora of Fennoscandia. II. Musci. Swedish Natural Science Research Council.

Ólafsson, E. & M. Ingimarsdóttir, 2009. The land-invertebrate fauna on Surtsey during 2002-2006. Surtsey Res. 12, 113-128.

Óskarsson, B.V., Jónasson, K., Valsson, G. & J.M.C. Belart, 2020. Erosion and sedimentation in Surtsey island quantified from new DEMs. Surtsey Res. 14, 63-77. https://doi.org/10.33112/surtsey.14.5

OSPAR, 2007. Atmospheric nitrogen in the OSPAR convention area in 1990-2004. In Eutrophication Series.

Ottósson, J.G., Sveinsdóttir, A. & M. Harðardóttir (eds), 2016. Vistgerðir á Íslandi. Fjölrit Náttúrufræðistofnunar, 54, 299.

Patiño J. & A. Vanderpoorten. 2021. Island biogeography: an avenue for research in bryology. Bryophyte Diversity and Evolution, 43, 206-20

Pearce, I.S.K., Woodin, S.J. & R. Van Der Wal, 2003. Physiological and growth responses of the montane bryophyte *Racomitrium lanuginosum* to atmospheric nitrogen deposition. New Phytol. 160(1), 145-155. https://doi.org/10.1046/j.1469-8137.2003.00875.x

Petersen, A., 2009. Formation of a bird community on a new island, Surtsey, Iceland. Surtsey Res. Prog. Rep. XII, 133-148.

Petersen, G.N. & T. Jónsson, 2020. The climate of Surtsey. Surtsey Res. 14(May), 9-16. https://doi.org/10.33112/surtsey.14.1

Sigurðsson, I.A. & S.P. Jakobsson, 2009. Vestmannaeyjar, Árbók Ferðafélags Íslands 2009 (J. V. Sigurðsson (*ed*)). Ferðafélag Íslands.

Thorarinsson, S., 1965. The Surtsey eruption: Course of events and the development of the new island. Surtsey Res. Prog. Rep. I, 51-55.

Weibull, H. & T. Hallingbäck, 2008. *Bryum*. In Encyclopedia of the Swedish Flora and Fauna, pp. 312-389. Swedish Species Information Center, SLU.

APPENDICES

Appendix A. Annotated checklist of bryophyte species found on Surtsey 1967 – 2022.

Here follows an annotated checklist for all bryophyte species, sub-species and varieties that have been encountered on Surtsey since its birth and up until April 2022 when this was written, no surveys were made between 2018 – 2022. Even uncertain identifications are included (e.g., *Cephaloziella* cf. *varians*, see Table 1 for further details on uncertain identifications). Accepted taxa are written in bold; synonyms are not bold. Only annotations pertaining to findings on Surtsey are included.

MARCHANTIOPHYTA

Anastrophyllaceae L.Söderstr., De Roo & Hedd.

1 ***Sphenolobus*** (Lindb.) Berggr.
    1 ***S. minutus*** (Schreb. ex D.Crantz) Berggr.

Cephaloziellaceae Douin

1 ***Cephaloziella*** (Spruce) Schiffn.
    1 ***C. divaricata*** (Sm.) Schiffn.
    2 ***C. hampeana*** (Nees) Schiffn. ex Loeske
    3 ***C. varians*** (Gottsche) Steph.

Lophoziaceae Cavers

1 ***Lophozia*** (Dumort.) Dumort.
    1 ***L. longidens*** (Lindb.) Macoun
    2 ***L. sudetica*** (Nees ex Huebener) Grolle
2 ***Lophoziopsis*** Konstant. & Vilnet
    1 ***L. excisa*** (Dicks.) Konstant. & Vilnet
        Lophozia excisa (Dicks.) Dumort. (Ingimundardóttir *et al.* 2014)
3 ***Tritomaria*** Schiffn. ex Loeske
    1 ***T. scitula*** (Taylor) Jørg.

Scapaniaceae Mig.

1 ***Scapania*** (Dumort.) Dumort.
    1 ***S. curta*** or ***S. scandica***[1]

Gymnomitriaceae H.Klinggr.

1 ***Nardia*** Gray N.
    1 ***N. scalaris*** Gray

Jungermanniaceae Rchb.

1 ***Jungermannia*** L.
    1 ***J. pumila*** With.

Aneuraceae H.Klinggr.

1 ***Aneura*** Dumort
    1 ***A. pinguis*** (L.) Dumort.

Aytoniaceae Cavers

1 ***Reboulia*** Raddi
    1 ***R. hemisphaerica*** (L.) Raddi

Marchantiaceae Lindl.

1 ***Marchantia*** L.
    1 ***M. polymorpha*** L.

BRYOPHYTA

Polytrichaceae Schwägr.

1 ***Atrichum*** P.Beauv.
    1 ***A. undulatum*** (Hedw.) P.Beauv.
2 ***Pogonatum*** P.Beauv.
    1 ***P. urnigerum*** (Hedw.) P.Beauv.
        P. urnigerum (Bjarnason & Friðriksson 1972)
3 ***Polytrichastrum*** G.L.Sm.
    1 ***P. alpinum*** (Hedw.) G.L.Sm.
        Polytrichum alpinum Hedw. (S. Magnússon & Friðriksson 1974)
    2 ***P. sphaerothecium*** (Besch.) J.-P.Frahm
        Polytrichum sphaerothecium (Besch.) Broth. (Magnússon & Friðriksson 1974)
4 ***Polytrichum*** Hedw.
    1 ***P. longisetum*** Sw. ex Brid.
        Polytrichastrum longisetum (Sw. ex Brid.) G.L.Sm. (Ingimundardóttir *et al*. 2014); *Polytrichum longisetum* Brid (Magnússon & Friðriksson 1974)
    2 ***P. piliferum*** Hedw.
5 ***Psilopilum*** Brid.
    1 ***P. laevigatum*** (Wahlenb.) Lindb.

Encalyptaceae Schimp.

1 ***Encalypta*** Hedw.
    1 ***E. ciliata*** Hedw.

Funariaceae Schwägr.

1 ***Funaria*** Schwägr.
    1 ***F. hygrometrica*** Hedw.
        F. hygrometrica (Bjarnason & Friðriksson 1972)

Distichiaceae Schimp.

1 ***Distichium*** Bruch & Schimp.
    1 ***D. capillaceum*** (Hedw.) Bruch et Schimp.

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[1] *Scapania curta* and *S. scandica* are related and morphologically variable species, separated primarily by differences in oil bodies and gemmae, which were missing in our dried samples (from quadrat O16) and also in a sample determined to the same species pair collected from a neighbouring quadrat in 2008 (P14).

Hymenolomataceae Ignatov & Fedosov

- 1 ***Hymenoloma*** Dusén
  - 1 ***H. crispulum*** (Hedw.) Ochyra
    - *Dicranoweisia crispula* (Hedw.) Milde (Ingimundardóttir *et al.* 2014); *Dicranoweisia crispula* (Hedw.) Lindb. (Magnússon & Friðriksson 1974)

Amphidiaceae M.Stech

- 1 ***Amphidium*** Schimp.
  - 1 ***A. lapponicum*** (Hedw.) Schimp.

Aongstroemiaceae De Not.

- 1 ***Aongstroemia*** Schimp.
  - 1 ***A. longipes*** (Sommerf.) Bruch & Schimp.
- 2 ***Dichodontium*** Schimp.
  - 1 ***D. pellucidum*** (Hedw.) Schimp.

Dicranellaceae M.Stech

- 1 ***Dicranella*** (Müll.Hal.) Schimp.
  - 1 ***D. crispa*** (Hedw.) Schimp.
  - 2 ***D. heteromalla*** (Hedw.) Schimp.
  - 3 ***D. schreberiana*** (Hedw.) Dixon
  - 4 ***D. subulata*** (Hedw.) Schimp.
  - 5 ***D. varia*** (Hedw.) Schimp.

Fissidentaceae Schimp.

- 1 ***Fissidens*** Hedw.
  - 1 ***F. adianthoides*** Hedw.

Rhabdoweisiaceae Limpr.

- 1 ***Oncophorus*** (Brid.) Brid.
  - 1 ***O. virens*** (Hedw.) Brid.

Ditrichaceae Limpr.

- 1 ***Ceratodon*** Brid.
  - 1 ***C. heterophyllus*** Kindb.
  - 2 ***C. purpureus*** (Hedw.) Brid.
- 2 ***Ditrichum*** Timm ex Hampe
  - 1 ***D. heteromallum*** (Hedw.) E.Britton
- 3 ***Trichodon*** Schimp.
  - 1 ***T. cylindricus*** (Hedw.) Schimp
    - *Ditrichum cylindricum* (Hedw.) Grout. (Magnússon & Friðriksson 1974)

Pottiaceae Schimp

- 1 ***Barbula*** Hedw.
  - 1 ***B. unguiculata*** Hedw.
- 2 ***Bryoerythrophyllum*** P.C.Chen
  - 1 ***B. recurvirostrum*** (Hedw.) P.C.Chen
    - *Barbula recurvirostra* (Hedw.) Dix. (Magnússon & Friðriksson 1974)
- 3 ***Didymodon*** Hedw.
  - 1 ***D. brachyphyllus*** (Sull.) R.H.Zander
  - 2 ***D. fallax*** (Hedw.) R.H.Zander
    - *Barbula fallax* Hedw. (Magnússon & Friðriksson 1974)
  - 3 ***D. icmadophilus*** (Schimp. ex Müll.Hal.) K.Saito
    - *Barbula ichmadophila* C.Muell. (Magnússon & Friðriksson 1974)
  - 4 ***D. insulanus*** (De Not.) M.O.Hill
    - *Barbula vinealis* Brid. var. *Cylindrica* (Tayl.)Boul. (Magnússon & Friðriksson 1974)[2]
  - 5 ***D. rigidulus*** Hedw.
  - 6 ***D. tophaceus*** (Brid.) Lisa
- 4 ***Tortula*** Hedw.
  - 1 ***T. hoppeana*** (Schultz) Ochyra
  - 2 ***T. mucronifolia*** Schwägr.
  - 3 ***T. muralis*** Hedw.
  - 4 ***T. subulata*** Hedw.
- 5 ***Trichostomum*** Bruch.
  - 1 ***T. brachydontium*** Bruch

Grimmiaceae Arn.

- 1 ***Racomitrium*** Brid.
  - 1 ***R. canescens*** (Hedw.) Brid.[3]
    - *R. canescens* (Bjarnason & Friðriksson 1972)
  - 2 ***R. ericoides*** (Brid.) Brid.
    - *R. canescens* (Bjarnason & Friðriksson 1972)
  - 3 ***R. fasciculare*** (Hedw.) Brid.
  - 4 ***R. lanuginosum*** (Hedw.) Brid.
  - 5 ***R. sudeticum*** (Funck) Bruch & Schimp.
    - *Racomitrium heterostichum* var. *sudeticum* (Funck) Grout. (Magnússon & Friðriksson 1974)
- 2 ***Grimmia*** Hedw.
  - 1 ***G. torquata*** Drumm.
    - *Grimmia torquata* Hornsch. (Magnússon & Friðriksson 1974)
- 3 ***Schistidium*** Bruch & Schimp.[4]

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[2] The finding of *Barbula vinealis Brid*. var. cylindrica (Tayl.) Boul. in 1972 (Magnússon & Friðriksson 1974) was mistakenly registered as *Didymodon brachyphyllus* (Sull.) R.H.Zander by Ingimundardóttir et al. (2014).

[3] Since 1972 no report exists of *R. canescens* at all from Surtsey (Appendix B). However, *R. ericoides* eventually appears in 1984, shortly after a revision of the *Racomitrium canescens* complex by Frisvoll (1983). Prior to this revision, there was a lot of confusion about how to delimit *R. canescens* against *R. ericoides* and it is therefore likely that samples from Surtsey denoted to *R. canescens* and sampled 1972 or earlier, have indeed been the same species as is now called *R. ericoides.* Unlike *R. ericoides*, *R. canescens* has not been found with spore capsules in Iceland (Jóhannsson 1993, 2003).

[4] Originally the genus *Grimmia* was widely defined, including species now placed in *Schistidium*. A revision of the genus *Schistidium* by Hans Blom (1998) expanded the genus from six (e.g. Nyholm 1975) to 38 species in the Nordic area (see: Blom (Blom 1998) in Nyholm 1998). Prior to 1998, the salt tolerant seashore specialist *S. maritimum* was recognized but the name *S. apocarpum* was used for most of the species growing

- 1 **S. apocarpum** (Hedw.) Bruch & Schimp.
    - *Grimmia apocarpa* Hedw. (Magnússon & Friðriksson 1974)
- 2 **S. confertum** (Funck) Bruch & Schimp.
- 3 **S. flexipile** (Lindb. ex Broth.) G.Roth
- 4 **S. frigidum** H.H.Blom
    - a var. ***havaasii*** H.H.Blom
- 5 **S. maritimum** (Sm. ex R.Scott) Bruch & Schimp.
    - *Grimmia maritima* Turn. (Magnússon & Friðriksson 1974)
    - a subsp. ***piliferum*** (I.Hagen) B.Bremer
- 6 **S. papillosum** Culm.
- 7 **S. pruinosum** (Wilson ex Schimp.) G.Roth
- 8 **S. strictum** (Turner) Loeske ex Mårtensson
    - *Grimmia stricta* Turn. (Magnússon & Friðriksson 1974)

Bartramiaceae Schwägr.

- 1 ***Bartramia*** Hedw.
    - 1 **B. ithyphylla** Brid.
- 2 ***Philonotis*** Brid.
    - 1 **P. capillaris** Lindb.
        - *Philonotis arnellii* Husn. (Ingimundardóttir *et al.* 2014)
    - 2 **P. fontana** (Hedw.) Brid.
    - 3 **P. tomentella** Molendo

Meesiaceae Schimp.

- 1 ***Leptobryum*** (Bruch & Schimp.) Wilson
    - 1 **L. pyriforme** (Hedw.) Wilson
        - *L. pyriforme* (Bjarnason & Friðriksson 1972)

Bryaceae Schwägr.

- 1 ***Anomobryum*** Schimp.
    - 1 **A. julaceum** (Schrad. ex P.Gaertn. *et al*.) Schimp.
        - *A. filiforme* (Dicks.) Husn. (Magnússon & Friðriksson 1974)
- 2 ***Bryum*** Hedw.[5]
    - 1 **B. argenteum** Hedw.
    - 2 **B. dichotomum** Hedw.
    - 3 **B. klinggraeffii** Schimp.
- 3 ***Ptychostomum*** Hornsch.
    - 1 **P. arcticum** (R.Br.) J.R.Spence ex Holyoak & N.Pedersen
        - *Bryum arcticum* (R.Br.) Bruch & Schimp. (Ingimundardóttir *et al.* 2014)
    - 2 **P. calophyllum** (R.Br.) J.R.Spence
        - *Bryum calophyllum* R.Br. (Ingimundardóttir *et al.* 2014)
    - 3 **P. capillare** (Hedw.) Holyoak & N.Pedersen
        - *Bryum capillare* Hedw. (Ingimundardóttir *et al.* 2014), *B. capillare* (Bjarnason & Friðriksson 1972)
    - 4 **P. compactum** Hornsch.
        - *Bryum algovicum* Sendtn. ex Müll.Hal. (Ingimundardóttir *et al.* 2014); *Bryum algovicum* Sendtn. (Magnússon & Friðriksson 1974)
    - 5 **P. elegans** (Nees) D.Bell & Holyoak
        - *Bryum elegans* Nees (Ingimundardóttir *et al.* 2014)
    - 6 **P. imbricatulum** (Müll. Hal.) Holyoak & N. Pedersen
        - *Bryum caespiticium* Hedw. (Ingimundardóttir *et al.* 2014), *B. caespiticium* (Bjarnason & Friðriksson 1972)
    - 7 **P. inclinatum** (Sw. ex Brid.) J.R.Spence
        - *Bryum stenotrichum* C.Muell (Magnússon & Friðriksson 1974); *Bryum archangelicum* Bruch & Schimp. (Ingimundardóttir *et al.* 2014)
    - 8 **P. pallens** (Sw. ex anon.) J.R. Spence
        - *Bryum pallens* Sw. ex anon. (Ingimundardóttir *et al.* 2014)
    - 9 **P. pallescens** (Schleich. ex Schwägr.) J.R.Spence
        - *Bryum pallescens* Schleich. ex Schwägr. (Ingimundardóttir *et al.* 2014)
    - 10 **P. pseudotriquetrum** (Hedw.) J.R.Spence & H.P.Ramsay ex Holyoak & N.Pedersen
    - 11 **P. salinum** (I.Hagen ex Limpr.) J.R.Spence
        - *Bryum salinum* I.Hagen ex Limpr. (Ingimundardóttir *et al.* 2014)

Mniaceae Schwägr.

- 1 ***Mnium*** Hedw.
    - 1 **M. hornum** Hedw.
- 2 ***Pohlia*** Hedw.
    - 1 **P. annotina** (Hedw.) Lindb.
        - *P. annotina* (Hedw.) Loeske var. *decipiens* Loeske (Magnússon & Friðriksson 1974)
    - 2 **P. bulbifera** (Warnst.) Warnst.
    - 3 **P. cruda** (Hedw.) Lindb.
    - 4 **P. filum** (Schimp.) Mårtensson
        - *P. schleicheri* Crum (Magnússon & Friðriksson 1974)
    - 5 **P. proligera** (Kindb.) Lindb. ex Broth.
        - *P. proligera* Kindb. (Magnússon & Friðriksson 1974)
    - 6 **P. wahlenbergii** (F.Weber & D.Mohr) A.L.Andrews
- 3 ***Plagiomnium*** T.J.Kop.
    - 1 **P. cuspidatum** (Hedw.) T.J.Kop.

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in dry and less saline habitats. However, Jóhannsson (1993), influenced by Blom, listed 8 Icelandic species, amongst those were *S. strictum* and *S. confertum*.

[5] In the most recent treatments, the genus *Bryum* is split into several genera (e.g., Holyoak 2021), two of those, *Bryum* sensu stricto and *Ptychostomum* occur on Surtsey. Delimitation of species is still controversial in some groups, for example: *Ptychostomum* inclinatum is a widely defined taxon and also closely related to *P. salinum* (see: Holyoak 2021, for a recent account). Likewise, morphotypes with multicellular bulbils have been separated into numerous taxa in the past, but most of them are now placed in the polymorphic taxon *Bryum dichotomum* (Weibull & Hallingbäck 2008).

Orthotrichaceae Arn.

1 ***Plenogemma*** Plášek, Sawicki & Ochyra
  1 ***P. phyllantha*** (Brid.) Sawicki, Plášek & Ochyra
    Ulota phyllantha Brid. (Ingimundardóttir *et al*. 2014)

Aulacomniaceae Schimp.

1 ***Aulacomnium*** Schwägr.
  1 ***A. palustre*** (Hedw.) Schwägr.

Plagiotheciaceae M.Fleisch.

1 ***Isopterygiopsis*** Z.Iwats.
  1 ***I. pulchella*** (Hedw.) Z.Iwats.
    Isopterygium pulchellum (Hedw.) Jaeg. & Sauerb. (Magnússon & Friðriksson 1974)

Amblystegiaceae G.Roth

1 ***Amblystegium*** Schimp.
  1 ***A. serpens*** (Hedw.) Schimp.
2 ***Drepanocladus*** (Müll.Hal.) G.Roth
  1 ***D. aduncus*** (Hedw.) Warnst.
  2 ***D. polygamus*** (Schimp.) Hedenäs
    Campylium polygamum (B.S.G.) C.Jens. (Magnússon & Friðriksson 1974)

Calliergonaceae Vanderp., Hedenäs, C.J.Cox & A.J.Shaw

1 ***Straminergon*** Hedenäs
  1 ***S. stramineum*** (Dicks. ex Brid.) Hedenäs
    Calliergon stramineum (Brid.) Kindb. (Magnússon & Friðriksson 1974)

Scorpidiaceae Ignatov & Ignatova

1 ***Sanionia*** Loeske
  1 ***S. uncinata*** (Hedw.) Loeske
    Drepanocladus uncinatus (Hedw.) Warnst. (Friðriksson *et al*. 1972)

Brachytheciaceae Schimp.

1 ***Brachytheciastrum*** Ignatov & Huttunen
  1 ***B. velutinum*** (Hedw.) Ignatov & Huttunen
3 ***Brachythecium*** Schimp.
  1 ***B. albicans*** (Hedw.) Schimp.
  2 ***B. rivulare*** Schimp.
  3 ***B. rutabulum*** (Hedw.) Schimp.
  4 ***B. salebrosum*** (Hoffm. ex F.Weber & D.Mohr) Schimp.
    B. salebrosum (Web. & Mohr.) B.S.G. (Friðriksson *et al.* 1972)
1 ***Kindbergia*** Ochyra
  1 ***K. praelonga*** (Hedw.) Ochyra
    Eurhynchium praelongum (Hedw.) Schimp. (Ingimundardóttir *et al.* 2014)

Pylaisiaceae Schimp.

1 ***Calliergonella*** Loeske
  1 ***C. lindbergii*** (Mitt.) Hedenäs
    Hypnum lindbergii Mitt. (Magnússon & Friðriksson 1974)

Hylocomiaceae M.Fleisch.

1 ***Rhytidiadelphus*** (Limpr.) Warnst.
  1 ***R. squarrosus*** (Hedw.) Warnst.

Appendix B. List of all bryophyte taxa found on Surtsey since the birth of the island. ¥: No herbarium specimens; Bold x: herbarium specimen in ICEL in addition to being mentioned in the main reference; A: Jóhannsson (1968); B: Friðriksson (1970); C: Bjarnason & Friðriksson (1972); D: Friðriksson, Sveinbjörnsson & Magnússon (1972); E & F: Magnússon & Friðriksson (1974); G: Magnússon, S. H. & Magnússon B. in Ingimundardóttir *et al*. (2014); H: Own data 2008; I: Friðriksson, Sveinbjörnsson & Magnússon (1972); J: Own data 2018. Note that 2008 and 2018 shows the number of quadrats the species was found in, previously unpublished. Note also that *R. ericoides* in ICEL in 1970 was labelled as *R. canescens* var. *ericoides*, now recognized as a synonym of *R. ericoides*. We presume it was included as *R. canescens* in the publications of the time and suspect other incidents of *R. canescens* are indeed equivalent to *R. ericoides*. We would also like to emphasize a couple of errors we encountered when working on this manuscript, namely the fact that in Table 1 in Ingimundardóttir *et al*. (2014), the authors missed marking two occurrences of *Schistidium strictum* in 1971 and 1972, then as *Grimmia stricta* Turn. (Magnússon & Friðriksson 1974); and that the finding of *Barbula vinealis* Brid. var. *cylindrica* (Tayl.) Boul. in 1972 (Magnússon & Friðriksson 1974) was mistakenly registered as *Didymodon brachyphyllus* (Sull.) R.H.Zander by Ingimundardóttir *et al.* (2014). For this reason, we here republish the table, with corrections and additional data from both the 2008 and 2018 expeditions. Population trends in terms of changes in number of encountered quadrats between 2008 and 2018, are presented in a separate column. Note that many records from 2008 were not determined to species in genera like *Bryum*, *Schistidium* and *Cephaloziella*, which means that increases in number of quadrats between 2008 and 2018 for these genera must be evaluated with caution. Indeed, the average trend was only +2. All specimens collected in 2008 and 2018 are preserved at The Icelandic Institute of Natural History and Lund University, respectively.

	Bryophyte taxa	1967 - A	1968 - B	1969 - C	1970 - D	1971 - E	1972 - F	1975 - ICEL	1976 - ICEL	1984 - ICEL	1990 - ICEL	1991 - ICEL	2003 - G	2006 - AMNH	2008 - H	2018 - J	**Trend '08-'18**
	Bryum argenteum	x	x	x	x	**x**	x			**x**	**x**		**x**		11	14	**3**
	Funaria hygrometrica	**x**	x	x	**x**	x	x			**x**					1	1	**0**
	Bryum spp.		I	I	x	x	x						x		26		**-26**
	Ceratodon purpureus		**x**		**x**	x	x	**x**		**x**	**x**		x		10	20	**10**
	Dicranella crispa		I	I	**x**	**x**	x				**x**					1cf.	**1**
	Leptobryum pyriforme		x	x	**x**	x	x			**x**							
¥	*Pohlia bulbifera*		x														
	Pohlia cruda		I		x	x	x	**x**		**x**	**x**						
¥	*Ptychostomum imbricatulum*			x													
¥	*Ptychostomum capillare*			x											1		**-1**
	Pogonatum urnigerum			x	**x**	x	x			**x**					2	5	**3**
	Racomitrium canescens			x	**x**	x	x										
	Racomitrium ericoides				ICEL					**x**	**x**		x		17	22	**5**
¥	*Aongstroemia longipes*				**x**		x									1	**1**
	Atrichum undulatum				x	x	x				**x**						
	Brachythecium salebrosum				**x**		x	**x**					x				
	Bryum dichotomum				ICEL			**x**		**x**	**x**		x		1	33	**32**
	Ptychostomum pallens				**x**	x	x			**x**							
	Dichodontium pellucidum				**x**	x	x	**x**		**x**					4	9	**5**
	Philonotis spp.				x	x	x										
	Pohlia wahlenbergii				**x**	x	x			**x**							
	Racomitrium lanuginosum				**x**	x	x		**x**	**x**	**x**		x		26	21	**-5**
	Sanionia uncinata				x	x	x			**x**	**x**		x		3	3	**0**
	Anomobryum julaceum					x	x			**x**						1	**1**
	Bartramia ithyphylla					x	x			**x**							
	Bryoerythrophyllum recurvirostrum					x	x			**x**	**x**				7	13	**6**
¥	*Ptychostomum compactum*					x	x										
	Ptychostomum inclinatum					x	x	**x**		**x**	**x**						
¥	*Ptychostomum arcticum*					x	x										
¥	*Dicranella schreberiana*					x											
	Dicranella varia					x	**x**				**x**						
	Distichium capillaceum					x	x			**x**	**x**					1	**1**
	Drepanocladus polygamus					**x**	x			**x**	**x**						
¥	*Encalypta ciliata*					x	x										
¥	*Fissidens adianthoides*					x											
	Mnium hornum					x	x				**x**				1	1	**0**
¥	*Oncophorus virens*					x	x										
¥	*Pohlia annotina*					x										1cf.	**1**
¥	*Polytrichastrum alpinum*					x	x										
¥	*Polytrichum longisetum*					x	x										
¥	*Rhytidiadelphus squarrosus*					x	x								1		**-1**
¥	*Schistidium apocarpum*					x	x										
	Schistidium maritimum					x	x			**x**	**x**		**x**	x	31	19	**-12**
	Schistidium strictum					x	x			**x**	**x**		x		5	11	**6**

¥	*Straminergon stramineum*	x	x									
¥	*Marchantia polymorpha*	x	x									
	Amblystegium serpens		x			**x**	**x**					
¥	*Amphidium lapponicum*		x								2	**2**
¥	*Aulacomnium palustre*		x									
	Barbula unguiculata		x		**x**					6	11	**5**
	Brachythecium albicans		x					x		5	9	**4**
¥	*Brachythecium rivulare*		x									
¥	*Ptychostomum calophyllum*		x									
	Bryum klinggraeffii Schimp.		**x**									
	Ptychostomum pallescens		x		**x**	**x**						
¥	*Calliergonella lindbergii*		x									
¥	*Dicranella heteromalla*		x									
¥	*Dicranella subulata*		x									
	Hymenoloma crispulum		x		**x**					1		**-1**
	Didymodon fallax		x		**x**					2	2	**0**
¥	*Didymodon icmadophilus*		x								8	**8**
	Ditrichum heteromallum		x	**x**	**x**							
	Didymodon insulanus		x		**x**	**x**						
¥	*Drepanocladus aduncus*		x					x				
	Encalypta sp.		x									
¥	*Grimmia torquata*		x									
¥	*Isopterygiopsis pulchella*		x									
¥	*Philonotis fontana*		x							1cf.		**-1**
¥	*Plagiomnium cuspidatum*		x									
¥	*Pohlia filum*		x									
¥	*Pohlia proligera*		x									
¥	*Polytrichastrum sphaerothecium*		x									
¥	*Polytrichum piliferum*		x									
¥	*Psilopilum laevigatum*		x									
¥	*Racomitrium sudeticum*		x							1	10	**9**
¥	*Trichodon cylindricus*		x								3	**3**
¥	*Trichostomum brachydontium*		x							1		**-1**
	Cephaloziella divaricata		ICEL					x	x	9cf.		**-9**
	Cephaloziella spp.		x								5	**5**
	Jungermannia sp. (*atrovirens* or *pumila*)		x									
	Scapania sp. (*curta* or *scandica*)		x							1	1	**0**
	Philonotis capillaris			**x**	**x**						3	**3**
	Racomitrium fasciculare			**x**	**x**	**x**		x		13	9	**-4**
	Reboulia hemisphaerica			**x**						1		**-1**
	Brachytheciastrum velutinum				**x**							
	Cephaloziella hampeana				**x**			x		1cf.	1cf.	**0**
	Jungermannia pumila				**x**						2cf.	**2**
	Lophoziopsis excisa				**x**							
	Brachythecium rutabulum					**x**						
	Philonotis tomentella					**x**						
	Schistidium frigidum					**x**					9	**9**
	Ptychostomum salinum							ICEL				
¥	*Schistidium flexipile*							x		5	33	**28**

	Plenogemma phyllantha												**x**		11	14	**3**
¥	*Brachythecium* sp.														1		**-1**
¥	*Ptychostomum elegans*														4	2	**-2**
¥	*Ceratodon heterophyllus*														1cf.		**-1**
¥	*Didymodon brachyphyllus*														2	15	**13**
¥	*Didymodon rigidulus*														4	3	**-1**
¥	*Didymodon* spp.														2		**-2**
¥	*Kindbergia praelonga*														1	3	**2**
¥	*Pohlia* spp.														1	1	**0**
¥	*Schistidium confertum*														1	1	**0**
¥	*Schistidium papillosum*														1	9	**8**
¥	*Schistidium* spp.														20		**-20**
¥	*Tortula hoppeana*														1	2	**1**
¥	*Tortula muralis*														1	8	**7**
¥	*Aneura pinguis*															1	**1**
¥	*Bryum arcticum / algovicum / archangelicum*															4	**4**
¥	*Cephaloziella varians*															4cf.	**4**
¥	*Didymodon tophaceus*															1	**1**
¥	*Lophozia longidens*															1	**1**
¥	*Lophozia sudetica*															2	**2**
¥	*Nardia scalaris*															1	**1**
¥	*Ptychostomum pseudotriquetrum*															2	**2**
¥	*Scapania* cf. *obcordata*															1	**1**
¥	*Schistidium frigidum* var. *havaasii*															2	**2**
¥	*Schistidium maritimum* subsp. *piliferum*															3	**3**
¥	*Schistidium pruinosum*															2	**2**
¥	*Sphenolobus minutus*															1	**1**
¥	*Tortula mucronifolia*															1	**1**
¥	*Tortula subulata*															1	**1**
¥	*Tritomaria scitula*															1	**1**
	Total number of taxa:	2	8	9	20	39	73	**10**	**1**	**33**	**24**	**1**	18	2	43	59	
	Cumulative number of taxa:	2	8	12	23	46	81	**84**	**84**	**88**	**91**	**92**	94	95	107	123	

MARINE BIOLOGY

Observations of cetaceans in the waters of the Surtsey Nature Reserve between 2008 and 2021

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ABSTRACT

The island of Surtsey originated from an underwater eruption in 1963 and has since been studied extensively, illustrating the colonization and succession by numerous species in both the terrestrial and marine habitats. However, there is little information on the cetaceans occurring near the island. Here we show that killer whales, pilot whales and minke whales are observed within the Surtsey Nature Reserve in June-August, although survey effort within this area has been lower than in other parts of the Vestmannaeyjar archipelago. Thus, we expect the list of species will increase with higher effort in the future. Killer whales were the species observed most commonly and were seen during the summer months, most often on the east and north coasts. Both observational and animal-attached tag data suggest killer whales were feeding within the reserve, and the only prey identified was herring. However, seasonal survey effort limits a comprehensive understanding of the prey killer whales may target within this area and particularly whether killer whales may target the seal colonies established here during autumn and winter. In the future, increased effort in summer and at other times of the year, would help fill in these gaps in our knowledge of the importance of the Surtsey nature reserve for cetaceans.

INTRODUCTION

Iceland sits at the confluence of warm and cold Atlantic water masses which contribute to the high productivity that creates a rich environment for top predators, such as cetaceans (Víkingsson *et al*. 2015). The occurrence of several species of cetaceans in coastal waters has led to the development of whale-watching in towns along the southwest, west and north coasts of Iceland (Rasmussen 2014). The waters off the south coast of Iceland are productive, rich in marine life, and have unique physical oceanographic characteristics with diverse marine habitats, such as areas of shallow and deep waters off the shelf (Astthorsson *et al*. 2007). It is, thus, a region expected to be suitable habitat for cetacean species. However, the occurrence of cetaceans along the south coast of Iceland is little monitored due to the lack of dedicated research effort or whale-watching activities.

The Icelandic Orca Project was initiated in the Vestmannaeyjar archipelago in 2008, becoming the longest-running dedicated research and monitoring programme of killer whales (*Orcinus orca*) in Icelandic waters (Samarra *et al*. 2017a). Killer whales are known to occur in the archipelago in the summer months to feed on the herring that spawns locally in July (Óskarsson & Taggart 2009). While the project had an initial focus on killer whales, it also collects information on other species sighted within the archipelago to record the cetacean biodiversity of the region. Several species of cetaceans have been recorded in this region, however their use of different areas of the archipelago has not been explored to date.

The island of Surtsey, the southernmost island of the Vestmannaeyjar archipelago and Iceland's southernmost outpost, was formed as a result of an oceanic eruption that occurred between 1963 and 1967. The island has been legally protected from its birth, creating a pristine natural laboratory where a long-term study of biological colonisation and succession has been established. To date, hundreds of species have been described on the island including moulds, bacteria, lichens, fungi, plants, invertebrates, breeding seabirds and seals (Magnússon *et al*. 2020). In the marine environment, several benthic marine algae, invertebrates, and fish species have also been reported (e.g., Jónsson & Gunnarsson 2000; Hauksson 1992, 2000; Baldursson & Ingadóttir 2007). The island is continuously changing as erosion leads to recession of the coastline, which is predicted to continue for at least another century (Jakobsson *et al*. 2000). Thus, the current composition of the benthic and pelagic communities will likely change in the future as the habitat matures into a more stable stage (Gunnarsson & Hauksson 2009). The island and surrounding marine area were inscribed to the World Heritage List of UNESCO in 2008 (Baldursson & Ingadóttir 2007). Here, we aim to report on observations of cetaceans sighted within the Surtsey Nature Reserve (SNR), to complement other studies that have documented the presence of different marine and terrestrial species present in this habitat.

MATERIAL AND METHODS

Whenever weather conditions permitted, small research vessels were used to search for whales in Vestmannaeyjar. The boat(s) departed from the harbour of Heimaey and effort was generally concentrated in the west and central part of the Vestmannaeyjar archipelago. Searches were conducted in an area bordered to the west by Þrídrangar and to the south by Surtsey. In some years, the search by boat was aided by observers based on land, that also searched for whales within the same study area and directed the boat to whale sightings. The focus of the fieldwork was on killer whales but as much as possible other species sighted were also recorded.

Between 2008 and 2016, fieldwork was only conducted in the month of July; from 2017 to 2021, fieldwork was conducted in June, July and August, although the effort in 2020 was constrained by the COVID-19 pandemic. Effort varied primarily due to weather and research priorities. Boat tracks during surveys were saved to collect information on survey effort and areas searched, although this was not conducted as consistently in 2008 and 2010 as it was in all other years. Despite varying research priorities from year to year, photographs of whales were collected every year for identification purposes. Photo-identification is a technique which uses unique markings on the bodies of individuals to identify them, making it possible to collect information at the individual level. In the case of killer whales, individuals were identified based on the size and shape of the dorsal fin, the presence of nicks and scars, saddle patch (the lightly coloured area below and behind the dorsal fin) pattern and body scars (Bigg et al. 1990). Photographs were collected continuously during boat surveys in an attempt to identify all the individuals present within an encounter. Photographs were collected using a variety of digital single-lens reflex cameras and lenses. Photographic cameras were synchronised with GPS time on a regular basis so that the location where pictures were collected could be determined. In recent years, cameras with integrated GPS sensors were used that recorded the GPS coordinates directly to the picture metadata.

To investigate the effort conducted within the SNR, boat tracks from every field season were plotted on a map to illustrate the proportion of the effort that occurred within this area. The SNR investigated here included the boundaries of the area nominated for the World Heritage List of UNESCO as well as a surrounding buffer zone, as determined in the nomination of Surtsey for the UNESCO World Heritage List document (Baldursson & Ingadóttir 2007). Maps were generated using QGIS v3.8 (QGIS.org 2022) and using data on land limits from the IS 50 V database of the National Land Survey of Iceland (2022). The locations of collection of pictures of different whale species were used to characterise the species observed within the nature reserve, as well as where these species were seen.

In 2009, killer whales were tagged with digital archival tags (Type B Suction-cup attached tag that includes DSL400-VDT II and PD3GT19, Little Leonardo, Aoki *et al.* 2012, Miller *et al.* 2016, and Dtags, Samarra & Miller 2015) attached to the whales with suction-cups using a 7 m carbon fibre pole from a small zodiac (<6 m length). The tags emitted a VHF signal that allowed the tagged whale to be tracked after deployment. The tagged whales were followed generally at distances of more than 100 m, from the tagging boat or from a 9.45 m observation motorboat, using the VHF signal and visual observations. The different types of tags included a different suite of sensors but all had a pressure sensor (sampling rate 1 Hz for Little Leonardo tags and 50 Hz for Dtags), which allowed for the diving behaviour of the tagged whale to be investigated. An animal-borne camera DSL400-VDT II (Little Leonardo) collected one still image every 4s.

RESULTS

Surveys around Vestmannaeyjar were conducted on a total of 213 days between 2008 and 2021, covering a distance of 17247 km. Approximately 3.3 % of this effort, or 572 km, were inside the SNR (Table 1). While all years, except 2010, had some effort inside the SNR, the amount of effort varied considerably between years.

Killer whales were sighted inside the reserve in 7 out of 11 summer seasons when there was effort in this area. A single minke whale (*Balaenoptera acutorostrata*) was also reported in the reserve in 2009 as was a group of long-finned pilot whales (*Globicephala melas*) in 2019. Across all years, killer whales were observed in June (n = 1), July (n = 7) and August (n = 4). Greater sightings in July reflect the effort occurring mostly in July in the earlier years of the project. Killer whales seem to have been observed most often on the east compared to the west coast

Table 1. Cetacean survey effort in the Vestmannaeyjar archipelago and within the Surtsey Nature Reserve (SNR) in 2008–2021. The maximum number of boats refers to the maximum number used within a given year but not all boats were used every day.

Year	Month	Total effort (days)	Effort inside SNR (days)	Total distance (km)	Distance inside SNR (km)	Max. number of boats	Species sighted inside SNR (n days)
2008	July	7	2	131.67	23.10	1	Killer whale (2)
2009	July	19	3	2474.86	324.68	3	Killer whale (1), minke whale (1)
2010	July	6	NA	NA	NA	2	-
2013	July	11	1	1090.16	24.88	2	-
2014	July	16	2	973.00	14.97	2	-
2015	July	20	1	1678.56	18.06	2	Killer whale (1)
2016	July	15	3	914.53	4.56	1	Killer whale (1)
2017	June	9	-	809.65	-	1	-
	July	12	-	727.42	-	1	-
	August	6	1	431.31	15.72	1	-
2018	June	4	-	223.20	-	1	-
	July	13	1	981.90	12.93	2	-
	August	7	3	631.72	40.88	1	Killer whale (3)
2019	June	9	1	727.78	2.23	1	Killer whale (1)
	July	11	1	867.55	3.46	2	-
	August	6	3	393.56	30.13	1	Pilot whale (1)
2020	July	9	1	518.53	0.37	1	-
	August	3	-	227.00	-	1	-
2021	June	8	-	566.88	1.15	1	-
	July	15	3	2228.68	39.84	2	-
	August	7	1	649.03	15.35	1	Killer whale (1)
Total		213		17246.99	572.31		

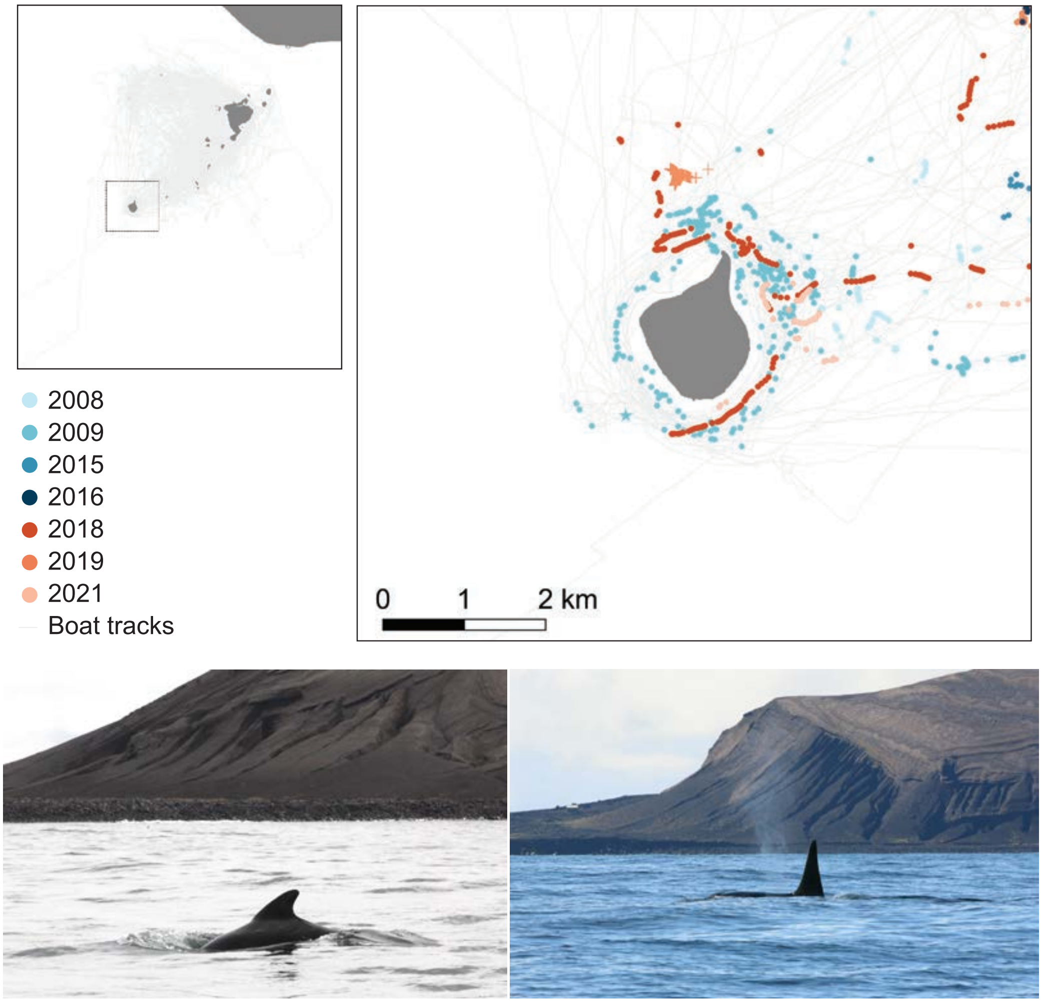

Figure 1. Map of Vestmannaeyjar displaying in light grey all boat tracks to illustrate the spatial distribution of effort (top left). Insert of the Surtsey Nature Reserve showing boat tracks within the reserve and locations where photographs of killer whales (•) and pilot whales (+) were collected between 2008–2021 (top right). A minke whale was observed from the research boat once (star) but no photographs were collected. A single pilot whale (bottom left) and a single killer whale (bottom right) can be seen within the Surtsey nature reserve.

of Surtsey (Fig. 1). Killer whale behaviour was not consistently sampled across the study period, except between 2016 and 2021. In these years, killer whales were observed feeding on herring in the waters around Surtsey in 2 out of 6 encounters. In other encounters, killer whales were observed travelling, with some instances of milling behaviour (travelling in circles, surfacing in different directions and lack of consistent directional movement).

On the 25th July 2009, a female killer whale was tagged at 12:22 inside the SNR. The tag recorded the whale's underwater behaviour for approximately 10h, during which the whale was continuously inside the SNR, thus providing an interesting case study for the use of this habitat by killer whales.

The tagged whale was female IS063, part of a group that is seen regularly in the waters of Vestmannaeyjar during the summer months (Fig. 2 top center). The female was accompanied by the remaining members of the group (cluster G, Tavares et al. 2017). During >10hr of observation, the whale and its group circled the island of Surtsey at least 5 times (Fig. 2 top left). Visual observers on board the research boats recorded occasional notes of the whales' behaviour as well as information from the vessel's echosounder display, as an indication of the potential presence of fish in the area. The echosounder was not on for the first 1.5 hrs of the deployment and it was intermittently off during the deployment when acoustic recordings were attempted. Between 18:36 and 19:35, the observers reported fish observed on the echosounder. However, the whale's diving behaviour during this period was not apparently different from other periods of time in the deployment, consisting of both shallow and deep dives but to similar depths as throughout the remainder of the deployment duration (Fig. 2 centre panel). The main difference is that around 19:00 the whale began a longer period of deeper dives (approx. 2.5hrs) than observed at any other point in the deployment (generally <1h), which could be indicative of feeding behaviour. The tag stopped recording at 22:44 due to a full memory but did not detach from the whale until the following day. Because the tag was still attached to the whale, the observational boat continued tracking the whales after sunset but had to leave the area soon after because it became too difficult to continue sighting the whales in low light. At this point, the whales appeared to be leaving the area, towards the southwest.

An analysis of the pictures collected by the tag could not confirm the presence of prey, due to low underwater visibility, which is characteristic of this

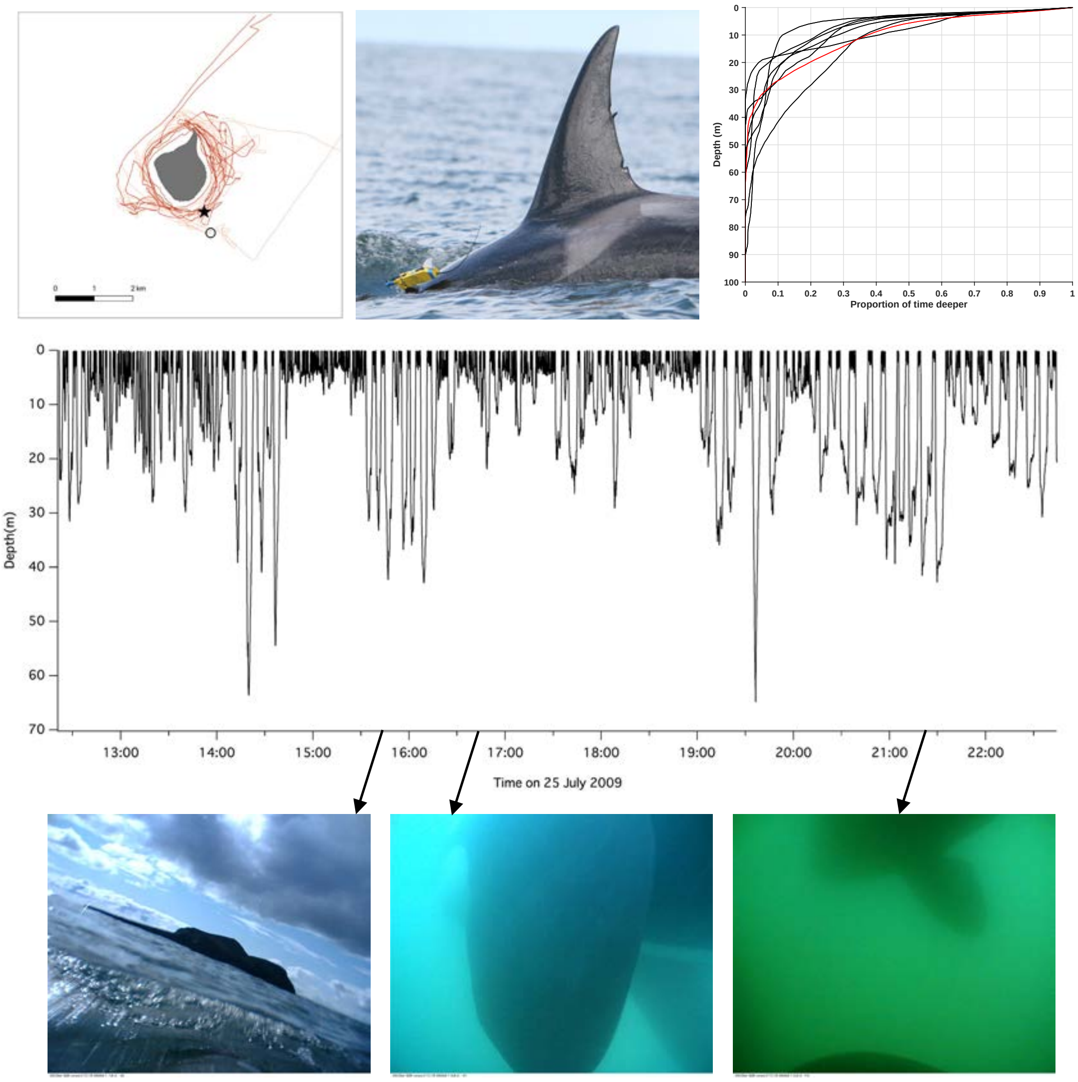

Figure 2. Top panel: left) map illustrating the boat tracks of the two research vessels on 25 July 2009 while searching, tagging and then tracking tagged whale IS063 (at a distance of >100 m) as a proxy for the movements of the tagged whale and its group; centre) photograph of IS063 carrying the tag; right) cumulative depth use of tagged whale IS063 (red) compared to another 7 whales tagged during the same field season (black). Note that the location where the tag was deployed (star) and the location where the tag stopped recording (circle) are marked on the map on the top left. The observation boat (orange line) followed the whales to the southwest until the light was too low to continue, at which point the boat made a sharp turn towards the northeast to leave the area. Centre panel: Dive profile of whale IS063 for the entire duration of the tag deployment. Bottom panel: Example photographs captured by the tag attached to whale IS063, showing the island of Surtsey during a moment when the whale surfaced to breathe, and the proximity of other members of the group to whale IS063 while swimming underwater, illustrating poor underwater visibility. The black arrows show when during the tag deployment the photographs were captured.

area, as a result of the outflow of large glacial rivers along the south coast of Iceland. Yet, the use of the water column exhibited by the whale throughout the deployment was similar to that observed in other whales tagged in the wider Vestmannaeyjar region in 2009, as illustrated in Fig. 2 (top right) by the cumulative depth use (as in Miller *et al*. 2010). Some of these whales were confirmed to be feeding by inspection of acoustic data recorded on some of the tags, or by visual observations. This suggests that whale IS063 and her group might have been feeding in the area around Surtsey during the tag deployment, even though that was not clearly obvious from surface observations. Indeed, the whales were not observed clearly milling with seabirds present flying above the whales in circles or plunge-diving into the water to feed on fish gathered by the whales – both common indications of herring feeding behaviour. Nevertheless, the circling behaviour observed may have been foraging effort, searching for prey within this environment.

DISCUSSION

This study illustrates the common occurrence of cetaceans in the waters around Surtsey. It confirms the presence of killer whales and minke whales, which had also been reported by Baldursson & Ingadóttir (2007) along with harbour porpoises, and adds pilot whales to the list of species observed in the SNR. It was particularly killer whales that were observed more regularly, with minke whales and pilot whales sighted only on one occasion each. However, the effort surveying the waters around Surtsey was very limited compared to the rest of the Vestmannaeyjar archipelago (Table 1), which limits our ability to detect different species occurring in this area. The boat effort was reduced and, in general, the waters around Surtsey were only surveyed if whales were not encountered in other parts of the Vestmannaeyjar archipelago closer to Heimaey or if observers on land directed the boat to whales sighted around Surtsey. Land observations were most commonly done from Stórhöfði, in the southern tip of Heimaey, approximately 20 km away from Surtsey. Even though the observers had binoculars with large magnification (15x), detecting whale presence around Surtsey was only possible during very good weather conditions. Thus, we expect that the list of species may increase in the future, and the patterns of which species more frequently occur in the SNR may also change with additional survey effort.

Killer whales were observed most often on the east and north compared to the south and west coasts of Surtsey. Though that could have been due to greater survey effort in those areas (Figure 1), the east coast of Surtsey is a more stable and sheltered area that has suffered less erosion from wave action than elsewhere on the island, which can be explained by the prevailing southwesterly winds in this region (Jakobsson *et al*. 2000). That has resulted, for example, in an increased diversity in algal cover (Jónsson & Gunnarsson 2000; Gunnarsson & Hauksson 2009) and a somewhat higher number of benthic species (Hauksson 2000). Thus, this could be habitat more suitable for killer whale prey, compared to elsewhere around the island, which could explain the apparently higher killer whale presence.

Killer whales were seen in every month of the summer (June to August), but most often in July. This reflects the study effort but also coincides with the expected period of higher abundance of spawning herring in the Vestmannaeyjar archipelago (Óskarsson & Taggart 2009). Both observational and tag data suggest that killer whales feed within the SNR, and that they are feeding on herring, similar to what is observed in the wider Vestmannaeyjar archipelago in the summer months (Samarra *et al*. 2017a, b). Herring distribution patterns around the Vestmannaeyjar archipelago during the spawning period have, to our knowledge, not been studied and thus there is little understanding of how often herring use the SNR and when in the season that happens. Nevertheless, the observations of herring predation by killer whales within the SNR reported in this study suggest at least part of the herring stock uses this area during the spawning season. Future studies that aim at quantifying the spatial distribution of herring within Vestmannaeyjar and how that may change throughout the summer should help determine the importance of the SNR for herring and, consequently, herring predators such as the killer whale.

It has been proposed that the presence of seals has attracted killer whales to the area of Surtsey. Both harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are seen in Surtsey at different times of the year (Hauksson 1992, 2009, 2015). Harbour seals appear to haul-out in great numbers in the winter-time on the northern shore of the island during feeding, but are not numerous during breeding time in summer (Hauksson 2009). Grey seals appear to make extensive use of the island as a breeding colony in October-November, and in fact in 2017 the breeding colony of Surtsey was the largest of all the colonies located in the south coast of Iceland, with an estimated pup production of 134 (Granquist & Hauksson 2019). Killer whales are known to predate on both seal species in Iceland (Samarra *et al*. 2018), and the analysis of dietary markers of some individual whales sighted in Vestmannaeyjar indicates that they have a mixed diet, including both fish and marine mammals (Samarra *et al*. 2017b). Thus, it is possible that killer whales predate upon seals in Surtsey. However, to date no observations of predation on seals have not been reported in the SNR, or in the Vestmannaeyjar archipelago as a whole. The lack of effort to visually monitor the presence of killer whales, or other cetacean species, in the SNR in any season outside of summer clearly limits any conclusions on potential seal predation, as seals appear to be using the area more intensively during autumn and winter.

Future observations of cetacean occurrence in Surtsey and its surrounding waters could reveal a broader range of species using this area as well as a larger range of prey being consumed by killer whales than what has been documented to date. Increased dedicated research in the SNR would be beneficial to understand how the various species of cetaceans occurring in the Vestmannaeyjar archipelago use this habitat. This could be achieved, for example, using passive acoustic monitoring techniques, that can be used year-round independent of weather conditions, or with increased effort on dedicated visual research at least during summer. Increased monitoring would also allow for a better understanding of how species occurrence and habitat use may change in the future as the island continues its recession.

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REFERENCES

Aoki, K., M. Amano, K. Mori, A. Kourogi, T. Kubodera & N. Miyazaki, 2012. Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. Mar. Ecol. Prog. Ser. 444, 289–301.

Astthorsson, O.S., A. Gislason & S. Jonsson, 2007. Climate variability and the Icelandic marine ecosystem. Deep-Sea Res. II 54, 2456-2477.

Baldursson, S. & Á. Ingadóttir (eds.), 2007. Nomination of Surtsey for the UNESCO World Heritage List. Icelandic Institute of Natural History, Reykjavík, 123 pp.

Granquist, S.M. & E. Hauksson, 2019. Aerial census of the Icelandic grey seal (*Halichoerus grypus*) population in 2017: Pup production, population estimate, trends and current status. Marine and Freshwater Research in Iceland, HV 2019-02, 19 pp.

Gunnarsson, K. & E. Hauksson, 2009. Succession and benthic community development in the sublittoral zona at the recent volcanic island, Surtsey, southern Iceland. Surtsey Res. 12, 161-166.

Hauksson, E., 1992. Observations on seals on Surtsey in the period 1980-1989. Surtsey Res. Prog. Rep. X: 31-32.

Hauksson, E., 2000. A survey of the benthic coastal fauna of Surtsey, Iceland, in 1997. Surtsey Res. 11, 85-88.

Hauksson, E., 2009. Seals in Surtsey, the period 1980-2005. Surtsey Res. 12, 167-170.

Hauksson, E., 2015. Observations on seals on the island of Surtsey in the period 1980-2012. Surtsey Res. 13, 41-43.

Jakobsson, S.P., G. Gudmundsson & J.G. Moore, 2000. Geological monitoring of Surtsey, Iceland, 1967-1998. Surtsey Res. 11, 99-108.

Johnson, M.P. & P.L. Tyack, 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J. Oceanic Eng. 28, 3-12.

Jónsson, S. & K. Gunnarsson, 2000. Seaweed colonisation at Surtsey, the volcanic island south of Iceland. Surtsey Res. 11, 59-68.

Magnússon, B., G.A. Gudmundsson, S. Metúsalemsson & S.M. Granquist, 2020. Seabirds and seals as drivers of plant succession on Surtsey. Surtsey Res. 14, 115-130.

Miller, P.J.O., A.D. Shapiro & V.B. Deecke, 2010. The diving behaviour of mammal-eating killer whales (*Orcinus orca*): variations with ecological not physiological factors. Can. J. Zool. 88, 1103-1112.

Miller, P., T. Narazaki, S. Isojunno, K. Aoki, S. Smout & K. Sato, 2016. Body density and diving gas volume of the northern bottlenose whale (*Hyperoodon ampullatus*). J. Exp. Biol. 219, 2458-2468.

National Land Survey of Iceland, 2022. IS 50V Strandlína. February 2022 https://gatt.lmi.is/geonetwork/srv/eng/catalog.search#/metadata/FE3E66F8-7749-409A-8795-02207CE27613

Óskarsson, G.J. & C.T. Taggart, 2009. Spawning time variation in Icelandic summer-spawning herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 66, 1666-1681.

QGIS.org, 2022. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

Rasmussen, M., 2014. The whaling versus whale-watching debate: the resumption of Icelandic whaling. *In* Higham, J., L. Bejder and R. Williams (eds) Whale-watching: sustainable tourism and ecological management. pp. 81-94. Cambridge University Press, Cornwall, UK

Samarra F.I.P. & P.J.O. Miller, 2015. Prey-induced behavioural plasticity of herring-eating killer whales. Mar. Biol. 162, 809-821.

Samarra F.I.P., S.B. Tavares, J. Béesau, V.B. Deecke, A. Fennell, P.J.O. Miller, H. Pétursson, J. Sigurjónsson & G. A. Víkingsson, 2017a. Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. Mar. Biol. 164, 159.

Samarra F.I.P., M. Vighi, A. Aguilar & G.A. Víkingsson, 2017b. Intra-population variation in isotopic niche in herring-eating killer whales off Iceland. Mar. Ecol. Progr. Ser. 564, 199-210.

Samarra F.I.P., M. Bassoi, J. Béesau, M.Ó. Elíasdóttir, K. Gunnarsson, M-T. Mrusczok, M. Rasmussen, J.N. Rempel, B. Thorvaldsson & G.A. Víkingsson, 2018. Prey of killer whales (*Orcinus orca*) in Iceland. PLoS ONE 13(12), e0207287.

Víkingsson, G.A., D.G. Pike, H. Valdimarsson, A. Schleimer, T. Gunnlaugsson, T. Silva, B.Þ. Elvarsson, B. Mikkelsen, N. Øien, G. Desportes, V. Bogason & P.S. Hammond, 2015. Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? Front. Ecol. Evol. 3, 1-18.

GEOLOGY

Human (boot) tracks preserved in volcanic deposits of Surtsey Island, Iceland

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ABSTRACT

Several human boot tracks and trackways are preserved in palagonitized tuff in Surtsey Island, south Iceland. The underlying palagonitized substrate is made of reworked tephra debris talus and slump material that lies partly on top of lava flows erupted in 1964–1965 in Surtungur tuff crater and 1966–1967 in Surtur tuff crater. This stratigraphic information along with other evidence from the nature of the sediments, alteration history of the deposits and the record of human presence on the island indicate the tracks were formed in the years between 1967 and 1970. The exquisite preservation and consolidation of the tracks coincide with a period of rapid geomorphic changes in the early stages of development of the island, when the newly formed tephra was still unconsolidated and easily mobilized by mass movements, wind and runoff. Furthermore, cooling magmatic intrusions generated hydrothermal activity on the island speeding up diagenesis of the tephra and the cementation of the boot tracks in the substrate. Expulsion rims preserved in some of the boot tracks suggests the tracks were formed in moderately cohesive substrate, followed by rapid burial of the prints in heavy wind and/or storm. Three boot sizes were identified suggesting the tracks were made by at least three persons, and documentation of the boot anatomy, measurements on angle of gait, stride and pace reveal the direction of movement for each trackway. Intense erosion of the tuff cones has exhumed the tracks to the surface that stand today as a testimony to impressively rapid geological cycles for preservation and exhumation and the role of unstable and rapidly changing environments, the aftermath of high-energy events, in capturing and preserving ichnites. These boot tracks are the first fossil tracks described for Iceland and the first record in the world of boot tracks preserved in sedimentary rocks.

INTRODUCTION

Surtsey is a recently formed volcanic island south of Iceland (Fig. 1). The eruption started visibly on November 14th, 1963, and Surtseyan type explosive activity generated tephra, lapilli and bombs, that accumulated weightily and rapidly building the island that grew to cover an area of 1.05 km^2 with height of 175 m above sea level toward the end of March 1964. From the beginning of April 1964, the eruption transitioned to effusive volcanism that continued intermittently until June 1967, expanding the surface of the island on top of a lava delta to 2.65 km^2, the total volume of the volcano reaching 1.1 km^3 (70% tephra and 30% lava), with subaerial volume of 0.1 km^3 (Thorarinsson 1965a, 1968b). During the eruption and after, intense weathering mobilized the tephra by mass wasting, aeolian activity and runoff, but decreased significantly after 1974 with consolidation and palagonitization of the tephra by hydrothermal alteration (Jakobsson 1978). Intense coastal erosion had also removed about 53% of the area of the island by 2019 (Óskarsson et al. 2020).

During the course of the volcanic activity Sigurður Þórarinsson of the Museum of Natural History of Reykjavík, Iceland (today the Icelandic Institute of Natural History), documented thoroughly the volcanic activity along with the physical changes in the island, but also registered all the early visits to the island (Thorarinsson 1965a, 1967a, b, 1968a, Helgadottir 2021). Þórarinsson states that he “arrived on the scene together with other geologists” on November 14th, 1963 (1967b, p. 15), although this visit was aboard a boat. According to his records, during the explosive

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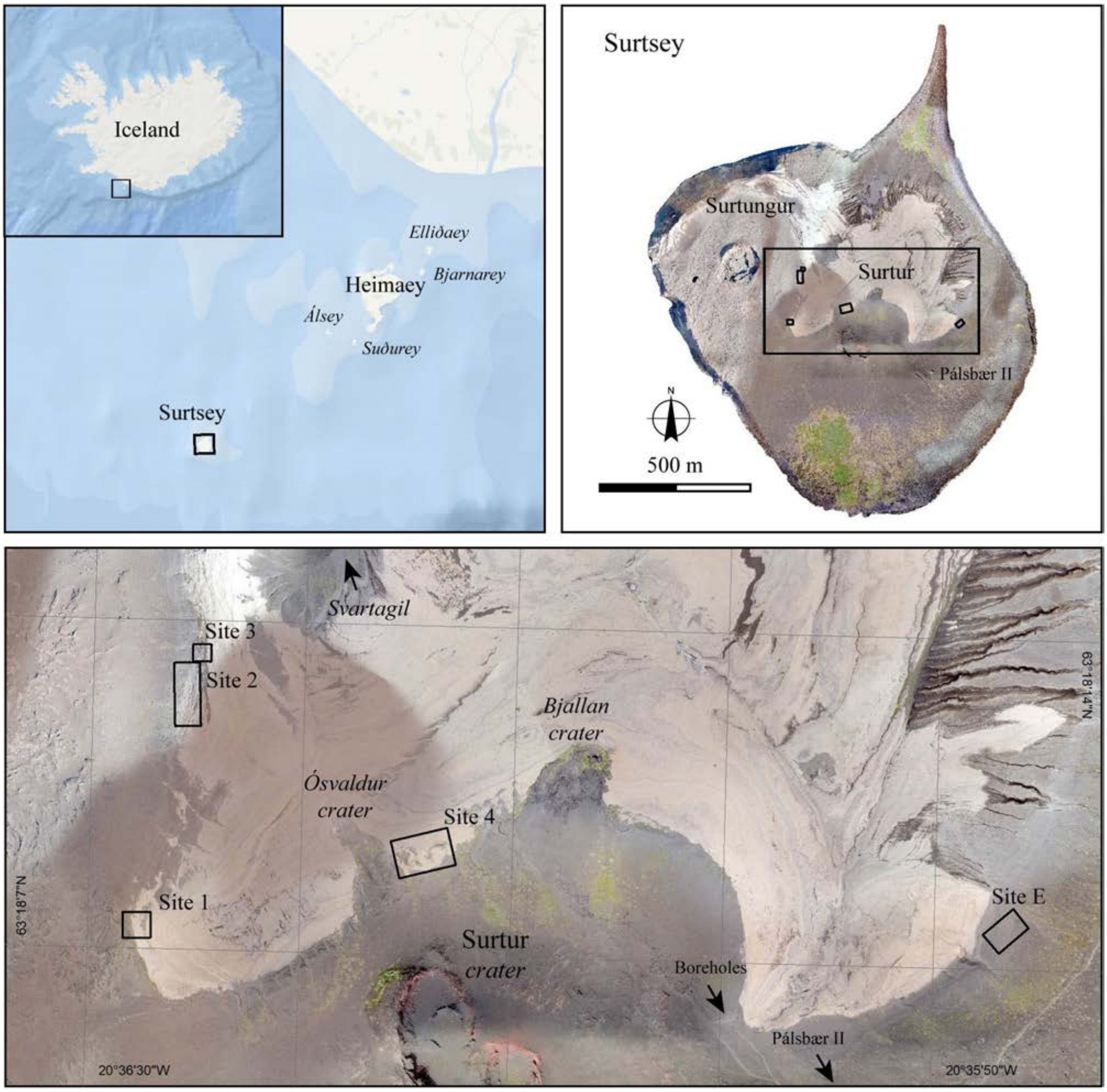

Figure 1. Geographic location of the Island of Surtsey and specific location of study sites on the island. Credit (upper left): Esri, Garmin, GEBCO, NOAA NGDC and other contributors. Credit (upper right and lower) Orthoimage from 2019 (Óskarsson et al. 2020).

phreatomagmatic phase the island was visited only four times mainly due to hazards associated with the phreatomagmatic explosions (Thorarinsson 1967b p.30). The first landing on Surtsey took place on December 6th, 1963, made by three French visitors but lasted ashore only a quarter of an hour before they had to depart as the volcanic eruption resumed intensity. A second very brief landing occurred on December 13th, 1963, when seven Vestmann Islanders went ashore Surtsey to vindicate naming the island as Vesturey (e.g. Lárusdóttir 2017, Friðriksson 2022). Because of the intense volcanic activity during those first weeks, early visitors did not venture far from shore. The third documented landing occurred on December 16th, 1963, when Icelandic geologists Sigurður Þórarinsson and Þorbjörn Sigurgeirsson went ashore to collected samples and walked on the slope of the volcanic cone that had been formed (e.g. Helgadóttir 2021). On February 19th, 1964, a group of seven scientists, journalists and “eruption enthusiasts” went ashore but apparently only stood on the sandy beach on the northeastern side and had to retreat in hurry due to the fall of ash and bombs (e.g. Pálmadóttir 2003, Helgadóttir 2021).

Table 1. Geological history of Surtsey Island from 1963 to 1980 and early visits onshore as recorded in the work of Thorarinsson (1965b and 1968b).

Date	Events, size and elevation of the island	Type of activity	Visits
1963			
14 Nov, 7:15 am	First signs of submarine eruption in Surtsey. Beginning of eruption that would form Surtur crater.	Phreatomagmatic	
1 Dec	First break, 4 hours.		Seaguls sat on the island for the first time.
6 Dec	Short break in eruption. 7 Dec. Lenght of island 1020 m and elevation of highest point about 112 m (elevation measured on Dec. 5).		Three French journalists sponsored by weekly Paris Match landed on the beach and placed a flag on the island. Residence about 45 min.
13 Dec	11 Dec. Length of island 1000 m and elevation of heighest point 106 m.		Seven Icelanders from Vestman Islands landed on the beach and placed a sign with the name Vesturey. Had to flee in hurry due to bomb shower and ash fall.
16 Dec	Break in eruption of 17 hrs. Longest break of all that year. Lengh of island 800 m and elevation of highest point 87 m. According to "Morgunblaðið" news on Dec. 22, 1963, additional 20 m of tephra were deposited on top of the island the day after the visit of Sigurður and Þorbjörn. 17 Dec. Elevation of island 106 m.		Two scientists Sigurður Þórarinsson and Þorbjörn Sigurgeirsson went on land from the vessel Óðinn to collect samples. Walked on the island but with short residence.
28 Dec	Beginning of Surtla submarine eruption 2 km ENE of Surtsey. Small fissure, did not emerge above sea.	Phreatomagmatic	
1964			
6 Jan	Surtla eruption over.		
End January	Activity ceased altogether in Surtsey and snow capped the highes poit for a few days.		
2 Feb, 11 pm	New vent NW of flank of Surtur. Beginning of eruption that would form Surtungur crater.	Phreatomagmatic	
19 Feb	17 Feb. Length 1350 m and area 102 ha.		Seven persons (5 men and 2 women) includsing S. Þórarinsson went on shore from vessel Haraldur but had to flee in hurry due to bomb shower and ash fall. No further attempts were made to go ashore on Surtsey while the explosive phase was still active. Residence of visitors was one hour and half and only on the beach.
4 Apr	Effusive phase began at noon.	Effusive	
15 Apr	11 Apr. Area 133 ha and highest point 173 m.		Three persons land on the island with a Cessna aircraft. Pilot Stéfan Þór Jónsson.
16 Apr			Scientists and filmakers land on Surtsey.
29 Apr	Break in eruption of Surtungur.		
9 Jul	Resumption of effusive activity in Surtungur.	Effusive	
19 Aug	25 Aug. Area 182 ha.		Helicopter from the Coast Guards lands first time on the island.
1965			
18 Jan			Aircraft Prestwick Twin Pioneer (Lóan) lands first time on Surtsey. Pilot Björn Pálsson. The aircraft made dozens of trips to the island.
20 Feb	Feb. Area 234 ha.		Aircraft from Civil Aviation Authority lands on Surtsey.
29 Apr			Last landing of aircraft Lóan.

17 May	Eruption ceased in Surtungur.		1965 to present. Surtsey declared a Nature reserve and from 2008 UNESCO World Heritage Site. Visits only allowed with special authorization.
22 May	Beginning of Syrtlingur submarine eruption 600 m ENE of Surtsey. According to isopach map in Thorarinsson 1967, about 5–10 cm of tephra from Syrtlingur was deposited over the sites in Surtsey Island. 24 Aug. Elevation of highest point 169 m and area 245 ha.	Phreatomagmatic	5 Jun. Páll Helgason, from the Westman islands adventured to the island of Syrtlingur during a short break in the explosive activity (Eyjafréttir Dec. 1995, Friðriksson 2022). 23 Jun. Páll Helgason, Viktor Sigurjónsson and Guðjón Sigurjónsson set up a tent in Surtsey and stamped 4500 envelopes with a newly released Surtsey stamp. They faced a charge for travelling to Surtsey without permission but were later acquitted of the charge (Morgunblaðið 27 Jun. 1965, Eyjafréttir Dec. 1995).
17 Oct	End of Syrtlingur eruption. Syrtlingur Island washed away by Oct. 24.		
26 Dec	Beginning of Jólnir submarine eruption 800 m SV of Surtsey. According to isopach map in Thorarinsson 1967, about 1–3 cm of tephra from Jólnir was deposited over the sites in Surtsey Island.	Phreatomagmatic	
1966	First signs of consolidation of the tephra.		
10 Aug	End of Jólnir eruption. Jólnir Island washed away by Oct. 31.		20 May. Páll Helgason, Hjálmar Guðnason, Hlöðver Pálsson and Ólafur Gräntz are first to adventure onshore the island of Jólnir (Eyjafréttir Dec. 1995).
19 Aug	Beginning of effusive activity at Surtur crater.	Effusive	
12–17 Dec	Minor lava flow from vent on inner NW wall of Surtur crater.	Effusive	
1967			
1–4 Jan	Lava flow from vent on outer north slope of Surtur cone.	Effusive	
1–8 Jan	Another lava flow from vent on inner wall of Surtur crater.	Effusive	
2 Jan	Lava flow from vent on outer NE slope of Surtur cone.	Effusive	
2–7 Jan	Minor lava flow from fault in wall of inner Surtur crater.	Effusive	
5 Jun	End of effusive activity in Surtur crater. Area 2.65 km^2 and highest point at 175 m.	Effusive	
1968	First signs of hydrothermal activity in the tephra.		
1969	First signs of palagonitization in the tephra east of Surtur.		
1977	Sites with tracks fully palagonitized.		
1980	Sites with tracks exhumed near the surface.		

After the explosive phase ceased and the effusive phase began on April 4th, 1964, many people visited the island to see the lava fountains and flows. Þórarinsson reports that from 1963–1964 he had landed there either by boat or aircraft eleven times, then eleven times in 1965, nine times in 1966 and eight times in 1967, each visit lasting for a few hours with a longer stay of four days (Thorarinsson 1965a, 1966, 1967, 1968a). In May 1965 the island was declared a Natural reserve and visits were restricted to authorized scientists and thus decreased significantly in number. Some of these visits are listed on Table 1 in the context of the geological events that occurred during the formation of the island.

Surtsey explorers did not envisage that one or several of these visits would leave permanent traces of its residence. Human (boot) tracks fossilized within the palagonitized tuff layers in Surtsey and exhumed at the surface with erosion were first reported by geologist Sveinn Jakobsson in the 1980s or 90s, while conducting geological research in Surtsey at the time. Sveinn introduced the tracks to geologist Lovísa Ásbjörnsdóttir in 2006 as man-made tracks; nevertheless, Sveinn was not entirely convinced of their authenticity. The first sites to be reported as holding man-made boot tracks were Site 4 (Fig. 1), photographed by geologists Hallgrímur D. Indriðason and Sigurður Sveinn Jónsson in 2001, and Site 1 photographed by geologist Kristján

Jónasson in 2011. The boot tracks in S1 were later documented photogrammetrically by geologist Birgir V. Óskarsson that mapped systematically the prints in collaboration with paleontologist Raúl Esperante in July 2021, which in addition discovered Site 2. In the same trip Þorgerður Ólafsdóttir discovered Site 3. The significance of the finding was remarkable as it posed a unique opportunity for studying the formation of ichnites in modern environments. The stages in the development of Surtsey from the beginning are well documented and the post-eruption changes by weathering and alteration are also well known. Thus, the aim of this study is to describe the tracks within the stratigraphy and environment they are found and to discuss their authenticity and the process of fossilization and preservation. Although others have mentioned the boot tracks in Surtsey before and taken photos, this study describes them for the first time in a scientific way.

THE RECORD OF FOSSIL HUMAN TRACKS IN VOLCANIC ROCKS

Fossil human tracks are very rare in the rock record, and even more rare those associated with volcaniclastic substrates (Lockley et al. 2008), with sites in Italy, Kenya, Turkey, United Kingdom and Tanzania. In Italy, the Middle Pleistocene (Chibanian age) ‘Devil’s Trails ichnosite outside the town of Foresta, on the northeastern slope of the Roccamonfina volcano, consists of 81 identified tracks in four trackways preserved on a zeolite-rich deposit formed by a pyroclastic flow. The human and some animal tracks are preserved in a zeolithified volcanic ash covered by coarser, granular material (Mietto et al. 2003, Avanzini et al. 2008, Avanzini et al. 2020). Late Pleistocene human footprints, hand tracks, knee and body impressions have been found in the cave named Grotta della Bàsura, about 1 km north of Toirano, at the foot of Mount Carmo of Loano. These traces are preserved on clay sediment and represent a complex set of motions on a difficult path of a group of adults followed by adolescents and children during both stance and progression phases while exploring the cave (Avanzini et al. 2020). Thousands of human and animal tracks are preserved in Afragola, Nola and Palma Campania in several stratigraphic levels of a pyroclastic flow deposit dated to 3780 yrs BP by ^{14}C (Avanzini et al. 2020). Casts of three human footprints were found in Moregine, about 600 m south of the walls of the ancient city of Pompei dated 79 AD (Avanzini et al. 2020). A series of adult and children footprints have been reported in the Aosta area (Armirotti et al. 2017).

In Turkey, a set of human footprints were found in 1969 on the surface of a tuff on the western flank of Çakallar Hill (a volcanic cone) west of the Manisa-Salihli-Demirkprü̈ Dam, with diastemas (significant separation between the toes) and clear erectus bipedalism characteristics (Ozansoy 1969). The relative age of these footprints has not been reported.

More than 400 human footprints have been found in Holocene deposits south of Lake Natron, Tanzania preserved on the surface of a volcaniclastic tuff consisting of moderately sorted fine ash to fine lapilli particles. These footprints are remarkably well preserved with prominent expulsion rims resulting from the deformation of the soft sediment under the weight of the pedestrians (Balashova et al. 2016). Various ages have been assessed for the ash ranging between 5760 ±30 yrs BP and 19.1 ±3.1 kyr BP based on ^{40}Ar/^{39}Ar analysis and ^{14}C dating techniques (Balashova et al. 2016, Liutkus-Pierce et al. 2016, Hatala et al. 2020).

Human footprints and animal tracks have been found in Pleistocene deposits with several layers of coarse basaltic volcanic ash in the Valsequillo Basin, south of Puebla, Central Mexico. Several short human trackways are recognized but incomplete due to poor preservation (González et al. 2006). The age of the ash and even the authenticity of the prints is controversial were Gonzalez et al. (2006) dated the ash layer to at least 40 kyr BP by OSL dating, wheile Renne et al. (2005) dated the layer as old as 1.3 myr based on ^{40}Ar/^{39}Ar dating and claimed that the footprints could not be human but the result of quarrying operations.

Hundreds of exceptionally preserved human footprints in twelve trackways and a trampled path are preserved in two small exposures of a surface of a Holocene volcanic ash in the site Acahualinca near the shores of Lake Managua, Nicaragua. Also present are tracks of deer, opossum and bird tracks. The estimated dates for the tracks range from 2120 to 6500 yrs BP (Lockley et al. 2009, Schmincke et al. 2009, Schmincke et al. 2010).

Véliz (1978) reported the finding of “fragmentary tracks of four feet, and thus dubious” tracks and “indisputable tracks of three human feet” in a rhyolitic layer in the hill named El Portillo de la Crucita, Guaimaca, Honduras. No dates have been estimated for these tracks.

THE RECORD OF BOOT TRACKS

The only reported boot tracks is from military structures in Trentino-Alto Adige Region in Northern Italy left by First World War soldiers (Avanzini et al. 2011). In Valmorbiaweerk (Forte Pozzacchio) the boot tracks are preserved in 2–3 mm on a thin layer of pure cement, and thus man-made and of less significance to this study. In the fortified complex of Monte Celva east of the city of Trento several human and small mammal tracks are preserved on the concrete floor. In both places the tracks record the imprint of boots with soles covered by rows of nails, leaving conical depressions outlining the contour of the shoe (see Avanzini et al. 2020, Figs. 9, 10).

METHODOLOGY

Surtsey Island was visited on July 16th to 19th, 2021 as part of an expedition led by the Icelandic Institute of Natural History. The accessible areas of the island were surveyed for preserved human tracks. Measurements were made with a tape measure and photogrammetrically and consisted of: 1) total length of trackway, 2) compass direction of trackway, 3) length of each track from the middle point of the heel rim to the middle point of the frontal (toe) end, 4) width of each track measured at half the length of the print, 5) pace as distance between individual tracks measured from the middle point of one print to the middle point of the following print, 6) stride measured as distance from the middle point of one print to the middle point of the next consecutive print of the same foot, 7) anatomical right and left identity of tracks in the trackways was determined by the shape and relative position to one another and the angle of gait which is the angle relative to the midline of the track. In this study we differentiate the left out-toeing by assigning a negative number and right out-toeing a positive number (see Table S in supplementary files).

High-resolution photographs were taken with digital cameras Olympus Tough TG-6, Canon 6D and with a Phantom 4 Pro drone. Photogrammetry processing of the drone images (20 MP camera FC6310, focal length 8.8 mm, image resolution 4864x3648 px) was made for each footprint site (images from 90 to 137 for each site) at the Icelandic Institute of Natural History (IINH) with software Agisoft Metashape (version 1.7.3). The resulting products were high-resolution georeferenced orthoimages (~ 2 mm/pix), digital elevations models (DEMs, ~8 mm/pix) and mesh models for three sites (Site 1, 2 and experiment). For scaling the orthoimages and models we used coded targets (12 bits from Agisoft Metashape) with known dimensions and for georeferencing ground control points that were measured with a high-precision GNSS instrument (Trimble R10) by the National Land Survey of Iceland. The methodology of the photogrammetry survey in Surtsey followed the 2019 survey described in Óskarsson et al. (2020). Photogrammetric methods for documenting the trackways were based on studies on hominid footprints (e.g. Masao et al. 2016).

Geological information of the island was extracted from aerial imagery of Surtsey from 1964 available at the National Land Survey of Iceland (www.lmi.is) and geological maps from the IINH (Lýsigagnagátt: NI_J5v Surtsey Jarðfræðikort jarðsaga 1963–2006 – 1:5.000, https://gatt.lmi.is/). A georeferenced 3D model of the island was available for additional observations on the geology of Surtsey and measurements, through the web platform V3GEO (Surtsey Island July 2021, Birgir Vilhelm Óskarsson; Guðmundur Valsson; Lovísa Ásbjörnsdóttir, https://v3geo.com/model/347) and through the software LIME (Buckley et al. 2019).

Orientation and dip of the trackways were measured with an iPhone 8S; for orientation we used the Compass application developed by Apple and for dip we used the Bubble Level application version 3.05 developed by Lemondo LLC. Angles could also be measured from a GIS based software.

In this study we used the following nomenclature to designate sites, trackways and tracks: Study sites are numbered S1, S2, S3 and S4. Site 4 is a single trackway with four tracks that was reported to the authors after field work was completed in July 2021 and thus details of the track could not be obtained. Trackways are named T1, T2 and T3 at each site. Individual tracks are named “t”, followed by a consecutive number beginning with 1 for the first occurrence and the letter “r” for right foot or “l” for left foot. As an example, the first track of trackway T1 in Site 1 is S1T1t1r.

EXPERIMENT

An experiment was conducted in a dry tephra debris fan east of the hut Pálsbær II (Site E in Fig. 1), where three trackways were made at different slopes, uphill 14°, subhorizontal 1°, and downhill 11° (Table 2). The trackways were photographed and processed photogrammetrically using coded targets for reference. The height of the person was 190 cm and boot size 32.5 cm in length and 11 cm width (46 EUR, foot length 27.5 cm). Measurements included boot track length and width, pace, stride, and angle of gait. The boot tracks in the experiment site were measured from the orthoimage only. Results are shown in Table 2 and in Table S in the Supplementary files.

GEOLOGICAL SETTING

Surtseyan geology

The eruption of Surtsey Island is divided into two main phases, the explosive Surtseyan phase that characterized the months from November 14th, 1963, to end of March 1964 and the effusive phase, that characterized the months from April 4th, 1964, to June 5th, 1967 (Table 1, Thorarinsson 1965a, 1967a, b, 1968a). During the eruption the activity migrated within Surtsey Island, but also to three other submarine eruptions located nearby Surtsey; Surtla, Syrtlingur and Jólnir, that formed ephemeral islands that were washed away within few months after their formation (see Table 1) and today exist as seamounts. The activity in Surtsey Island began forming the eastern tephra cone, Surtur. The almost unlimited availability of water in the submarine setting of the eruption led to powerful and explosive magma-coolant interactions generating fine-grained tephra and lapilli deposited in finely-bedded layers by air fall, pyroclastic density currents and by base-surge flows (Lorenz 1974). On February 2nd the activity migrated NW and established a new vent forming the western tephra cone, Surtungur. After the tephra closed the access of sea water into the vent beginning of April 1964, the eruption transitioned to effusive beginning first in the Surtungur cone that eventually formed a lava shield building out to the south from the tephra cone. On May 17th, 1965 the eruption ceased at Surtungur and on August 19th, 1966, effusive activity was reestablished in Surtur crater forming a second lava shield, and with five minor eruptions breakouts in the inner and outer cone of Surtur in late December 1966 and early January 1967. The effusive activity in Surtsey Island was terminated altogether on June 5th, 1967.

About one third of the exposed part of Surtsey was made up of basaltic (alkaline) tephra (Jakobsson 1972). The analysis by Jakobsson (1978) indicates that the tephra is very poorly sorted, with about 19% of the particles being fine ash (<0.06 mm), 67% as coarse ash (0.06–2 mm), about 14% as lapilli (2–64 mm), and less than 0.5% of blocks and bombs (>64 mm), according to the classification of Fisher (1961). Microscopic examination of the tephra shortly after deposition (Summer 1964) indicated that 82–88% volume consisted of unaltered and unpalagonitized basaltic glass, the rest consisting of fragments of autogenic hyalobasalt and phenocrystals of plagioclase, olivine and Cr-spinel, with initial porosity of the tephra at surface as high as 45–50% (Jakobsson 1972). Glass, when under hydrothermal alteration, is subject to palagonitization, a post-eruptional hydrolytic alteration process occurring at relatively low temperatures whereby basaltic glass is dissolved producing various authigenic minerals including palagonite, zeolites and smectites (Fisher & Schmincke 1984). Palagonite, the main product of this process, is a vitreous, transparent, but usually yellow to brown authigenic mineral that results in the compaction of the loose tephra (Jakobsson & Moore 1986).

During the build-up of the tephra cones, the steepening of the crater margins and outer slopes resulted in tephra slip, slumps and landslides forming a debris apron at the base and later top of the lava shields which partially filled the craters. Post-eruption degradation of the tephra cones with mass wasting continued to erode the cones and in Surtsey this process was intensive until consolidation with compaction and later palagonitization decreased the rates of surface erosion significantly. In the process, parts of the aeolian and talus sediments got palagonitized leaving only the outermost shell of reworked tephra unconsolidated. Since the termination of the volcanic activity, destructive forces have prevailed causing severe geomorphic changes. Coastal wave erosion is extreme, and the island had decreased by over 53% in 2019 (Óskarsson et al. 2020). Moreover, extreme weather conditions in Surtsey have removed over 4 m of palagonitized tuff from the cones at certain locations exposing the inner layering and sediments have accumulated at the base of the cones (Óskarsson et al. 2020).

LOCATION OF TRACKS IN THE TUFF CONES

Five boot trackways and two single tracks have been documented on palagonitized tuff on the SE slope of the island in four separate sites, Site 1, Site 2, Site 3, and Site 4 (Fig. 1, 2 and 3). Site 1 has two trackways (Fig. 2), Site 2 has three trackways, S2T1 and S2T2

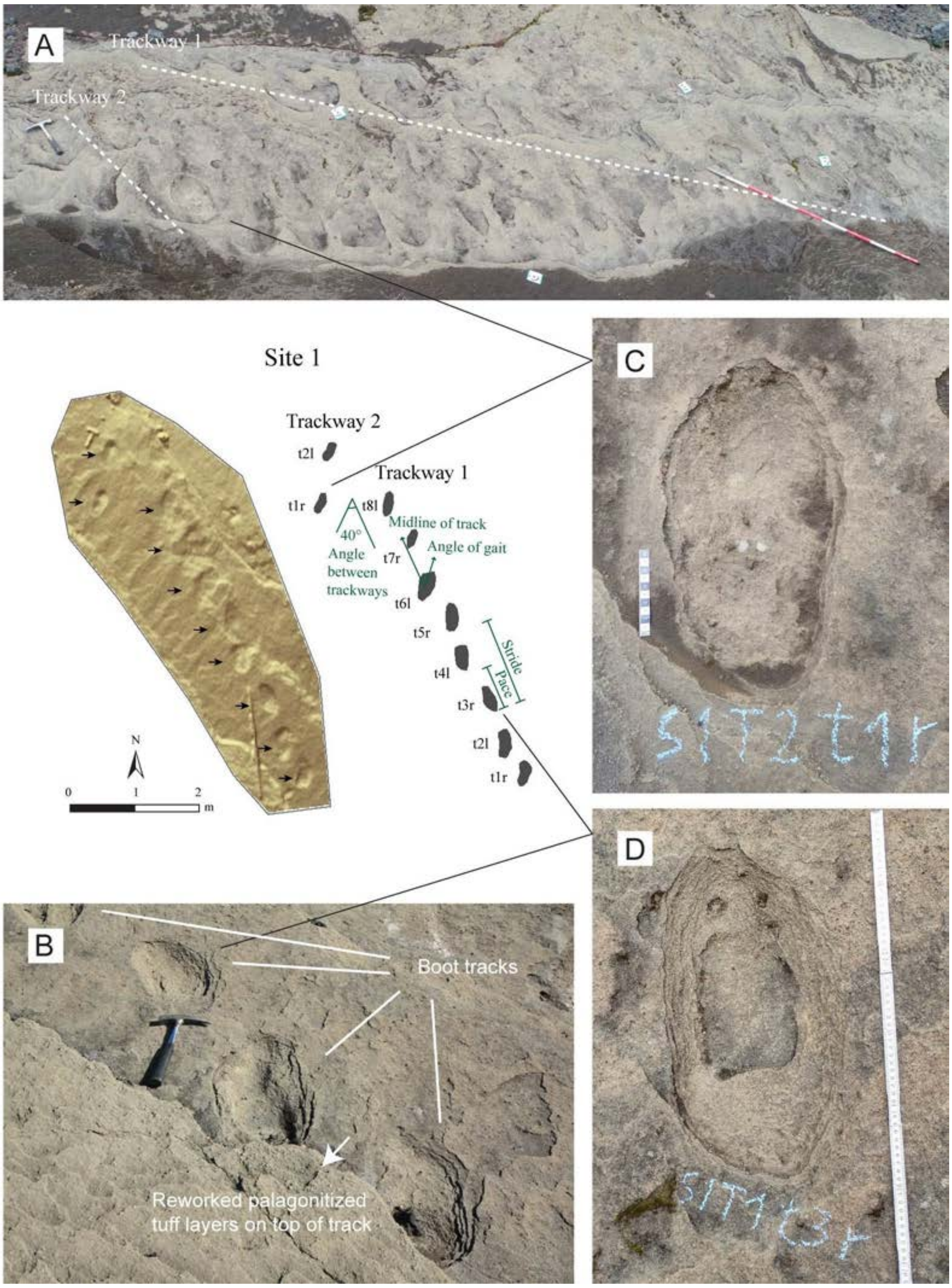

Figure 2. General view and details of Site 1 with trackways S1T1 and S1T2. Centered in the figure is a digital elevation model of the site with the trackways. Arrows point the location of the tracks. A) View of S1T1 in the foreground and S1T2 near the upper left corner. Notice the variation in orientation of the individuals tracks as the trackmaker walked to stay in a straight path while walking on soft ground. Notice other structures similar to tracks that resulted from the erosion of the track layer and both overlying and underlying layers. These pseudo tracks are easily distinguishable from true tracks because they do not show a pattern of alignment as tracks in trackways do. Some tracks show approximately 35° rotation with respect to the trackway midline. B) Four tracks of S1T1. C) Track S1T2t1r. Scale bar 10 cm. D) Track S1T1t3r. Scale bar 30 cm.

being well defined while S2T3 is inferred from the position of three tracks (Fig. 3), Site 3 has one single boot track and Site 4 was reported to have four tracks, but only one was documented (Fig. 4).

The tracks of all sites are positioned at seemingly the same stratigraphic level in the tuff cones within the uppermost (youngest) layers of palagonitized tuff cones (Fig. 5A). Site 1 (63.302081°, –20.607695°) is found at about 90 m.a.s.l. on an 18° slope along the crest of the ridge between Surtur and Surtungur tuff cones. Site 2 (63.303419°, –20.607159°) is found at about 106 m.a.s.l. along a 2° slope inside the eastern flanks of the Surtungur tuff cone. Site 3 (63.30371°, –20.60694°) is in straight northward continuation of Site 2 but slightly above, and Site 4 (see Fig 1 for approximate location) is located on a 20° slope at 75 m.a.s.l. in between two small craters within the inner walls of the Surtur tuff cone (Ósvaldur and Bjallan, Fig. 1) but the exact location of the boot tracks that are likely eroded today, is not known to the authors. The layer with the boot tracks of Site 1 is partially overlaid by 40 cm of palagonitized tuff (Fig. 5B) but 20 m below, the same layer is covered by about 1.2 m of palagonitized tuff beds (Fig. 5C and D). The overlying tuff includes numerous thin and discontinuous 1–5 cm beds of alternating fine ash and lapilli, sometimes with grading and cross bedding. The beds below and on top of Site 1 lack lithics and evidence of impact sags (Figs. 5 and 6). On Site 2 the layer with boot tracks is partially covered by 10–20 cm thick palagonitized tuff beds of lapilli and fine grained tephra (Fig. 5E) but within blocks of slumped material (Fig. 5A).

THE SURTSEY BOOT TRACKS

All the boot tracks studied are true tracks or surface tracks *sensu* Romano and Whyte (2003, Fig. 2 and 3), preserved as concave epichnia and epirelif, not underprints or subsurface tracks. Two main traits indicate that they are boot tracks and not footprints: the absence of toe marks and the occurrence of the mark of the waist or shank, which is the break in the outsole that separates the heel from the toe sections of the shoe.

All tracks in Site 1 have been modified by erosion but nevertheless remained relatively well preserved at the time of study (Figs. 2 and 3). Despite the best exposed tracks occur in Site 2 (Fig. 3). The tracks lack features observed in some vertebrate fossil and modern tracks, including stria, tension fractures,

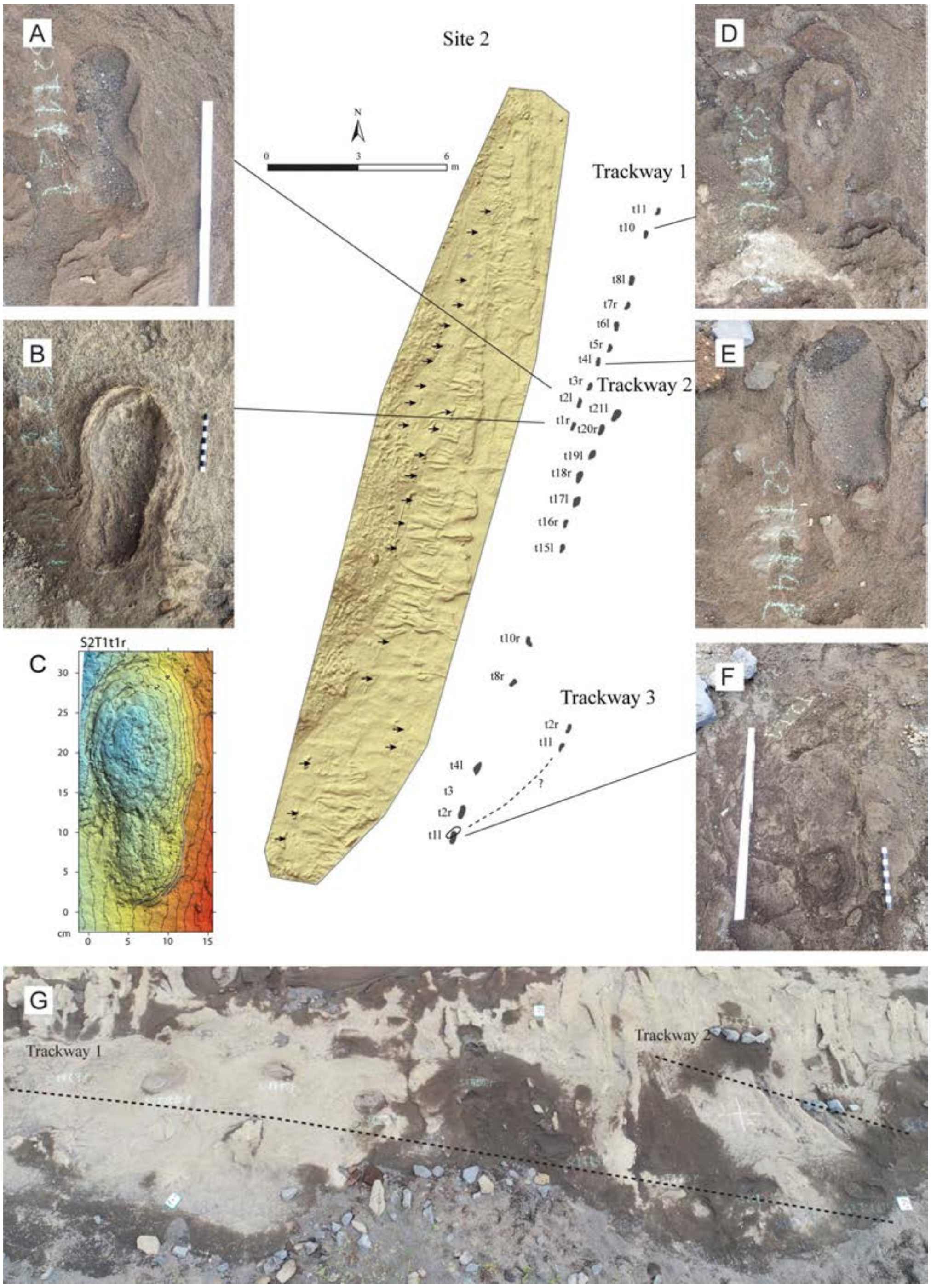

Figure 3. General view of Site 2. Centered a digital elevation model of the tracks in Site 2. Arrows point the location of the tracks. The different tracks show various degrees of preservation, spanning from well-preserved t1r (B) and t2l (A) to poorly preserved t10 (D) and t4l (E). C) A digital elevation model of boot track S2T1t1r. Black contour lines at 5 mm intervals. Notice the well-preserved expulsion rims of the track. F). Beginning of trackway S2T2 showing isolated S2T3 partially overlapping track t1l of S2T2. White scale bar is 42 cm, small scale bar 10 cm. G) Image showing parts of Trackways 1 and 2.

Table 2. Trackways, stride, gait and boot track measurements.

Site	**Site 1**	**Site 1**	**Site 2**	**Site 2**	**Site 2**	**Experiment**	**Site E**	**Site E**	**Site E**
Trackway	Trackway 1	Trackway 2	Trackway 1	Trackway 2	Trackway 3	**Trackway**	Trackway 1	Trackway 2	Trackway 3
Nr. of tracks	8	2	15	21	2	**Nr. of tracks**	17	23	13
Avg. length (cm)[1]	(3) 41±8.2	(2) 34.4±2.7	(4) 32.3±1.5	(5) 38.7±5.3	(2) 30.7±0.3	**Avg. length (cm)**	(8) 37.7±1.5	(7) 38.2±2.4	(10) 42±3.4
Avg. width (cm)	19.7±4.0	15.5±0.2	17±1.7	16.9±3.2	11.2±1.1	**Avg. width (cm)**	17.5±1.5	20.6±2.5	22.3±3.4
Trackway length (m)	5	1,2	8.1 (10.6)	14,3	1	**Trackway length (m)**	12,5	19,4	12,5
Trackway azimuth (degrees)[2]	333	28	21	23	22	**Trackway azimuth**[2]	2	221	77
Slope of trackway (degrees)	18	14	2	2	2	**Slope of track (degrees)**	14	1	11
Avg. angle of gait (degree)[3]	30.4±16.2	0.8±1.01	-2.2±9.14	-1.7±4.5	-0.2±0.4	**Avg. angle of gait (degree)**[3]	18.3±13.3	-6.5±14.2	-0.08±17.5
Avg. stride (m)	1.36±0.1		1.5±0.12	1.6±0.11		**Avg. stride (m)**	1.38±0.08	1.56±0.16	1.79±0.09
Avg. pace (m)	0.67±0.1	0,82	0.79±0.05	0.83±0.05	0,67	**Avg. pace (m)**	0.70±0.09	0.77±0.13	0.90±0.08
Estimated movement	uphill	uphill	uphill	uphill	uphill	**Movement**	uphill	horizontal	downhill
Estimated boot size[4]	45-46 (EUR)	40-42 (EUR)	40-42 (EUR)	45-46 (EUR)	~40 (EUR)	**Boot size**	32.5 cm (46 EUR)	32.5 cm (46 EUR)	32.5 cm (46 EUR)
Estimated stature (cm)[5]	177-190	167-175	167-175	177-190		**Stature (cm)**	190	190	190

[1] Number of tracks used in calculation in parenthesis.

[2] Azimuth direction of trackway.

[3] The angle between the trackway midline and the long axis of the track. Negative values are left out-toeing and positive right out-toeing.

[4] Boot length x boot width divided by 2. Factor is derived from comparison with the boot track in experiment and the actual bootsize that is 32.5 cm in length and 11 cm max width.

[5] Derived from simple foot length x height correlation charts.

marginal thrusts, and ejecta (Melchor 2015). The associated sediment lacks ripple marks, raindrop marks, desiccation cracks, rhyzoliths (traces of plant roots), insect trails, traces left by other vertebrates, and markings made by wind-blown vegetation.

Site 1

Site 1 has two preserved trackways, S1T1 and S1T2, both highly modified by erosion but still well recognizable (Fig. 2). S1T1 dips 18°SW, is oriented 333°N and has nine tracks, the first three with the contour well marked and the other six with the contour of the heel poorly preserved. The first track is a right print S1T1t1r.

S1T2 dips 14°SW, is oriented 28°NE and has two exposed tracks. An oval depression after the second print may be inferred as the third track in the sequence but it is poorly preserved and it could also be a structure resulting from erosion or the empty depression left after the impact of a lithic block, as other such structures are common on the slopes of Surtsey Island. This trackway starts with a left print (S1T2t1l).

Site 2

Three trackways, S2T1, S2T2, and S2T3 occur on this site (Fig. 3). S2T1 and S2T2 have direction about 21°W. The total length of the two trackways combined is 22.4 m as they are currently exposed. Table 2 shows dimensions, pace and stride of the tracks.

The orientation of both the two trackways and individual tracks is unambiguous because of their asymmetry, which show both the prints of the heel and the toe end of the boot track.

Trackway S2T1 is 8.11 m long and consists of eleven exposed tracks. The shape of each track determines whether they are left or right sides. Trackway S2T2 is 14.29 m long and consists of twenty-one exposed tracks with the first track corresponding to the left foot. The trackway occurs behind S2T1, and it distinguishes from S2T2 because the last two tracks of S2T2 (t20r and t21l) occur parallel and at a few tens of centimeters distanced to the right side of the first two tracks of S2T1 (t1r and t2l).

Tracks in trackway S2T2 occur in three different degrees of preservation: 1) as true prints, 2) as prints filled with sediment (t1l, t2r, t4r, t8r, t10r), and 3) as partially filled with sediment (t15l, t17l, t19l, t20r, t21l). Missing tracks in the trackway are t3l, t5l, t6r, t7l, t9l, t12r, t13l, and t14r.

The southernmost track of S2T3 is partially overlapping the heel impression of track t1l of trackway S2T2 (Fig. 3F). The orientation of this single track is 22°N (Fig. 3F). The track is well impressed with a sharp outline and the mark of the shank, clearly distinguishing the heel and toe sections of the boot. The impression on the right side of the track (toward the slope) is 3.5 cm deeper than on the left side (away from the slope). Based on the orientation of the track and the difference in depth within the track, we infer that the trackmaker was walking downhill at an approximate 30° angle with respect to the strike of the slope.

Site 3

About 25 m north of the last exposed track of S2T2 a single, well-preserved boot track, here named S3T1,

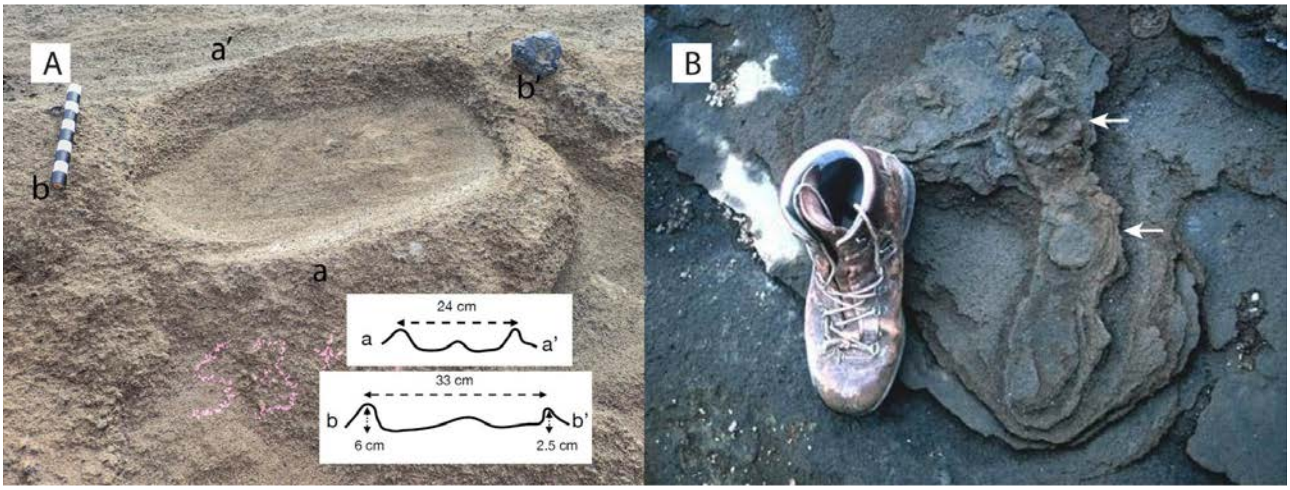

Figure 4. A) Single track in Site 3 with two cross sections. Scale bar is 10 cm. B) Site 4. Arrows point to the position of the heel of two overlapping tracks. Boot for scale size 45 (EUR), comparable in size to the track. Photo credit Hallgrímur D. Indriðason 2001.

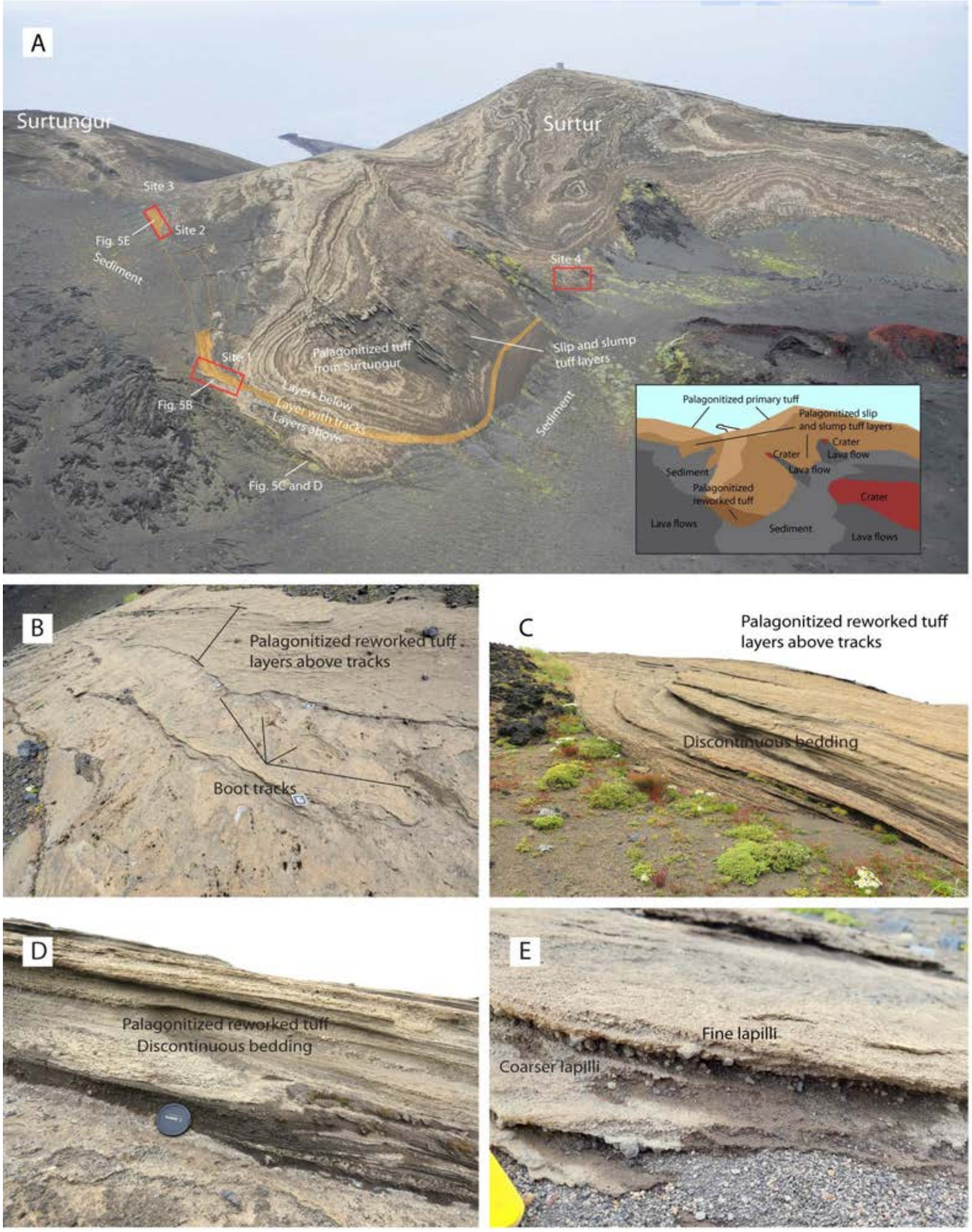

Figure 5. A) Stratigraphic location of the tuff layers with the tracks of this study and sketch showing the main lithologies. B) Trackway 1 in Site 1 showing the palagonitized reworked tuff layers above the track. The layer is about 40 cm thick at this location but 20 m below it thickens to about 1.2 m (C). D) The bedding is discontinuous, and the layers lack lithic clast and blocks and bombs unlike the primary tephra of Fig. 6. E) A close-up of the palagonitized tephra beds within slump layers above site 2.

occurs roughly in the opposite direction to S2T1 and S2T2 trackways (Fig. 4A). The track is fully exposed with a deep track wall surrounding the shaft, a well-formed marginal rim, uniform depth, and absence of sediment filling.

Site 4

Four boot tracks were preserved on this site, whose occurrence was made known to us after we left the island and thus was not studied (see one track in Fig. 4B with estimated boot size of 45–46 EUR). The tracks were seen in the site with a downhill direction towards the south (Hallgrímur D. Indriðason, pers. comm.).

STRIDE AND GAIT MEASUREMENTS

The results from these measurements were useful for determining the direction of the walk and if the walk was uphill or downhill (Table 2 and Table S in Supplementary files). When a line is placed centered in the trackway a left and right out-toeing can be observed. A slender out-toeing is more common in human bipedalism than in-toeing (Morton 1932) and thus we infer the orientation from the out-toeing indicates the direction of the trackways of Site 2 was northwards and uphill. This direction is also observed from the shape of t1r of Trackway 1 in Site 2 (Fig. 3). A clear difference is seen in the angle of gait from the shallow slope of Site 2 and the steep slope of Site 1, the same pattern observed in the trackways of the experiment site. The

Figure 6. A) Uniform bedding of primary tephra with lithic and impact sags in the gully Svartagil north of Surtsey. Notice the irregular distribution of lithics in the tuff. B) Sags formed by lithic blocks colliding into uncemented tuff. The figure shows a sag left after a bomb was eroded away. Small scale bar 10 cm. C) In-situ lithic block and adjacent sag of another lithic block that was eroded. Scale bar 42 cm.

average angle of gait is low and near zero (from the midline of the track) in shallow slopes while the angle is greater and the rotation unidirectional in the steeper slopes. In Trackway 1 of Site 1 and Trackway 1 of the experiment Site E the angle of gait is unidirectional to the NE, and pace and stride shorter, thus suggesting an uphill motion for the walk of Trackway 1 of Site 1. The estimated boot size, stride and pace length of Trackway 1 were also compared to the boot size (size 46), stride and pace measurements of the experiment, likely indicating a person with similar stature as the person of the experiment (190 cm). The stride and pace length of the downhill walk of Trackway 3 in the experiment Site E was longer, and perhaps a longer stride would be observed in the sites studied if the person had been walking downhill.

DISCUSSION

The boot tracks in Surtsey Island offer an exceptional opportunity for studying ichnites within geological formations formed in recent, well-documented events. The following points were investigated: the nature of the boot tracks and trackways, the stage in the construction of Surtsey Island relative to the elevation of the location and trackways, the lithology of the tephra and timing of fossilization, the nature of the tuff/sediments on top of the layers with the boot trackways, the location of the sites as sediment traps, the location of the sites relative to alteration and palagonitization history of the tuff, the history of visits to the island and potential persons involved in the making of the boot trackways.

The nature of the tracks: boot tracks versus impact structures

Numerous bombs and lithic blocks are seen exposed on the surface of the tephra layers, many of which have been eroded and rolled down the slope (Fig. 6A - C). Some of those bombs and blocks do not show impact sags in the underlying beds and others show deformation of the underlying beds, indicating that they landed ballistically, and the tephra layer was wet, cohesive, and plastically deformable (Fig. 6B - C). The sags are commonly elongated with the long axis orientally radially to center of the crater Surtur I (Lorenz 1974).

In the places where the tephra layer has just been eroded, some blocks and bombs are still attached to the surface, encircled by a rim of the ash layer in which the ejecta impacted. Some of those blocks and bombs are still attached to the ground surrounded by an expulsion rim. The pattern of shapes, structure and preservation of the impact structures differ significantly from the boot tracks. The undulated shape, the preservation of the impression of the shank, and their alignment of the tracks forming a trackway

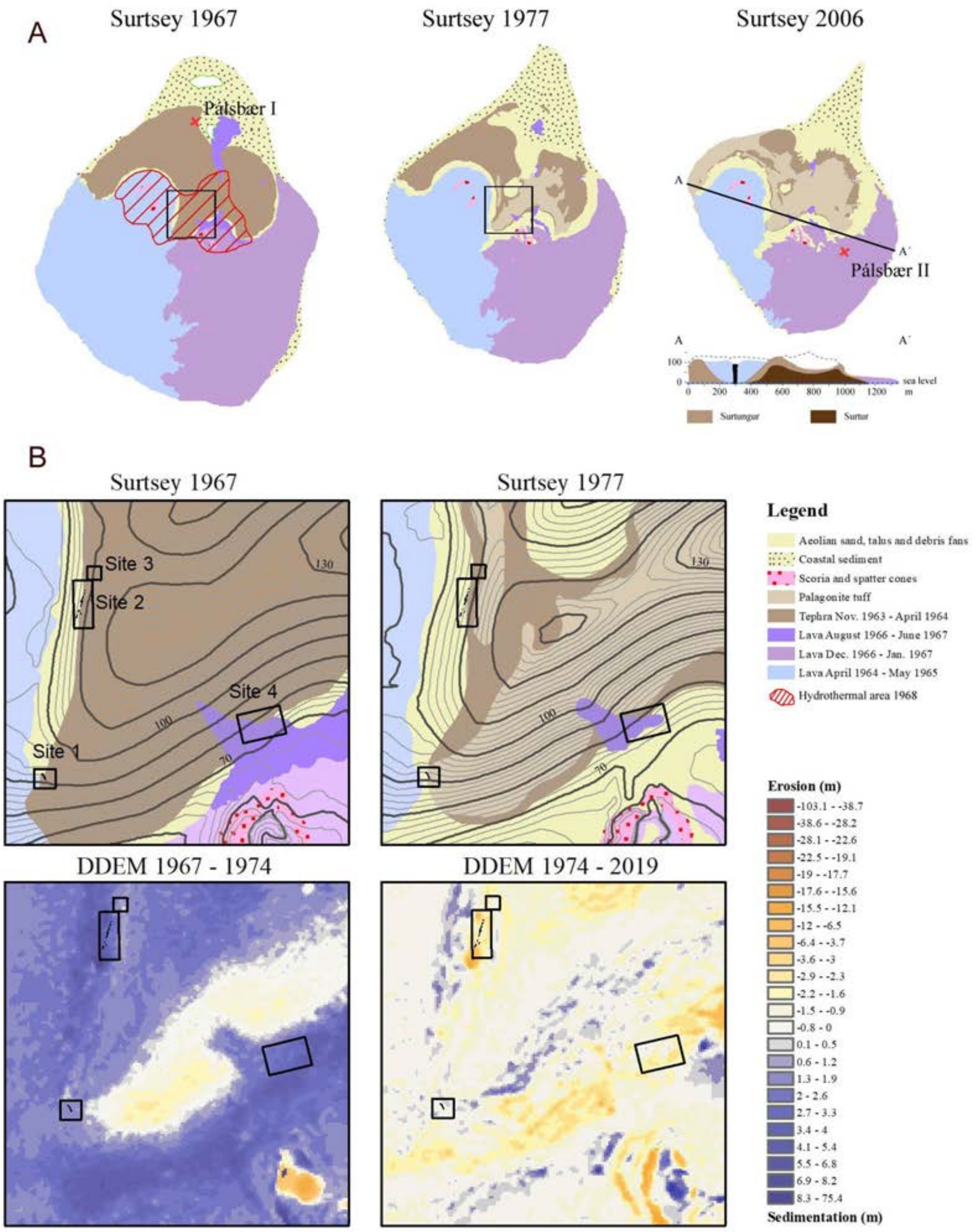

Figure 7. Geological maps of Surtsey from 1967, 1977 and 2006. Note the different palagonitization stages in the maps. Location of Pálsbær I and Pálsbær II shown for reference. Hydrothermal area from 1968 mapped with red lines. Cross sections of the island show how the tephra of Surtungur covers the older Surtur cone. B) (Above) Maps showing a close-up of the sites at different stages of palagonitization. (Below) DEM differencing from Óskarsson et al. (2020) showing the amount of erosion and sedimentation at each site at two periods, 1967–1974 and 1974–2019.

strongly indicate that the studied structures were the result of humans walking and leaving boot tracks and not fortuitous alignment of volcanic bombs.

The stratigraphic position of the boot tracks

As mentioned above the tracks are found seemingly at the same stratigraphic position (Fig. 5A). Their position lies within palagonitized tuff layers that cover the western side of Surtur tuff cone and eastern side of Surtungur tuff cone. The final phreatomagmatic activity of Surtsey was in Surtungur depositing tephra radially away from the vent and burying the older Surtur cone (see cross section in Fig. 7A), meaning that the tephra forming the substrate of the sites is from Surtungur. The thickness of the tuff from Surtungur draping the Surtur cone is unclear near the vent but has been estimated to be about 10 meters in the boreholes east in Surtur tuff cone (Fig. 1, Jackson et al. 2019). The boot tracks are thus posterior to the phreatomagmatic phase of Surtungur. The tracks could have formed towards the end of the Surtungur phreatomagmatic phase; however, the nature of the underlying and overlying tuff beds is reworked as discussed below and no visit to the island is recorded at this time (around March of 1964). The tracks are also found lying on top of the lava shields inside both cones meaning that they formed after the formation of the lava shields and the formation of the reworked tuff beds.

The elevation of the boot track sites relative to the stage of development of the island

We can infer from the location and elevation of the sites with the boot tracks at what stage of development Surtsey Island was when the boot tracks were formed. From Fig. 8 a comparison of maps is shown between the stages of February 17th 1964, late August 1964, July 1967, and the actual position of the boot tracks in July 2019. Around February 17th the location of the boot tracks does not match the current locations as they are 30 meters below current elevations at Sites 1 and 4, and about 10 meters below at Sites 2 and 3. On February 17th the eruption was phreatomagmatic, and the tephra cones were still under construction. Visits to the island were only four during the phreatomagmatic phase and none seem to have reached the elevation of the sites as discussed below. Moreover, it is unlikely that any visitor would have taken the risk of walking on the steep crater walls. On 25th of August 1964 the eruption had transitioned to effusive in the Surtungur vent and the tephra cones had largely been eroded to current form, and the location of the sites match to

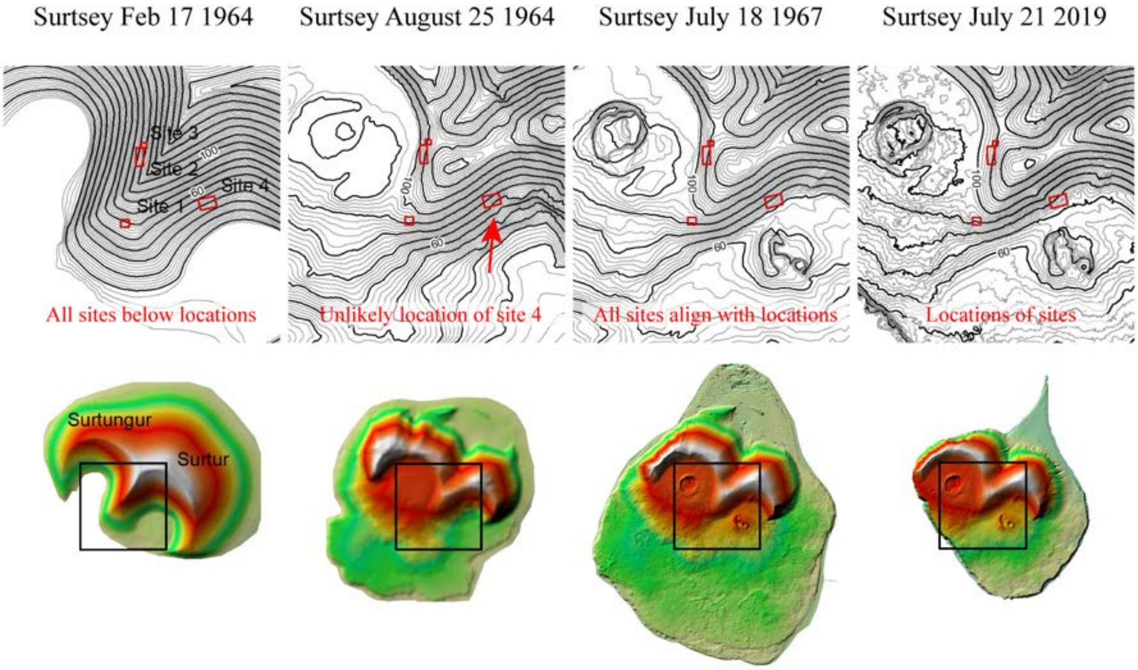

Figure 8. The location of sites placed on top of three different stages of development of Surtsey. The map from 2019 shows the true location of the sites. The stages from Feb 1964 and August 1964 are unlikely whereas the tracks do not align with the true location. The DEMs of 1964 were generated from 2 m contour maps provided by the Icelandic Institute of Natural History. The DEMs of 1967 and 2019 were generated from vertical images (Óskarsson et al. 2020).

some extent the current location. Nevertheless Site 1 was slightly off likely lacking the reworked tuff that would accumulate later at that location, and Site 4 was high up in the inner wall of Surtur tephra cone. If someone walked at Site 4 in late August 1964, the sediment would not accumulate easily to cover the boot tracks for preservation. Nevertheless, in July 1967 the lava shield of Surtur was completely formed and all sites align with current location. Sediment began to accumulate at the sites, and all were easily accessible by pedestrians including Site 4.

Thus, judging from these maps, the stage in which the sites were correctly positioned relative to their present-day elevation and accessible to pedestrians that walked along the margins of the lava shields, is after the formation of the Surtur shield in July 1967. The trackways are found on a route that was common in the early years due to accessibility and led to the hut Pálsbær I (Fig 7A and 9A), build in the north part of Surtsey in 1967. It is common that visitors in Surtsey prefer to walk on top of the sediments instead of walking on the fragile rough lava, and today the palagonite ridge with Site 1 is still the most accessible route up to the top of both Surtur and Surtungur tuff cones.

The physical condition of tephra at the time of track formation and the timing of fossilization

The formation of the Surtsey tracks would have involved the following sequence of events (modified from Thulborn 1990): 1) initial deposition of tephra sediments, 2) halt of the deposition of tephra, 3) surface of the sediment trodden by humans, 4) track molds consolidated, and 5) influx of sediment that covers the tracks.

The formation and successful preservation of tracks depends on multiple factors including the geography of the area, the type and stage of geological events forming the substrate and burying the tracks, the physical conditions of the substrate, the depth of the tracks, the behavior of the trackmaker and the climatic conditions. In the fossil record tracks were commonly preserved in environments that experienced rapid and/or periodic accumulation of sediments (Thulborn 1990).

The physical conditions of the substrate determined whether the tracks were formed at first. If the substrate had been too hard and dry, humans would not have left tracks on the surface. On the other extreme, if substrate had been excessively soft or wet, sediment would have collapsed, and tracks would not have been preserved with well-defined shafts, outline, and expulsion rims. The existence of the Surtsey tracks attest to a substrate of medium consistency and cohesiveness.

If the sediment had been highly cohesive, the humans walking on its surface would have disfigured their tracks as they tried to pull out their boots. Sticky sediment most likely would have recorded large and shapeless tracks and ejecta on the outside of the tracks.

The fossil record of vertebrate tracks shows that the best-preserved tracks occur in fine-grained sediments such as mudstones, siltstones, very fine sandstones, and fine volcanic ash. Tracks may form and be preserved in coarser sediments, but they are rare and of moderately or poor quality (Thulborn 1990). The Surtsey boot tracks are preserved in tephra sediment of medium to very coarse grain size, in which grains have a higher degree of mobility than in finer sediments. The fact that the Surtsey boot tracks are well formed and most of them with clear outlines (except for Site 1, which are modified by erosion), indicates that the substrate had adequate physical conditions for track formation despite having been formed in coarse grained sediments.

As indicated above, many tracks show well-preserved features, including a relatively deep shaft (e.g. track S3T1, Fig. 4), and a well-defined contour line. These traits indicate that the tracks remained mostly morphologically unaltered for the span of time between their formation and their consolidation. However, tracks in unconsolidated sediment do not last a long time, as observed in modern unconsolidated sediments where tracks have a short life span because they are subject to rapid modification or utter destruction by the growth of vegetation, wind, rain, and gravitational processes like grain creeping and slumping, which are likely to be more intense in coarse-grained sediments such as tephra. Sedimentary structures like desiccation cracks and raindrop impressions indicative of a relatively long permanence on the substrate prior to hardening of the substrate are absent in the Surtsey boot tracks.

Slump structures are generally associated with rapid sedimentation (Reineck & Singh 1975), a fact consistent with their occurrence in tephra layers on the slopes of Surtsey Island. Slumping was observed in the tephra layer immediately below the layer with boot tracks on site 2 but not above. Both the relatively high degree of preservation and the lack of slump structures associated with the boot tracks indicate an excellent degree of cohesiveness and a short time between track formation and consolidation.

The tephra/sediment layers above and below the boot tracks

The palagonitized tuff layers on top and below the boot tracks tell us that the tracks were buried by tephra/sediment after they were formed, deposits that were later palagonitized. The nature of the tuff on top is interpreted as twofold: 1) the layers on top and below the boot tracks of Site 1 and 4 is reworked tuff/sediment, that lack lithic and juvenile bombs, and have discontinuous bedding that reflects transport and deposition of tephra grains with slip, aeolian and runoff processes (Fig. 5C and D). 2) The layers below and on the sides of boot tracks of Sites 2 and 3 appear primary tuff layers but within slump deposits that had stabilized on top of the lava field (Fig. 5E).

The reworked tuffs below the boot tracks classify here as sedimentary and were formed after the lava shields were emplaced, because they are located at higher elevations in the craters and needed to have been trapped above the lava flows to be preserved at their present position. These sediments began accumulating on top of the lava flows quickly after their emplacement in Surtungur in May 1965 and December 1966 in Surtur.

Judging from the thickness of the sediments still preserved on top of the layer with the boot track on Site 1 we know that over 0.4 m of sediments overlaid the tracks at this location and 1.2 m slightly below. Extracting thickness change values from the DDEM of Fig. 7B (Óskarsson et al. 2020) we see that during the period of 1967–1974 about 1.6 m of sediment was deposited on top of Site 1, about 3–5 m of sediment deposited on top of Site 2 and 3, and 2–4 m on Site 4. The same figure shows that during the period of 1974–2019, about 0.4 m was removed from Site 1, 2–3 m from Site 2 and 3, and 1–3 m from Site 4. Subtracting these values and comparing them to the present thickness of the sediment on top of these sites, we get about 1 m of remaining sediment that would have accumulated sometime after 1967 but underlying the boot tracks.

Sediment accumulation at the base of the tephra cones and margins of lava shields was high during the first years prior to the consolidation and palagonitization of the cones. This is vividly seen in Fig. 9A that shows sediment over one meter in thickness deposited in one winter season, blocking the entrance of the hut Pálsbær I sometime around 1967–1970. Over 60% of the cones were palagonitized in 1974 meaning sedimentation rates decreased significantly after 1974. From these observations, within this time window of 1967 and 1974, we think the boot tracks formed shortly after 1967 and before 1970 due to the little amount of accumulated sediments.

The location of the sites and the alteration and palagonitization history of the tephra

Jakobsson (1972) reports that the first signs of consolidation in the tephra were seen in 1966, affecting the 10–15 cm of the exposed tephra layers and the first observed palagonitization was observed in September 1969, a process he attributes to local heating of the tephra. Jakobsson (1978) indicated that elevated temperatures were first noticed in April 1968 in areas north of the Surtur lava shield, which had been cool in July 1967. Temperatures in this thermal field, within which the two current study sites occur, were 48–84˚C at approximately 5 cm depth in the hottest areas, and 40–60˚C at 20 cm depth, with a very steep gradient temperature in the uppermost 40 cm but with a flattening out curve at 100˚C temperature. The heating of the tephra was explained as a result of steam at 100˚C originating from either precipitated water that subsequently vaporized after seeping down to the 100˚C level or vaporized seawater which mixes with meteoric water near the surface (Moore and Jackson 2020). The area north of the saddle near Site 2 is called "Svartagil" which means the black gully, because it was humid and black all year around due to steam and elevated temperatures. This area was malleable and could retain imprints for longer periods (Erling Ólafsson, pers.comm).

Consolidation of tephra continued through 1971 with common precipitation of opal and zeolite in the resulting tuff and in 1976 most of the tephra within the thermal area was palagonitized (Jakobsson 1978). By 1979 the surface temperature at 20 cm depth exceeded 20˚C in areas north of both Surtur and Surtungur lava fields. Deposits within this warm zone became lithified as glassy tephra underwent palagonitization. After palagonitization tephra is more evenly resistant to wind and marine erosion (Jakobsson 1978) and studies on the other islands of the Vestmannaeyjar archipelago have shown that the palagonitized tephra (tuff) is more resistant to marine abrasion than the lavas (Jakobsson 1968).

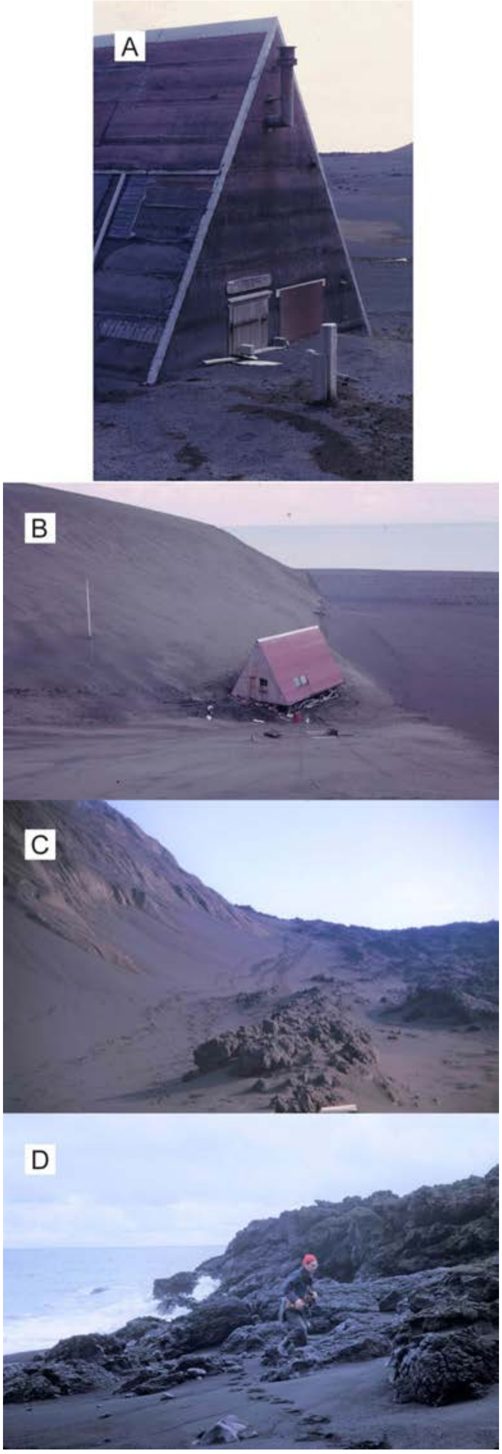

Figure 9. A) Hut Pálsbær I partially buried by remobilized tephra sometime between 1967 and 1970. This hut was dismantled and a new one was built on the SE slope of the island (Photo: Sturla Friðriksson). B) A distant view of hut Pálsbær I (Photo: Sturla Friðriksson). C) Many trackways were formed on the slopes of the volcanic cone during the early visits. The trackways in this photo occur in lose, unconsolidated tephra nearshore and were rapidly modified and destroyed by wind (Photo: Sturla Friðriksson). D) Icelandic geologist Sigurður Þórarinsson wearing water boots onshore in one of the early visits to the island (Photo: Sturla Friðriksson).

The geological maps with the boot track sites of Fig. 7A show the sites were unconsolidated in 1967 while partly or entirely palagonitized in 1977. Thus, palagonitization of the boot track sites is believed to have begun earlier than 1977, underneath 1–4 m (depending on the site) of unconsolidated sediments.

Visits to the island and the makers of the boot tracks

As summarized in Table 1 visits to the island were many and frequent after the termination of the explosive phreatomagmatic phase end of March 1964, and thus it is difficult to identify the makers of the boot tracks. In terms of preservation potential, the explosive phreatomagmatic phase was the most ideal for burying tracks quickly. However, only four visits were made to the island at this stage, three of them with short residence on the coast of Surtsey, and one with longer residence following a 17 hr eruption break in the explosive activity (Table 1). The one with longer residence, on December 16th, 1963, was made by geologists Sigurður Þórarinsson and Þorbjörn Sigurgeirsson, that had been waiting in the coast guard vessel Óðinn and adventured into the island for sample collection landing at 2:00 pm when they saw the eruption had entered a break. With them were two coast guard crew, steersman Kristinn Árnason and seaman Jónas Ragnarsson. Judging from photographs from this date, they landed on the northern coast and only Sigurður and Þorbjörn walked on the island, the other two waited by the boat. It is not known how far into the island they went but the residence was short due to the eminent danger of renewed explosive activity. This visit potentially left boot tracks that were preserved in the Surtur tuff cone because renewed explosive activity on the next day deposited 20 m of tephra on top of the Surtur tephra cone as reported by Sigurður (in Morgunblaðið newspaper, December 22nd, 1963). Images from this day also show the weather was humid and the tephra well consistent for capturing the prints. The height of the cone was about 86 m when they walked on the island, meaning their tracks would be located at this elevation if they reached the top of the island and at lower elevations at the sides of the cones. These height measurements were conducted from the vessel of the Coast Guard on a regular basis with good precision. Thus, the elevation of the tracks from the 16th of December are to be found at lower stratigraphic levels of the tuff cones than the tracks of this study.

Following the explosive phase in the end of March

1964, visits to the island were frequent both from sea and by small aircraft although after 1965, visits were controlled to minimize the impact of humans on the natural development of the island. (Table 1). The size of the boot tracks has been estimated and gives two sizes, 41–42 and 46 (EUR) and the third seems in the range of 40 but is unclear. Both Sites 1 and 2 have two trackways with boot sizes 42 and 46, and boot size of Site 4 is 45–46, which could suggest that the same two people walked on the sites. The stature of the person with shoe size 41–42 is in the range 167–175 cm in height and of the person of shoe size 46 is 177–190 cm in height according to simple height x foot length correlation charts (Giles & Vallandigham 1991). One potential owner of Trackway 1 in Site 2 and Trackway 2 in Site 1 is Sigurður Þórarinsson. Sigurður visited the island eight times in 1967 (Thorarinsson 1968a) and used 41–42 (EUR) in shoe size (Sven Þórarinn Sigurðsson, pers. comm.), which is 25.4–26.3 cm in length that matches the size found in this track. He was about 170 cm tall and wore Wellington boots in his visits (Fig. 9D). He was often accompanied by other scientists, journalists, filmmakers, photographers, and others (Helgadóttir 2021). Figure 9 shows Sigurður Þórarinsson walking on the recently deposited volcanic sediment and several trackways formed by the early visitors to the island.

The tracks in Sites 2 and 3 are relatively well-preserved so that it is possible to determine the direction of movement both from the anatomy of the boots and the angle of gait (Fig. 4–8). From the analyses of the angle of gait, the out-toeing gives a northerly direction for Trackways 1 and 2 in Site 2 in agreement with the anatomy of the best-preserved boot. The two trackways in Site 2 run parallel to one another, indicating that two people walked in the same direction very likely at the same time. Two additional boot tracks above in Trackway 3 indicate a third person. This trackway is possibly connected to a print that intersects Trackway 2 (Fig. 3F) which appears from its anatomy to have an orientation westward. Thus Trackway 3 in Site 2 could be of a person walking in a counter direction to Trackways 1 and 2 and then trending west. In Site 1, despite the high degree of erosion of the tracks, the angle of gait is unidirectional with a relatively short pace and stride. The length x width of the weathered boot tracks divided by a factor of 2 to account for deformation of the sand, a factor derived from the experiment site, indicates a boot size about 46 (EUR). The results are strikingly similar to the result of the experiment indicating the same size person and the short stride would support uphill movement as in the uphill experiment. The two trackways occur at a 42° angle, indicating that there was some intersection in their routes. All tracks are found within common hiking routes within the island, either along the sediment talus at the break of slope between the lava fields and the steeper tuff cones or walking up the ridge between the tuff cones and up to the saddle and possibly towards the hut Pálsbær I (Fig. 9B) at the north shore or hiking up to the top of the cones. In Site 4, the person might have been visiting the newly formed crater on the inner side of Surtur named Ósvaldur (Fig. 1).

Were the tracks of all sites made on the same day?

It is difficult to assert if the tracks in all sites formed on the same day despite that they seemingly form at the same stratigraphic level in the tuff cones. Nevertheless, the environmental conditions for preservation that involve deformation of humid sediments followed by rapid sedimentation triggered potentially by a storm, that coincide with human activity, are less common and would have been restricted to a few days a year. Most boot tracks are made in dry sand and are quickly erased by wind. Thus, it is not unlikely that the boot tracks formed during one visit where the ideal conditions for capture and preservation were met.

Synthesis and broader application

In synthesis, the evidence presented suggests the human boot tracks in Surtsey are authentic and their formation coincides with a period of rapid geomorphic changes following the volcanic event, sometime in between 1967 and 1970. Ideal conditions for capture and preservation of ichnites are rare as most ichnites are obliterated shortly after formation. Preservation of tracks require a soft, deformable substrate wherein an imprint is made and an environment in which minimal erosion of the imprinted surface occurs. However, the capture of the ichnites is best achieved with rapid burial for preservation as well as rapid consolidation of the substrate.

In Surtsey, the early years post-eruption met all these conditions. According to Sigurður Þórarinsson extreme rates of erosion and sedimentation characterized the first years syn- and post-eruption with rapid erosion of the uncompacted and unconsolidated tephra as well as rapid erosion of the lava margins by wave loading (e.g. Norrman 1978, Ingólfsson 1982). Óskarsson et al. (2020) estimated that about 300.000

m^3 of tephra was mobilized from the tephra cones by mass movement, aeolian and runoff in between 1967 and 1974 deposited in taluses at the margins of the cones. These conditions decreased dramatically after the tephra cones palagonitized. As shown vividly in Fig. 9A, the hut Pálsbær I, was often found partly buried in sediment after the winter months and had to be dug out (Fig. 9B, Erling Ólafsson, pers. comm.). This implies that the likelihood of ichnites being rapidly buried after formation was greater under these unstable initial conditions of the young island.

Hydrothermal activity in the early years was also imperative in the preservation and later cementation and consolidation of the sites. The initial steam-saturated tephra of large areas within the cones including the sites is likely to have contributed to the cohesiveness of the tephra that facilitated the preservation of the imprints in the substrate. These conditions deteriorated as the tephra cones consolidated with palagonitization and the hydrothermal activity focused into open fissures, yet on the other hand the boot tracks already captured in the substrate were permanently cemented in the cones.

The observations in Surtsey show that the conditions favorable for capturing and preserving the ichnites were those associated with high-energy events, or those following the aftermath of those events in the form of unstable environments, but with the ichnites somehow protected from being destroyed by those same processes. In this context, volcanic intrusions affected the local hydrological system and hydrothermal venting and steaming formed cohesive substrates and prompted rapid alteration and lithification of the substrate. Imprints susceptible to alteration consolidated rapidly increasing their resistance to erosive processes.

CONCLUSION

The boot tracks preserved in reworked palagonitized tuff layers in Surtsey Island are a case of exceptional occurrence of ichnites. As they date back to the years between 1967 and 1970, they may be the most recent fossils known to exist to this date. Their human origin is unmistakably attributed by their morphological traits and their occurrence forming a linear succession of tracks that is highly unlikely to have had a non-biological origin. Those characteristics and their particular shape make them clearly distinct from the circular and elongate deformations derived from the impact of volcanic bombs and lithic blocks in the soft tuff. They are identified as boot tracks because of their clear anatomical boot-like shape and/or the sediment filling show the outline of the boot outsole and the mark of the waist or shank.

The boot tracks occur in four different sites: Site 1 with two trackways, Site 2 with three trackways, Site 3 with one track and Site 4 four tracks. Because they have been partially affected by erosion, the boot tracks show various degrees of preservation, ranging from well-preserved tracks, to tracks that show a faint outline.

Formation of tracks of any kind requires a relatively soft and humid sediment susceptible to deformation by the trackmaker and an appropriate degree of cohesiveness to maintain the shape of the deformation after the print is formed. Also, fresh tracks are susceptible to rapid destruction due to wind, rain, gravity processes and biological alteration. The occurrence of boot tracks in tuff layers in Surtsey Island and the lack of evidence of deformation or desiccation cracks strongly suggest that the tuff layers in which they occur consolidated relatively rapidly soon after the tracks were formed. The early stages of Surtsey tephra cones underwent rapid erosion due to the uncompacted and unconsolidated nature of the tephra prior to palagonitization, that was imperative in capturing the boot tracks burying them rapidly within reworked tuff sediments. Moreover, steaming, and hydrothermal activity within the tephra prompted cohesiveness to the tephra allowing the preservation of the imprints and rapid consolidation increasing the resistance of the hosting substrate to erosion. These conditions were met in the years following the volcanic event and underline the role of high-energy events and their post-stabilization aftermath creating the suitable conditions for capturing and preserving ichnites.

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REFERENCES

Armirotti, A., C. De Davide, & D. Wicks, 2017. Scavi per dell'Ospedale regionale Umberto Parini Aosta: sintesi dei principali risultati. Bolletino della i Beni e le Attività Culturali, Regione d'Aosta 14, 14–31.

Avanzini, M., M. Bernardi, & F. M. Petti, 2011. Soldier tracks in a World War Fort (Valmorbiawerk, Trento, Italy). Ichnos 18, 72–78. https://doi.org/10.1080/10420940.2011.573602

Avanzini, M., P. Citton, P. Mietto, A. Panarello, P. Raia, M. Romano, & I. Salvador, 2020. Human footprints from Italy: the state of the art. Journal of Mediterranean Earth Sciences 12, 213–232. https://doi.org/10.3304/JMES.2019.003

Avanzini, M., P. Mietto, A. Panarello, M. De Angelis, & G. Rolandi, 2008. The devil's trails: Middle pleistocene human footprints preserved in a volcanoclastic deposit of southern Italy. Ichnos 15(3–4), 179–189. https://doi.org/10.1080/10420940802470458

Balashova, A., H. B. Mattsson, A. M. Hirt, & B. S. Almqvist, 2016. The Lake Natron Footprint Tuff (northern Tanzania): volcanic source, depositional processes and age constraints from field relations. Journal of Quaternary Science 31(5), 526–537. https://doi.org/10.1002/jqs.2876

Buckley, S. J., K. Ringdal, N. Naumann, B. Dolva, T. H. Kurz, J. A. Howell, & T. J. B. Dewez, 2019. LIME: Software for 3-D visualization, interpretation, and communication of virtual geoscience models. Geosphere 15(1), 222–235. https://doi.org/10.1130/GES02002.1

Fisher, R. V., 1961. Proposed classification of volcaniclastic sediments and rocks. Bulletin Geological Society of America 72(9), 1409–1414. https://doi.org/10.1130/0016-7606(1961)72[1409:PCOVSA]2.0.CO;2

Fisher, R. V. & H.-U. Schmincke, 1984. Alteration of volcanic glass. *In* Pyroclastic Rocks. Springer, New York, pp. 312–345

Friðriksson, Á., 2022. Strand í gini gígsins, Ugla útgáfa, Reykjavík (in Icelandic).

Furnes, H., 1975. Experimental palagonitization of basaltic glasses of varied composition. Contributions to Mineralogy and Petrology 50(2), 105–113. https://doi.org/10.1007/BF00373330

Giles, E. & Vallandigham, P. H., 1991. Height Estimation from Foot and Shoeprint Length, Journal of Forensic Sciences 36(4), 1134–1151.

González, S., D. Huddart, M. R. Bennett, & A. González-Huesca, 2006. Human footprints in Central Mexico older than 40,000 years. Quaternary Science Reviews 25(3–4), 201–222. https://doi.org/10.1016/j.quascirev.2005.10.004

Hatala, K. G., W. E. Harcourt-Smith, A. D. Gordon, B. W. Zimmer, B. G. Richmond, B. L. Pobiner, D. J. Green, A. Metallo, V. Rossi, & C. M. Liutkus-Pierce, 2020. Snapshots of human anatomy, locomotion, and behavior from Late Pleistocene footprints at Engare Sero, Tanzania. Scientific Reports 10(1), 1–12. https://doi.org/10.1038/s41598-020-64095-0

Hay, R. L. & A. Ijima, 1968a. Nature and origin of palagonite tuffs of the Honolulu Group on Oahu. Geological Society of America Memoir 116, 331–376. https://doi.org/10.1130/MEM116-p331

Hay, R. L. & A. Ijima, 1968b. Petrology of palagonite tuffs of Koko Crater, Oahu, Hawaii. Contributions to Mineralogy and Petrology 17, 141–154. https://doi.org/10.1007/BF00373206

Helgadóttir, S., 2021. Sigurður Þórarinsson, Mynd af manni, Náttúruminjasafn Íslands og Sigrún Helgadóttir, Reykjavík (Biography of Sigurður Þórarinsson in Icelandic).

Jackson, M. D., M. T. Gudmundsson, T. B. Weisenberger, J. M. Rhodes, A. Stefánsson, B. I. Kleine, P. C. Lippert, J. M.Marquardt, H. I.Reynolds, J. Kück, V. T. Marteinsson, P. Vannier, W. Bach, A. Barich, P. Bergsten, J. G. Bryce; P. Cappelletti, S. Couper, M. F. Fahnestock, C. F. Gorny, C. Grimaldi, M. Groh, Á. Gudmundsson, Á. T. Gunnlaugsson, C. Hamlin, T. Högnadóttir, K. Jónasson,; S. S. Jónsson, S. L. Jørgensen, A. M. Klonowski, B. Marshall, E. Massey, J. McPhie, J. G. Moore, E. S. Ólafsson, S. L. Onstad, V. Perez, S. Prause, S. P. Snorrason, A. Türke, J. D. L. White & B. Zimanowski, 2019. SUSTAIN drilling at Surtsey volcano, Iceland, tracks hydrothermal and microbiological interactions in basalt 50 years after eruption, Scientific Drilling, 25, 35–46. https://doi.org/10.5194/sd-25-35-2019

Ingólfsson, Ó., 1982. Some observations on the sediments of Surtsey. Surtsey Research Progress Report IX, 133–141.

Jakobsson, S. P., 1968. The geology and petrography of the Westman Islands. A preliminary report. Surtsey Research Progress Report IV, 113–129.

Jakobsson, S. P., 1972. On the consolidation and palagonitization of the tephra of the Surtsey volcanic island, Iceland. Surtsey Research Progress Report VI, 121–128.

Jakobsson, S. P., 1978. Environmental factors controlling the palagonitization of the Surtsey tephra, Iceland. Bulletin Geological Society of Denmark 27(Special Issue), 91–105.

https://doi.org/10.37570/bgsd-1978-si-11

Jakobsson, S. P. & J. G. Moore, 1986. Hydrothermal minerals and alteration rates at Surtsey volcano, Iceland. Bulletin Geological Society of America 97, 648–659. https://doi.org/10.1130/0016-7606(1986)97<648:HMAARA>2.0.CO;2

Lárusdóttir, B. 2017. Að nema land með nafni – Sagan af Surtsey, Skírnir, 166–185.

Liutkus-Pierce, C., B. Zimmer, S. Carmichael, W. McIntosh, A. Deino, S. Hewitt, K. McGinnis, T. Hartney, J. Brett, & S. Mana, 2016. Radioisotopic age, formation, and preservation of Late Pleistocene human footprints at Engare Sero, Tanzania. Palaeogeography, Palaeoclimatology, Palaeoecology 463, 68–82. https://doi.org/10.1016/j.palaeo.2016.09.019

Lockley, M., G. Roberts, & J. Y. Kim, 2008. In the footprints of our ancestors: an overview of the hominid track record. Ichnos 15(3–4), 106–125. https://doi.org/10.1080/10420940802467835

Lockley, M. G., R. G. Vasquez, E. Espinoza, & S. G. Lucas, 2009. America's most famous human footprints: history, context and first description of mid-Holocene tracks from the shores of Lake Managua, Nicaragua. Ichnos 16(1–2), 55–69. https://doi.org/10.1080/10420940802470755

Lorenz, V., 1974. Studies of the Surtsey tephra deposits. Surtsey Research Progress Report VII, 72–78.

Masao, F. T.; Ichumbaki, E. B.; Cherin, M.; Barili, A.; Boschian, G.; Iurino, D. A.; Menconero, S.; Moggi-Cecchi, J.; Manzi, G. & Perry, G. H., 2016. New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins, eLife Sciences Publications, Ltd, 5, e19568. https://doi.org/10.7554/eLife.19568

Melchor, R. N., 2015. Application of vertebrate trace fossils to palaeoenvironmental analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 439, 79–96. https://doi.org/10.1016/j.palaeo.2015.03.028

Mietto, P., M. Avanzini, & G. Rolandi, 2003. Human footprints in Pleistocene volcanic ash. Nature 422, 133. https://doi.org/10.1038/422133a

Moore, J. G. & M. D. Jackson, 2020. Observations on the structure of Surtsey. Surtsey Research 14, 33–45. https://doi.org/10.33112/surtsey.14.3

Morton, D. J., 1932. The angle of gait: A study based upon examination of the feet of central African natives, The Journal of Bone & Joint Surgery 14(4), 741–754.

Norrman, J.O. 1978. Coastal changes in Surtsey Island, 1972–75. Surtsey Research Progress Report VIII, 53–59.

Óskarsson, B. W., K. Jónasson, G. Valsson, & J. M. C. Belart, 2020. Erosion and sedimentation in Surtsey island quantified from new DEMs. Surtsey Research 14, 63–77. https://doi.org/10.33112/surtsey.14.5

Ozansoy, F., 1969. Pleistocene fossil human footprints in Turkey. Bulletin of the Mineral Research and Exploration 72, 146–150.

Pálmadóttir, E., 2003. Eins og ég man það, Vaka-Helgafell, Reykjavík (Biography in Icelandic).

Reineck, H.-E. & I. B. Singh, 1975. Depositional sedimentary environments. Springer, New York.

Renne, P. R., J. M. Feinberg, M. R. Waters, J. Arroyo-Cabrales, P. Ochoa-Castillo, M. Perez-Campa, & K. B. Knight, 2005. Age of Mexican ash with alleged fooootprints. Nature 438, E7-E8. https://doi.org/10.1038/nature04425

Romano, M. & M. A. Whyte, 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. Proceedings of the Yorkshire Geological Society 54(3), 185–215. https://doi.org/10.1144/pygs.54.3.185

Schmincke, H.-U., S. Kutterolf, W. Perez, J. Rausch, A. Freundt, & W. Strauch, 2009. Walking through volcanic mud: the 2,100-year-old Acahualinca footprints (Nicaragua). Bulletin of Volcanology 71(5), 479–493. https://doi.org/10.1007/s00445-008-0235-9

Schmincke, H.-U., J. Rausch, S. Kutterolf, & A. Freundt, 2010. Walking through volcanic mud: the 2,100 year-old Acahualinca footprints (Nicaragua) II: the Acahualinca people, environmental conditions and motivation. International Journal of Earth Sciences 99(1), 279–292. https://doi.org/10.1007/s00531-009-0438-0

Thorarinsson, S., 1965a. The Surtsey eruption: course of events and the development of the new island. Surtsey Research Progress Report I, 51–55.

Thorarinsson, S., 1965b. Sitt af hverju um Surtseyjargosið [Some facts about the Surtsy eruption]. Náttúrufræðingurinn 35:153–181 (in Icelandic with English summary).

Thorarinsson, S., 1966. The Surtsey eruption: course of events and the development of Surtsey and other new islands. Surtsey Research Progress Report II, 117–123.

Thorarinsson, S., 1967a. The Surtsey eruption: course of events during the year 1966. Surtsey Research Progress Report III, 84–90.

Thorarinsson, S., 1967b. Surtsey. The new island in the North Atlantic. The Viking Press, New York.

Thorarinsson, S., 1968a. The Surtsey eruption: course of events during the year 1967. Surtsey Research Progress Report IV, 143–148.

Thorarinsson, S., 1968b. The last phases of the Surtsey Eruption [Síðustu þættir Eyjaelda]. Náttúrufræðingurinn 38, 113–135 (in Icelandic with English summary).

Thulborn, T., 1990. Dinosaur tracks. Chapman and Hall, London.

Véliz, V., 1978. Huellas humanas en Guaimaca, Honduras. Yaxkin 2(4), 263–269.

Supplementary files

Table S. Measurements of stride, gait and boot track measurements.

Measurements of the inclination of the SE-03 Borehole on Surtsey Volcano

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ABSTRACT

The inclined SE-03 borehole drilled in 2017 provides a unique opportunity to further examine the stratigraphy and submarine structure of Surtsey. The borehole was drilled towards west (azimuth 264°) with inclination of 35° from vertical. Downhole measurements conducted in August 2021 using a STP-8 inclinometer confirmed that any discrepancy in the orientation of the borehole is minor and does not affect the overall interpretation of the location of the SE-03 drill core. The average inclination of the borehole from vertical is 33.4±0.2°. The bottom of the borehole at 354.05 m measured depth corresponds to a total vertical depth of 294.7±1.2 m. This is 4.7 m deeper than the designed borehole path. The horizontal length from the well head to the point vertically above the bottom of the borehole is 195.1±1.0 m, which is about 8 meters less than the designed borehole path (203.1 m). Correcting for this 1.4-1.8° discrepancy between the planned inclination and the actual value gives greater accuracy in the location of the units cored. The results confirm the location of an intrusion directly beneath the Surtur crater, considered to be the feeder dyke for its eruption in 1966-67.

INTRODUCTION

In the summer of 2017, the International Continental Scientific Drilling Program (ICDP) SUSTAIN project drilled three cored boreholes through Surtsey at sites about 10 m from a cored borehole drilled in 1979 (Jackson *et al.* 2019; Weisenberger *et al.* 2019). Two of the holes were vertical (SE-02a and SE-02b) and one (SE-03) was inclined i.e. drilled at an angle. Drilling of all three holes through the still hot subsurface was conducted from the same drilling platform, adjacent to the 1979 hole (SE-01, Jakobsson & Moore 1982). Table 1 provides a summary of the 1979 and 2017 boreholes.

The purpose of the cored SE-03 borehole was to study the existence of a possible diatreme underlying Surtur crater (Moore 1985) through examining tephra deposits, dykes and other vent facies that can provide additional information on deep stratigraphy and submarine structure. It was planned as 300 m long inclined hole with steel casing (Jackson *et al.* 2015). SE-03 was the last hole drilled during the drilling campaign in 2017; coring took place between August 28th and September 4th. The hole was directed towards west (azimuth 264°) and had an angle of 35° from vertical. It reached a measured depth of 354.05 m, giving a presumed 290 m vertical depth under the eastern sector of Surtur crater. The core thus traverses the deep conduit and intrusions (feeder dyke) of the Surtur eruptions (McPhie *et al.* 2020;

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Table 1: Boreholes drilled in Surtsey in 1979 (SE-01) and 2017 (SE-02a, SE-02b, SE-03) (based on Weisenberger *et al.* 2019).

Bore-hole name	Hole ID	Coordinates (WGS84)	Flange height (m a.s.l.)*	Reference level during drilling (m a.s.l.)*	East** North** (m)	Horizontal Distance from SE-01 (m)	Depth** * (m)
SE-01	73552	63° 18.09749’N 20° 35.98221’W	58.40	-	419756.79 311669.86	0.00	180.6
SE-02a	73553	63° 18.09659’N 20° 35.99063’W	58.01	57.57	419749.70 311668.38	7.08	152.01
SE-02b	73554	63 18.09739’N 20° 35.99020’W	57.86	57.65	419750.11 311669.85	6.86	191.85
SE-03	73555	63° 18.09649’N 20° 35.99170’W	58.13	57.65	419748.81 311668.22	9.92	354.64

* a.s.l.: above sea level; ** Reference coordinate system: ÍSN93; *** SE-03 is inclined 35° from vertical; depth is along hole axis.

Weisenberger *et al.* 2019). Investigations of the SE-03 core will further clarify the internal structure and facies architecture of the type locality of Surtseyan volcanism (Thorarinsson 1967).

Due to logistical issues no downhole logging apart from temperature measurements could be carried out in 2017 after drilling of SE-03. However, as the orientation of the hole is an important parameter when it comes to locating the core within the internal structure the Surtur crater and diatreme, measurements of the inclination of the borehole were conducted on August 5th, 2021.

BOREHOLE SE-03

The 2017 drilling was carried out by DOSECC Exploration Services of Salt Lake City, Utah, USA, using an Atlas Copco CS-1000 drill rig assembled on site after having been transported to the Surtsey island in parts by helicopter from the Icelandic Coast Guard vessel Þór moored offshore.

The SE-03 cored borehole was pre-drilled at 35° from vertical and azimuth 264° with a 6⅛” tricone rotary drill bit to a measured depth of 12.6 m. After lowering the 4½” HWT conductor casing to a casing shoe depth of 11.91 m, the conductor casing was cemented in place. After waiting on cement,

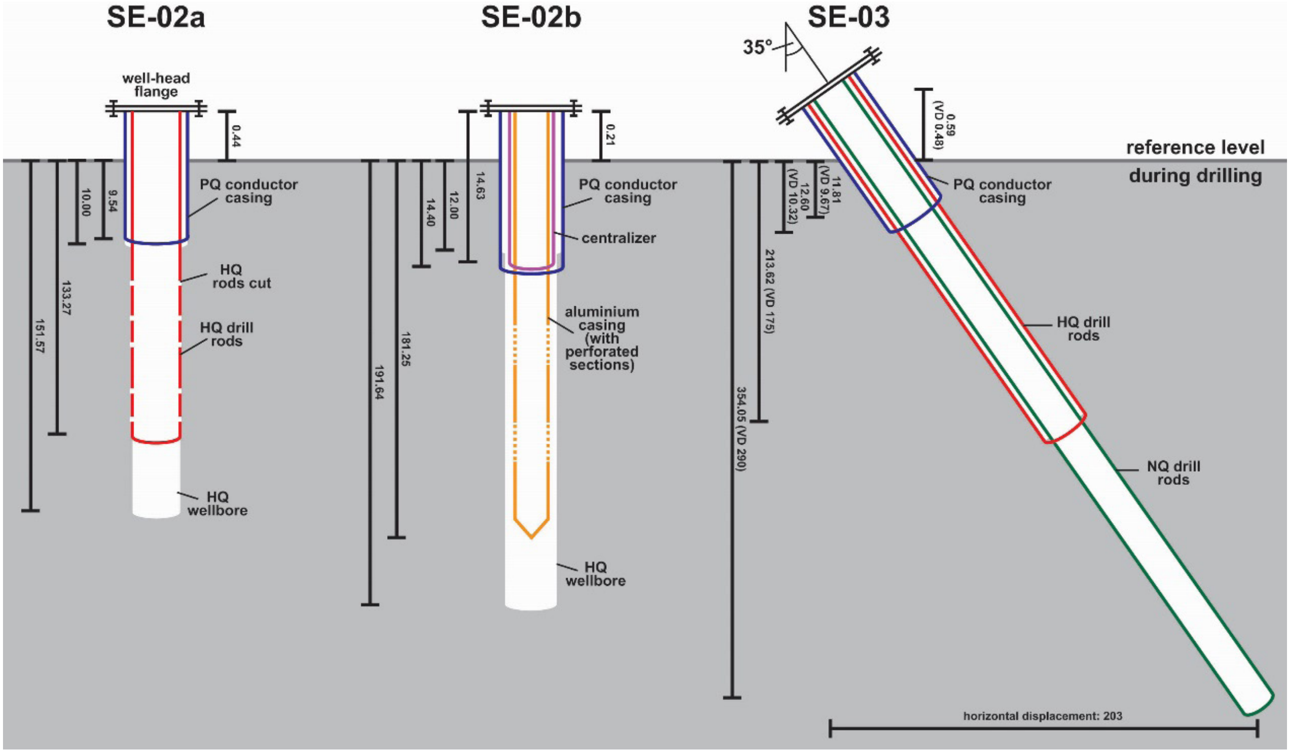

Figure 1. Schematic drawing of boreholes drilled on Surtsey in 2017. The inclined borehole dimensions are based on the planned 35° inclination (adapted from Weisenberger *et al.* 2019).

drill coring with a HQ3 bit tagged top of cement at 11.39 m. HQ coring (outer diameter: 88.9 mm, inner diameter: 77.8 mm) continued to 213.89 m measured depth, when the supply of HRQ drilling rods was fully exhausted. The HQ rods remain in the borehole to a measured depth of 213.62 m. Coring continued with an NRQ string (outer diameter: 69.9 mm, inner diameter: 60.3 mm). Coring with a NQ3 drill bit reached a total measured depth of 354.05 m. This corresponds to a presumed 290 m vertical depth below the ground surface and a horizontal displacement of about 203 m (Fig. 1). The NRQ coring string was left in the hole as permanent casing, including the NQ3 bottom-hole assembly. An extension of the HWT conductor casing was added and a flange was installed, at 0.48 m above the reference ground level. This corresponds to an additional borehole length of 0.59 m. Table 2 provides a detailed overview of the borehole design.

METHODS

Inclination measurements were carried out on August 5th, 2021, by an ÍSOR logging engineer using tools transported by helicopter to Surtsey (Fig. 2). The equipment consisted of a trip unit that was suitable for counting depth, a wireline line, logging instrument, and processing unit. The instrument was operated using the electrical generator stored at the Pálsbær II hut.

Table 2. Borehole specifications (based on Weisenberger *et al.* 2019).

Well name	**SE-03**
Total measured depth (m)*	354.05
Well-head flange height above drilling reference level (m)	0.59 (0.48 vertical height)
Total measured depth (m)**	354.64
6⅛” tricone rotary drilling (m)*	0-12.6
HQ drilling (m)* coring	11.39-213.89
NQ drilling (m)* coring	213.89-354.05
Casing information	
HWT conductor casing shoe depth (m)* (OD: 114.3 mm, ID: 101.6 mm)	11.91
HRQ drill rods left in hole (m)* (OD: 88.9 mm, ID: 77.8 mm)	213.62
NRQ drill rods left in hole (m)* (OD: 66.9 mm, ID: 60.3 mm)	354.05

* Drilling reference level, ** Reference level: flange, abbreviations: OD: Outer diameter, ID: inner diameter

Figure 2. Photograph showing ÍSOR logging engineer conducting inclination measurements of the inclined borehole (SE-03) on August 5th, 2021.

The inclination tool (SPT-08 inclinometer) is a product manufactured by SPT (Stockholm Precision Tools) with the following specifications: inclination (dip) from 0-360° to within ± 0.1°, gravity toolface from 0-360° ± 0.1°, magnetic toolface from 0-360° ± 0.2°, total magnetic field from 0-100,000 nT accurate to ± 50 nT, dip from -90° from horizontal within ± 0.2°, tool temperature (borehole temperature) from -40 °C to +125 °C accurate to ± 1 °C, pressure 80 MPa, and length dimension 1650 mm with outer diameter 42 mm (in the pressure barrel). The tool weighs 10 kg.

The logging run was planned based on the existing temperature conditions in the hole, indicating a temperature maximum of about 140 °C at a measured depth of about 145-150 m (Weisenberger *et al*. 2021).

The inclination was measured every twenty meters during the downhole logging, except for the interval between 100 and 200 m measured depth where no readings were taken. The high temperatures within this interval largely exceed the operational range of the instrument. To avoid any temperature related damage the tool was lowered through this interval as quickly as possible. This was successful as no damage occurred.

Individual measurements were also made on the outrun, which confirmed the data obtained during the inrun measurements.

RESULTS

The results of the inclination measurements are shown in Table 3 and Figure 3. The data show a slight deviation from the planned inclination of 35°,

Table 3. Inclination measurements conducted on August 5th, 2021, comparison with planned inclination of 35°.

Depth	Inclination (from vertical)	Vertical depth	Vertical depth 35°	Vertical error (m)	Horizontal displacement	Horizontal length (35°)	Horizontal error (m)
0.00	36.54	0	0	0.00	0	0	0.00
10.00	36.39	8.0	8.2	-0.15	5.9	5.7	0.21
20.00	36.32	16.1	16.4	-0.29	11.9	11.5	0.38
40.00	35.56	32.3	32.8	-0.48	23.5	22.9	0.53
60.00	34.88	48.6	49.1	-0.52	34.6	34.4	0.19
80.00	34.40	65.1	65.5	-0.45	45.5	45.9	-0.41
100.00	34.24	81.6	81.9	-0.32	56.4	57.4	-0.98
200.00	32.70	165.0	163.8	1.19	110.3	114.7	-4.42
220.00	32.21	181.9	180.2	1.68	118.1	126.2	-8.13
240.00	32.36	198.8	196.6	2.21	128.2	137.7	-9.47
260.00	32.40	215.7	213.0	2.71	139.2	149.1	-9.89
280.00	32.40	232.6	229.4	3.22	150.0	160.6	-10.57
300.00	32.48	249.5	245.7	3.71	160.9	172.1	-11.15
320.00	33.16	266.3	262.1	4.14	173.4	183.5	-10.10
340.00	33.44	283.0	278.5	4.47	186.7	195.0	-8.35
354.05*	33.44	294.7	290.0	4.68	195.1	203.1	-7.97

*projected using same angle as at depth 340 m

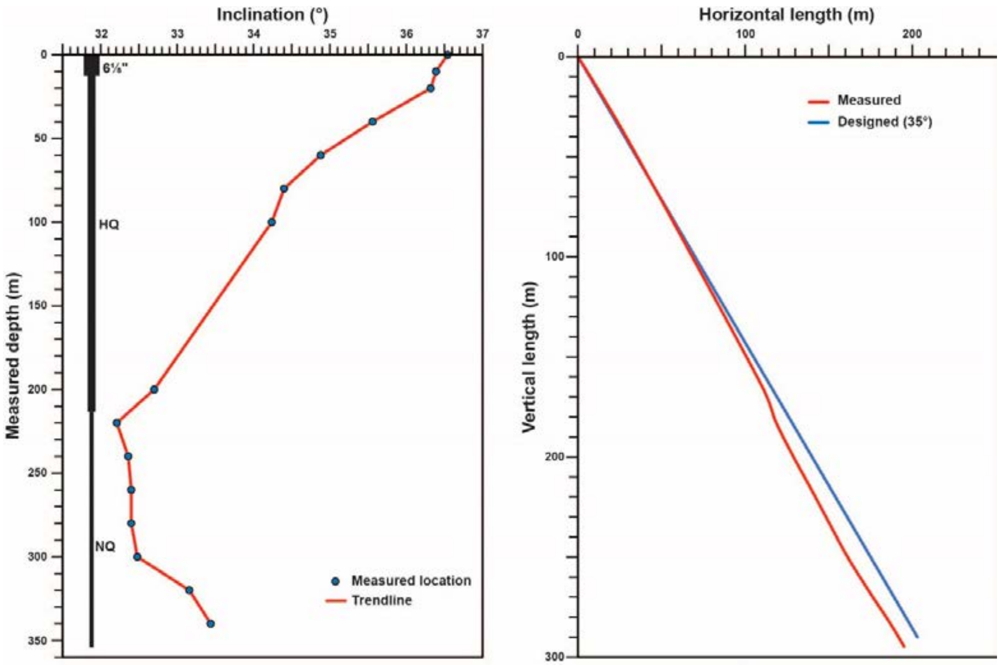

Figure 3. Diagram showing the measured inclination of the SE-03 borehole (left). The right graph shows the planned borehole path in comparison with the measured borehole path.

with the measured values ranging between 32.2° and 36.5°. This range is within the expected error margin for the drilling.

At the top, the borehole is inclined at a slightly higher angle, 36.5°, compared to the planned angle of 35°. With increasing depth and HQ drilling, the borehole inclination drops slightly by about 2° per 100 m measured depth. At 220 m measured depth the borehole has an inclination of 32.2°. The borehole inclination then increases again, at a rate of approximately 1° per 100 m measured depth. Overall, the average inclination is 33.4±0.2° from the surface to the bottom of the borehole. We cautiously assume that the average error in inclination may be 0.2°.

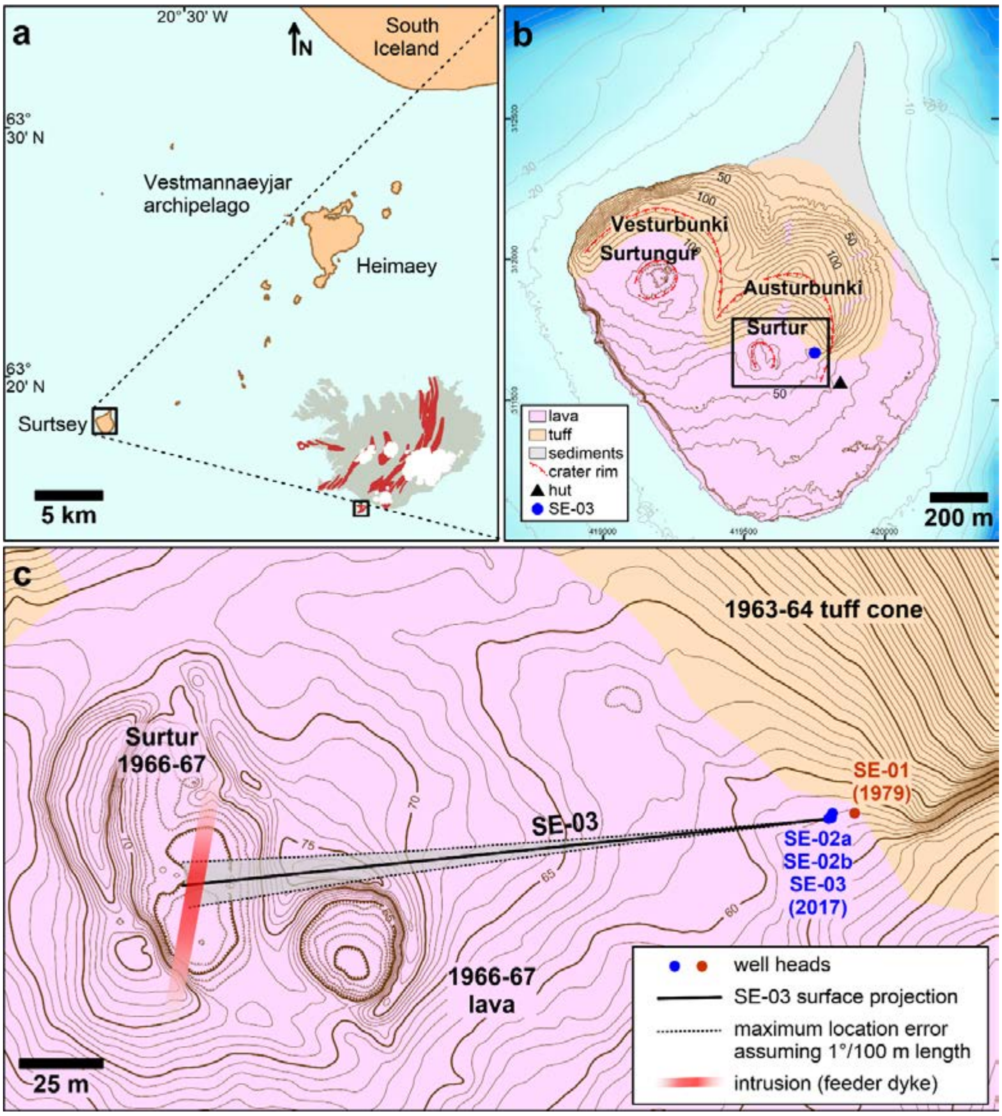

Figure 4. Location maps. (a) Vestmannaeyjar archipelago and Surtsey volcano. (b) The island of Surtsey. (c) Location of the inclined borehole SE-03 and its relation to the Surtur crater of 1966-67. The location of the intrusion encountered at 343-352 m measured depth is indicated with its likely orientation, based on Sigurður Þórarinsson's measurements of the 1966 volcanic fissure.

A build-up of inclination is observed within the section drilled with the smaller diameter NQ3 bit. The change of drilling diameter from HQ to NQ occurred at a measured depth of 214 m (Figure 3, Table 2). The change in the inclination trend from dipping to building up inclination at 220 m can apparently be related to the drilling activity and associated reduction of borehole diameter. The HQ drill pipe remained in the borehole, while drilling with the NQ3 bit commenced. Drilling with a smaller string and within a casing-supported upper section are plausible explanations for the observed change in inclination.

The measured difference in vertical orientation for the HQ section corresponds to an increase of 1.7 m at the end of the drilled section. A greater deviation in orientation results in a higher rate of vertical displacement for the NQ section. The corrected vertical depth at the bottom of the borehole is 294.7±1.2 m. This is 4.7 m deeper than the designed borehole path (Tables 2 and 3). The discrepancy in horizontal direction follows the same trend. The bottom of the borehole thus has a horizontal displacement of 195.1±1.0 m, about 8 meters less than the designed path of 203.1 m.

Figure 4 shows the surface projection of SE-03. The location of the approximately 5 m wide intrusion entered at a measured depth of 343-352 m (Weisenberger *et al*. 2019) is shown, using the initial trend of the eruptive fissure (N10°E) as measured by Sigurður Þórarinsson on August 20,1966 (Thorarinsson 1967) to indicate its likely trend. The intrusion lies directly beneath the Surtur crater, consistent with it being the feeder dyke of the 1966-67 eruption. Again, using a maximum error of 0.2° for the average angle, the uncertainty in the dyke location is ±1 m.

SUMMARY

Measurements of the actual angle from vertical of the SE-03 cored borehole drilled on Surtsey in 2017 used a STP-8 inclinometer, carried out on August 5th, 2021. The results show that deviations from the planned angle of 35° from vertical are minor, with an average 33.4±0.2° inclination of the hole from vertical. The vertical depth of the bottom of the borehole at 354.05 m measured depth is 294.7±1.2 m and the horizontal length from the drill head to the point vertically above the bottom is 195.1±1.0 m. By correcting for the 1.4-1.8° discrepancy between the planned inclination and the actual value, greater accuracy in the location of the lithological units in the SE-03 core is achieved. However, this discrepancy is minor and does not affect the overall interpretation of the core. In particular, the results strongly support the interpretation that the intrusion at a measured depth of 343-352 m is the feeder dyke of the Surtur 1966-67 eruption.

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REFERENCES

Jackson, M.D., M.T. Gudmundsson, W. Bach, P. Cappelletti, N.J. Coleman, M. Ivarsson, K. Jónasson, S.L. Jorgensen, V. Marteinsson, J. McPhie, J.G. Moore, D. Nielson, J.M. Rhodes, C. Rispoli, P. Schiffman, A. Stefánsson, A. Türke, T. Vanorio, T.B. Weisenberger, J.D.L. White, R. Zierenberg & B. Zimanowski. 2015. Time-lapse characterization of hydrothermal seawater and microbial interactions with basaltic tephra at Surtsey Volcano. Scientific Drilling 20, 51-58.

Jackson, M.D., M.T. Gudmundsson, T.B. Weisenberger, J.M. Rhodes, A. Stefánsson, B.I. Kleine, P.C. Lippert, J.M. Marquardt, H.I. Reynolds, J. Kück, V.T. Marteinsson, P. Vannier, W. Bach, A. Barich, P. Bergsten, J.G. Bryce, P. Cappelletti, S. Couper, M.F. Fahnestock, C.F. Gorny, C. Grimaldi, M. Groh, Á. Gudmundsson, Á.T. Gunnlaugsson, C. Hamlin, T. Högnadóttir, K. Jónasson, S.S. Jónsson, S.L. Jørgensen, A.M. Klonowski, B. Marshall, E. Massey, J. McPhie, J.G. Moore, E.S. Ólafsson, S.L. Onstad, V. Perez, S. Prause, S.P. Snorrason, A. Türke, J.D.L. White & B. Zimanowski, 2019. SUSTAIN drilling at Surtsey volcano, Iceland, tracks hydrothermal and microbiological interactions in basalt 50 years after eruption. Scientific Drilling 25, 35-46.

Jakobsson, S.P. & J.G. Moore, 1982. The Surtsey Research Drilling Project of 1979. Surtsey Research Progress Report IX, 76-93.

McPhie, J., J.D.L. White, C. Gorny, M.D. Jackson, M.T. Gudmundsson & S. Couper, 2020. Lithofacies from the 1963-1967 Surtsey eruption in SUSTAIN drill cores SE-2a, SE-2b and SE-03. Surtsey Research 14, 19-32.

Moore, J.G., 1985. Structure and eruptive mechanism at Surtsey Volcano, Iceland. Geological Magazine 122, 649-661.

Thorarinsson, S., 1967. The Surtsey eruption. Course of events during the year 1966. Surtsey Progress Report III, 84-90.

Weisenberger, T.B., M.T. Gudmundsson, M.D. Jackson, C.F. Gorny, A. Türke, B.I. Kleine, B. Marshall, S.L. Jørgensen, V.T. Marteinsson, A. Stefánsson, J.D.L. White, A. Barich, P. Bergsten, J.G. Bryce, S. Couper, M.F. Fahnestock, H. Franzson, C. Grimaldi, M. Groh, Á. Gudmundsson, Á.T. Gunnlaugsson, C. Hamelin, T. Högnadóttir, K. Jónasson, S.S. Jónsson, A. Klonowski, J. Kück, R.L. Magnússon, E. Massey, J. McPhie, E.S. Ólafsson, S.L. Onstad, S. Prause, V. Perez, J.M. Rhodes & S.P. Snorrason, 2019. Operational Report for the 2017 Surtsey Underwater volcanic System for Thermophiles, Alteration processes and INnovative concretes (SUSTAIN) drilling project at Surtsey Volcano, Iceland. GFZ German Research Centre for Geosciences.

Weisenberger, T.B., S. Prause, C.F. Gorny, B.I. Kleine, P. Bergsten, A.M., Klonowski, V. Perez, A. Barich. M.T. Gudmundsson, K. Jónasson, V. Marteinsson, A. Stefánsson, M.D. Jackson & Surtsey OnSite Team, 2021. The SUSTAIN ICDP Drilling Project on Surtsey. Proceedings World Geothermal Congress 2020+1, Reykjavik, Iceland. http://www.geothermal-energy.org/pdf/IGAstandard/WGC/2020/12068.pdf.

Fifty year evolution of thermal manifestations at Surtsey Volcano, 1968 – 2018

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ABSTRACT

The geothermal activity in Surtsey over the decades provides a very valuable record of the evolution of a volcanic geothermal system following its development and its relation to the process of palagonitization. The present study compiles all published as well as unpublished data on the surface manifestations of geothermal activity and measurements in the drill hole completed in 1979, to give a comprehensive account of the evolution of the thermal area at Surtsey during the period of 1968-2018. Most of this work was done by the late Sveinn P. Jakobsson. Overall, the time series demonstrates a slow but clear trend of cooling of Surtsey with time: the thermal activity within the lava rapidly cooled from recorded emission temperatures in fumaroles of up to 460°C in 1970, to ambient temperatures within 30-40 years after emplacement. In contrast, the thermal area within the tephra/tuff exhibits a gradual onset of geothermal activity. The onset on Surtur (Austurbunki) was first detected in 1968 and high temperatures still prevail at the surface where temperatures have only declined from 100 to 80-90 °C in 50 years. The onset on Surtungur (Vesturbunki) was detected in 1974 and the maximum temperatures recorded have remained within the 90-100 °C range since 1979. The intermediate area between Surtur/Austurbunki and Surtungur/Vesturbunki has exhibited activity broadly in the same way as Surtur/Austurbunki and maximum temperatures that remained within the 90-100 °C range from 1979-2000, are now clearly declining. Maximum temperatures in the 1979 drillhole were 141 °C in 1980 but they have been steadily declining, reaching 123 °C in 2018.

INTRODUCTION

The volcanic island of Surtsey forms part of the Vestmannaeyjar volcanic system at the southern end of Iceland’s Eastern Volcanic Zone. Surtsey’s volcanic eruption is estimated to have started about 40 hours before the first visible explosive activity broke the sea surface on November 14, 1963 (Sayyadi *et al*. 2021). During this four and a half month long phreatomagmatic explosive phase, tephra of alkali olivine-basalt composition was produced. The deposition of the tephra resulted in the formation of the two crescent-shaped cones (Fig. 1) of Austurbunki (at the time of the eruption the name Surtur I was used - Thorarinsson, 1965) and Vesturbunki (previously named Surtur II), each with a diameter of about 400 m and a height of 150 – 170 m above sea level. (Jakobsson & Moore 1982).

The names of localities have evolved with time since the Surtsey eruption. The two vents that formed on Surtsey were originally called Surtur I and Surtur II. This was then changed to Surtur for the eastern lava crater and Surtungur for the western lava crater, and in later years, the tephra cones have been called Austurbunki and Vesturbunki, while Surtur and Surtungur are still used for the lava vents. For simplicity, and ease of reference to some of the early publications, we use the names Surtur for the

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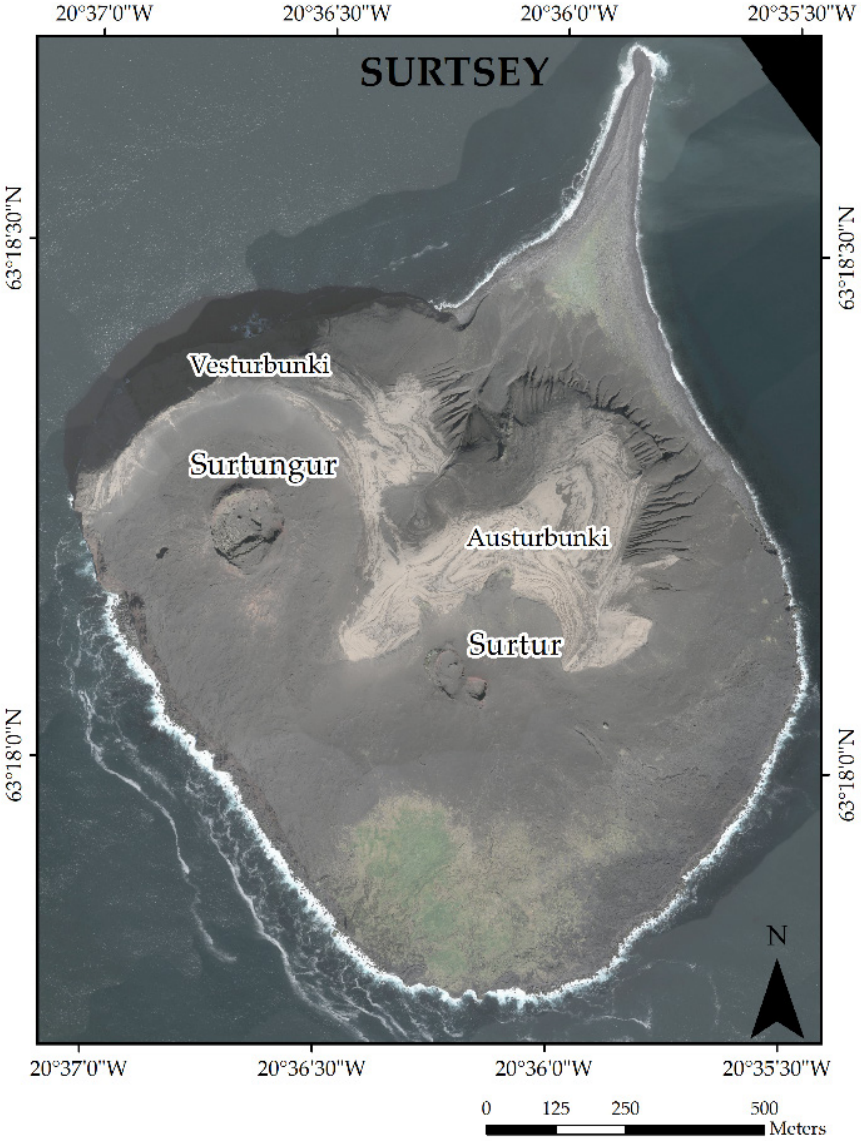

Figure 1. Aerial photograph of Surtsey taken in September 2018 (Loftmyndir ehf. 2018).

present day Austurbunki+Surtur, and Surtungur for Vesturbunki+Surtungur. Care is taken to differentiate between the tephra cones and the lava craters in the text.

On April 4, 1964, when seawater could no longer access the Surtungur vent (Surtur II), the eruption style changed from explosive to effusive, forming the Surtungur lava crater. Lava deposition on Surtsey occurred in three distinct phases (Jakobsson & Moore 1982). The first one lasted 13 months (April 1964-May 1965), building a lava shield. This eruptive phase was followed by a 15-month hiatus of activity on the Surtsey island, as explosive, phreatomagmatic activity built the new islands of Syrtlingur and Jólnir, both of which were quickly washed away by marine erosion (e.g., Thorarinsson 1968). The second phase of effusive activity on Surtsey lasted about 10 months (August 1966-June 1967), when a 220 m long fissure opened along the floor of Surtsey's eastern crater. The third phase occurred in December 1966-January 1967 when new fissures became active, and lava broke through at four additional sites in Austurbunki tephra cone. These third phase eruptions were all very minor (Baldursson & Ingadóttir 2007). When the volcanic activity on Surtsey finally ceased on June 5, 1967, the oceanic island that formed reached 175 m above sea level. Considering that the sea water depth before the eruption had been about 130 m, the total height of Surtsey volcano was 305 m in 1967 (Jakobsson 1972).

The island of Surtsey has changed considerably since the end of the eruption in 1967. Its shape is constantly modified by the harsh conditions of intense wave action in winter, prevailing in the sea south of Iceland (Jakobsson & Moore 1982). In 1968, Thorarinsson estimated that by the end of the eruption in 1967, Surtsey had reached a size of 2.65 km^2 and that the total production of eruptives during the eruption was 1.1 km^3, about 60-70 % of which was tephra (Thorarinsson 1969). By 2019, gradual erosion of the island had reduced its size to 1.22 km^2 (Óskarsson *et al.* 2020).

One of the main objectives of the initial studies at Surtsey was to closely follow the processes of consolidation and palagonitization of basaltic tephra to describe how these processes take place under the local physical conditions (Jakobsson & Moore 1982). Since its formation, Sveinn P. Jakobsson visited the island almost every year. He frequently inspected the area of primary tephra and sampled various localities to determine the start and the conditions of the expected process of consolidation and palagonitization of the tephra (Jakobsson & Moore 1982).

The first signs of consolidation in the tephra were observed in August 1966 in a few places such as the top of Surtur. When this observation was made, only the outermost 10-15 cm of the exposed tephra layers were consolidated. This was believed to be the result of the frequent oscillations in temperature and moisture that the surface experienced, as it faced the main direction of precipitation and sun exposure (Jakobsson & Moore 1982). In April of 1968, Sigurður Thorarinsson discovered heating of tephra with emanations of steam at the surface of Surtur (Jakobsson 1978). Additionally, this thermal anomaly was also observed in the infrared images taken on August 22, 1968, during a study conducted by Friedman and Williams (1970). It was then suggested that a geothermal system was being developed as a consequence of intrusive activity in the eastern tephra crater during December 1966-January 1967 (Jakobsson & Moore 1986).

A year after the thermal anomalies were discovered, Sveinn P. Jakobsson observed the first signs of palagonitization on the surface at the southeast corner of Surtur in September 1969. The geothermal activity caused the basalt tephra to alter rapidly into palagonite. Consequently, upon the discovery of the first signs of palagonitization, a program was established to monitor the expansion of palagonite tuff on Surtsey (Jakobsson 1972). This was the first time that the process of palagonitization was monitored in a natural setting (Jakobsson 1972, Jakobsson 1978). The program consisted of measuring areas of tephra and tuff on average every third year. Rock samples were taken and the expanding area of palagonite tuff was mapped in every expedition (Jakobsson 1978, Jakobsson *et al.* 2000).

The palagonitization and consolidation rates of the Surtsey tephra were estimated by Sveinn P. Jakobsson based on surface observations made during the period of 1969 – 1977. The results indicated that at 100 °C, it takes one to two years for the tephra within the greater part of the tephra cone above sea level, to convert into dense palagonitized tuff with the volume fraction of palagonite exceeding 10%. However, the rate of palagonitization was considerably slower at lower temperatures, particularly where the temperature had dropped below 40 °C (Jakobsson 1978).

In 1979, a 181 m deep hole was drilled, and a core extracted through the eastern rim of the Surtur tephra cone (present day Austurbunki), reaching close to the pre-eruption seafloor. This scientific drilling project was originated because of the exceptional opportunity to study the development of a historic, well-studied, oceanic volcano from its inception on the seafloor, through the formation of a volcanic island, to the modification of the volcanic edifice by geothermal processes (Jakobsson & Moore 1982). A second drilling program took place in 2017, the ICDP-supported SUSTAIN project where three cores were extracted at the same location as the 1979 drillhole to further study the structure and evolution of the island (Jackson *et al.* 2019, Weisenberger *et al.* 2019, Prause *et al.* 2020, Kleine *et al.* 2020, McPhie *et al.* 2020, Bergsten *et al.* 2021). The present study contributes to the overall aim of this work of documenting and further understanding the evolution of a volcanic island after its formation.

METHODS

During these geologic expeditions, the surface of Surtsey has been mapped in detail using conventional methods to follow the extent of the thermal area and the extent of the palagonite tuff. The first temperature measurements were performed by Sveinn P. Jakobsson in September 1969, and by August 1970, the thermal field was mapped in detail for the first time (Jakobsson 1972). Ævar Jóhannesson, at the Science Institute of the University of Iceland, contributed significantly to the mapping of the thermal area in 1970 and 1975, by making temperature measurements on both Surtur and Surtungur’s tephra and lava fields (Jóhannesson 1972, Jóhannesson 1978).

Throughout four decades, Sveinn P. Jakobsson continued to perform thermal surveys and contribute to the logging of the surficial temperatures of the geothermal area. His records show that conventional mapping was performed until 2006, when more modern techniques started to be implemented. After Jakobsson’s last visit to Surtsey in 2008, Icelandic Institute of Natural History (IINH) geologists, Lovísa Ásbjörnsdóttir and Kristján Jónasson, took over the thermal monitoring. Additionally, the 2018 survey was conducted by Velveth Perez, as a part of her master’s by research project at the University of Iceland.

Here the term palagonite is used as a synonym for altered, hydrated, basaltic glass, of brown or yellow color. The term is related to the alteration process,

Figure 2. Images taken during the 2018 thermal survey: A) Photograph of a steaming fissure located at the top of Surtungur tephra cone (Vesturbunki). B) Temperature measurement taken with the thermocouple sensor-stick. C) Trimble tablet with integrated GPS allows logging of the temperature reading. D) Additional record of the temperature measurement coordinates made with handheld GPS.

called palagonitization. Móberg (palagonite tuff), is an Icelandic term for brownish, consolidated tephra, of basaltic or intermediate composition (Jakobsson 1978, Stroncik & Schmincke 2002). Thermal field refers to the area at the surface of Surtsey that presents thermal anomalies.

During the most recent geologic expeditions at Surtsey, the thermal surveys are completed using an electronic thermometer that features an infrared sensor with a laser pointer, and a temperature-sensor thermocouple stick attachment (Fig. 2). In addition to a Trimble tablet with integrated GPS, the exact location of the temperature measurements is logged with the aid of a handheld GPS. This technology has improved the monitoring surveys by replacing the conventional mercury thermometers and the topographic paper maps that were used in the past.

As a consequence of the highly consolidated state of the palagonite tuff, temperature measurements are taken along a network of open fissures that are located throughout Surtur and Surtungur's palagonitized tuff cones. This network is clearly noticeable due to their elevated topography in contrast with the surrounding area, as well as the altered coloration of most of the fissures. In some cases, these active fissures also present condensation and emanation of steam. The temperature measurements in the open active fissures are performed by introducing the thermocouple temperature-sensor stick deep (approx. 15-20 cm) into the ground. A fair number of fissures are non-active and have been closed by scaling that has been deposited along the opening. Surface temperatures of these closed fissures were logged using an infrared laser gun thermometer.

Nineteen original paper maps that are part of the unpublished data by Sveinn P. Jakobsson on the surface manifestations of the thermal activity were digitized using GIS software. Nine additional maps were created with the temperature data that is available in the digital record of the IINH. Jakobsson's geological maps of Surtsey in scale 1:5000 were used and different features of the thermal manifestations that he tracked during the thermal monitoring surveys include: the palagonite tuff, thermal area extension, steaming fissures and temperature measurements. Additionally, the extent of the palagonite tuff was mapped with the aid of aerial photographs taken usually every other year.

The extent of the thermal area and how it changes with time is an important parameter in describing the evolution of Surtsey. In this study, the area at any given time is defined with three methods: when available, with the 20 °C isotherm line; with the defined area according to Jóhannesson's (1972) and Jakobsson's field data; and with thermal data extrapolation to 20 °C.

During the spatial and temporal analysis of the thermal area at Surtsey, the maximum temperatures recorded for the lava and the tephra are listed separately to monitor their course individually. For better comprehension and due to its volume and extent, the tephra thermal region is further subdivided into three separate areas: the Surtur (Austurbunki) tephra cone, the Surtungur (Vesturbunki) tephra cone, and the intermediate tephra zone. Six thermal survey maps from the following years were chosen for further analysis due to their substantial amount of thermal data in comparison with the rest: 1970, 1979, 1988, 2000, 2011, and 2018. The time elapsed between these surveys is suitable for analysis of the progression of the thermal area and its manifestations.

Additionally, the temperature in the 181-m-deep drill hole from 1979 has been monitored regularly for the past forty years by measuring the temperature. The record shows seventeen logs. However, only five of these will be used in this study to tie the evolution of the surface manifestations of the geothermal system to the subsurface temperatures: 1980, 1990, 2000, 2009, 2018. These surveys were strategically chosen to be about one decade apart.

RESULTS

The lava fields

Surtungur: The thermal data shows that the maximum recorded temperature of vapor/gas emitting from fissures in the Surtungur's lava pile was 460 °C in 1970 (Fig. 3) (Jóhannesson 1972), about 40% of the initial magma temperature estimation of 1150 °C. Vapor emissions decreased rapidly, and in 1974, the highest temperature recorded reached 160 °C (data not shown).

Temperatures remained constant for some years, until a slow increase was observed between 1983 – 1985 (data not shown). An even slower but steady decrease in temperature began after that. A substantial gap in the thermal record of the entire lava thermal region was observed for most of the 1990's, and by the year 2000, the maximum temperature recorded was already down to near-ambient values with a maximum of 16 °C (Fig. 3). No thermal anomalies were observed in the lava fields in 2018.

Surtur: The thermal record for Surtur's lava field was not as consistent nor as complete as the monitoring of the thermal area on Surtungur. The maximum temperature found within Surtur's lava field in 1970 reached 63 °C, at a location within a fissure that had been active in January 1967 (Fig. 3). Additionally, Jakobsson's thermal records from this area focused on the fissures located at the slopes of the tephra cone (Austurbunki). The highest maximum temperature value of 100 °C was recorded in 1979-1980 (Fig. 3). This temperature measurement was not from the lava field and was taken from vapor emitted from a fissure that is located within Surtur's cone inner wall.

The maximum temperature values oscillate during the following years and the recorded temperature never reached similarly high values again. Regardless of these temperature fluctuations, an overall decrease in temperature was observed in the thermal record and the last surface temperature measurement was taken in 2008, at a value of 55 °C (data not shown).

The Surtur (Austurbunki) tephra cone

The first thermal survey made on the tephra formation was done in November 1969. At that time, the maximum temperature at the surface of Surtur´s tephra cone was 84 °C. By the following year, temperature values between 98 °C and 100 °C were reported by Ævar Jóhannesson (1972) and Sveinn P. Jakobsson (1972), near the location where the first signs of palagonitization were observed (Fig. 3). In August 1970, only the inner wall of Surtur's tephra cone showed consolidation, and within this consolidated area, an even smaller volume of tephra showed signs of palagonitization.

The thermal records of the following years showed a period of substantial temperature fluctuations during the first decade after the onset of the thermal activity. Surface temperature values gained stability in 1979 and temperatures stayed within 90– 98 °C until 1992. There was a substantial gap in the data for the following years, but a survey performed in 2000 placed the maximum temperature value at 98 °C (Fig. 3). Another period of stable temperatures within the 84 – 100 °C range began in 2008 (data not shown). Surface temperature measurements made in 2018, placed the maximum temperature value at 88.9 °C (Fig. 3). Additionally, most of Surtur's tephra cone had been palagonitized, except for the distal parts of the eastern and the north-facing slopes where the tephra still presented a very low degree of consolidation.

The Surtungur (Vesturbunki) tephra cone

In 1970, the maximum temperature recorded in Surtungur's tephra only went as high as 10 °C (Fig. 3). Temperature values for the next few years presented an overall increase and by 1979, the temperature reached 98 °C (Fig. 3). There was a period of stable values, within the 90-99 °C range, during the following decade, and a temperature of 100 °C was reached in 1992 and 2008 (data not shown). The maximum temperature value that was measured during the 2018 thermal survey reached 92.4 °C (Fig. 3) and by then, palagonitization had altered Surtungur's entire inner wall. If the geothermal activity continues in this area, palagonitization can be expected to fully cover the north-facing slope of the cone in the years to come. Additionally, a value of 88.9 °C was measured at the top of Surtungur's rim during the thermal survey performed in 2018 (Fig. 3)**.**

The intermediate tephra zone

The thermal record for the zone where the Surtungur tuff cone overlaps the Surtur cone is referred in this study as the intermediate tephra geothermal area. Thermal activity has been observed within this zone since the onset of the thermal manifestations at the surface of the tephra in 1968. The first thermal monitoring performed in 1969 covered this area and placed the maximum temperature value at 80 °C (data not shown). Between 1969 and 1976 the thermal record showed a substantial temperature fluctuation around 85 °C, within the 15 – 100 °C range. In 1979, maximum temperatures gained stability, with values staying within the 90 – 100 °C range (Fig. 3). This continued until 2000, when the maximum temperature value dropped to 80 °C (Fig. 3). Fluctuations were also observed in the following years, but in 2018 the maximum temperature value was still 80 °C (Fig. 3).

Changes in the extent of Surtsey's thermal field

Using a combination of Jakobsson and Jóhannesson's (1972) records, the surface area of the thermal heat anomaly was calculated to be around 0.42 km^2 in 1970 (Fig. 4e). At this time, most of the anomaly was concentrated within the lava thermal region, specifically that of Surtungur's lava field and in the small craters in the tephra cone that erupted for a few days in 1966/67. The surface manifestations were present on Surtur's tephra cone as well as the intermediate tephra zone, but only ambient temperatures were recorded at the surface of Surtungur's tephra cone (Fig. 3).

In 1979, the surface manifestations of the thermal heat anomaly covered a surface area of about 0.39 km^2 (Fig. 4e) Spatial analysis placed the largest extent of the thermal anomalies within the entire tephra region. A decrease in surface area was observed in the following years, especially within the lava thermal region (Fig. 3). By 1988, the extent of the thermal heat only covered about 0.01 km^2 of the lava region (Fig. 4a), and the entire thermal field had been reduced to 0.33 km^2 (Fig. 4e).

In 2000, the lava thermal region presented only ambient temperatures (Fig. 3). At this time, the thermal field was 0.21 km^2 (Fig. 4e) and most of its manifestations were localized at the surface of Surtur's tephra cone (Fig. 3). A considerable change in the extent of the thermal field was also observed in 2011. The entire thermal field was then confined to 0.04 km^2 (Fig.4e) along the rim of both tephra cones (Fig. 3). Additionally, the thermal anomaly of the lava field region had completely disappeared (Fig. 3).

The 2018 spatial and temporal analysis of the field observations and temperature measurements placed the extent of the thermal field at about 0.021 km^2 (Fig. 4e). Most of the manifestations were still observed along the rims of both tephra cones.

Surtsey 1979 drill hole analysis

The temperature measurements that have been gathered in the 181-m-deep drill hole since 1980 have shown a general cooling trend of the geothermal system deep inside the island with a

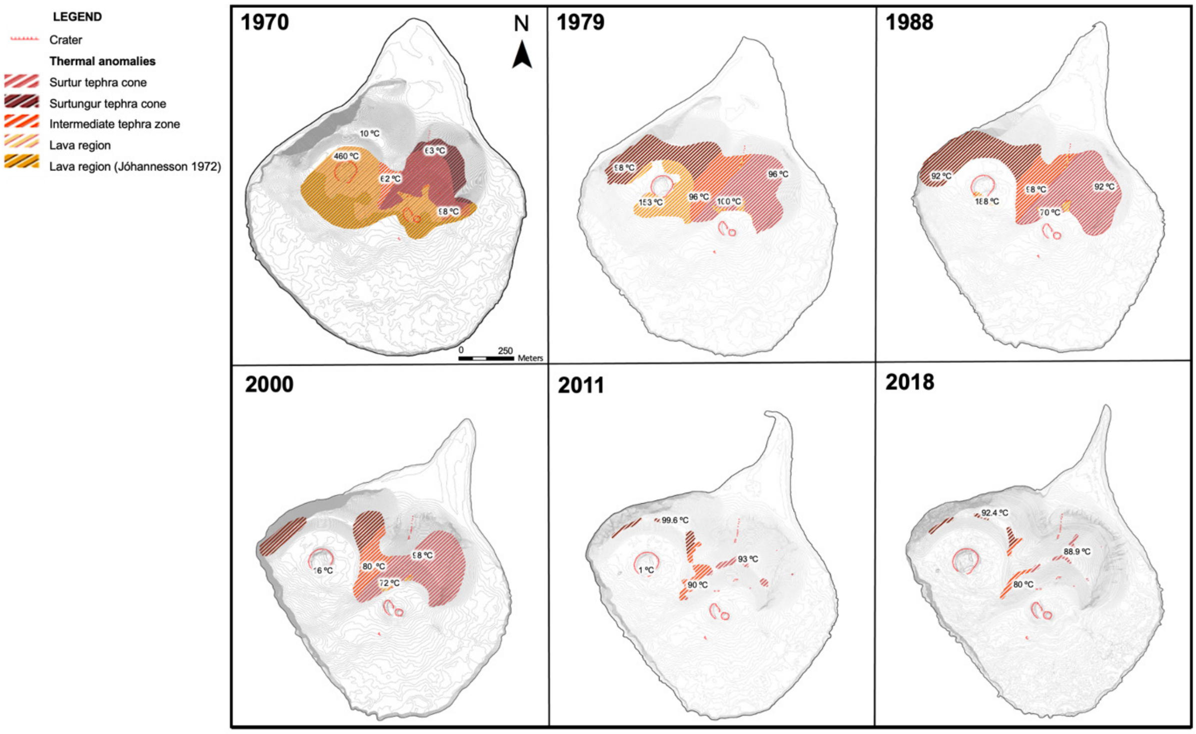

Figure 3. Extent of thermal field from 1970 to 2018, according to Jakobsson's map records and later survey data, and Jóhannesson's thermal survey (1972). Different colors correspond to different locations.

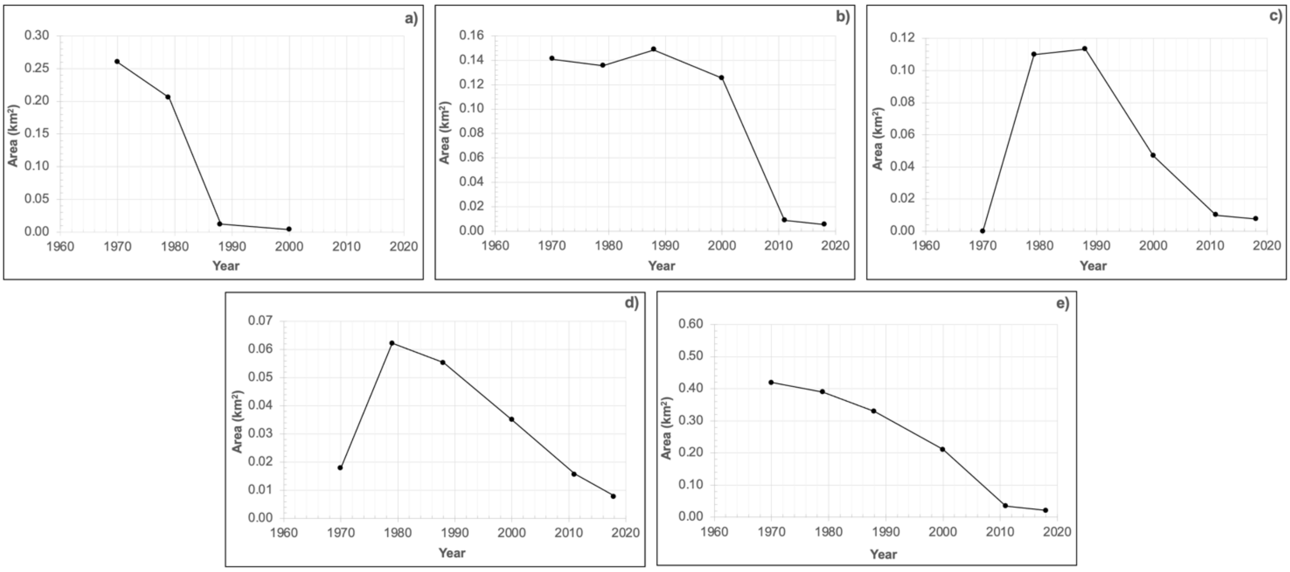

Figure 4. a) Extent evolution of the thermal area in the lava field region. The largest surface area is observed in 1970. A markedly decrease in surface area follows and by 2000, the thermal anomalies at the surface of the lava fields are about to disappear. **b)** Thermal evolution of Surtur's tephra/tuff geothermal area from 1969-2018. A gradual decrease in surface area is observed since 1969 with a marked decrease in the period from 1988-2011. **c)** Thermal evolution of Surtungur's tephra/tuff geothermal area from 1969-2018. A steep increase in the surface area is observed from 1969–1988, followed by a gradual decrease that is still observed by 2018 when the thermal manifestations on Surtungur declined to 0.008 km^2. **d)** Thermal evolution of the intermediate tephra/tuff zone geothermal area from 1969-2018. A steep increase in the surface area is observed from 1969–1979, followed by a gradual decrease that is still observed by 2018 when the thermal manifestations only extended as far as 0.008 km^2. **e)** The surface evolution of the extent of the entire thermal field on Surtsey. The surface area was largest in 1970, 0.42 km^2, but gradually decreased after that. Based on the thermal survey performed in 2018, the extent of the thermal field is about 0.02 km^2. Note the different scaling on the y-axes of the diagram.

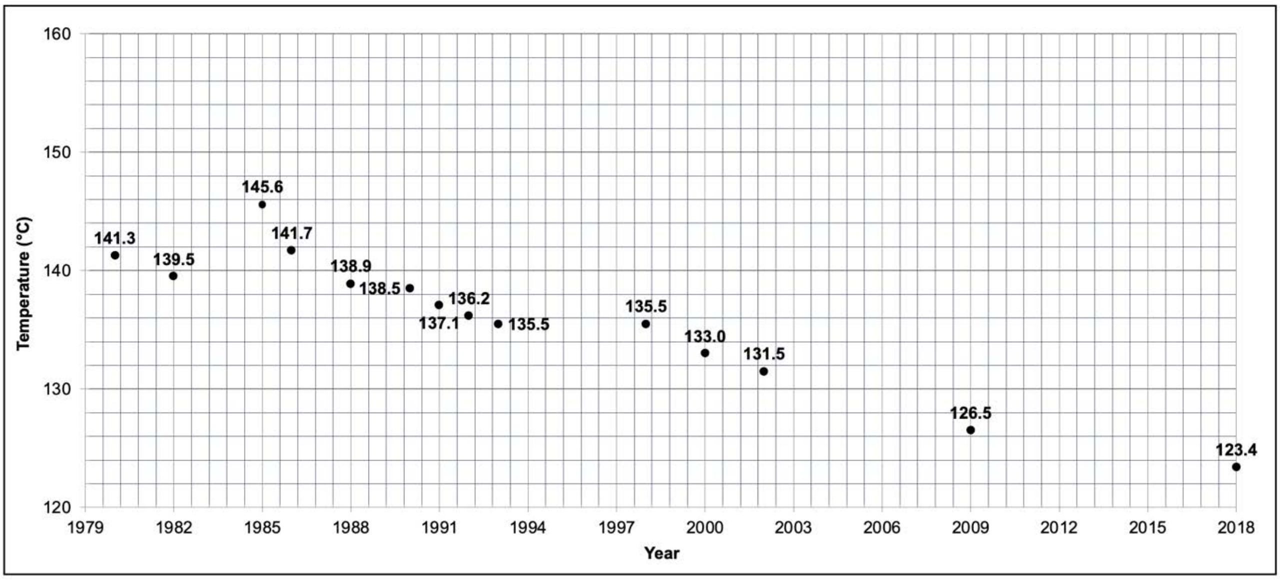

Figure 5. Graph showing the maximum temperatures measured in the 1979 drill hole during 39 years of thermal monitoring. Note that the y-axis only shows 120-150 °C.

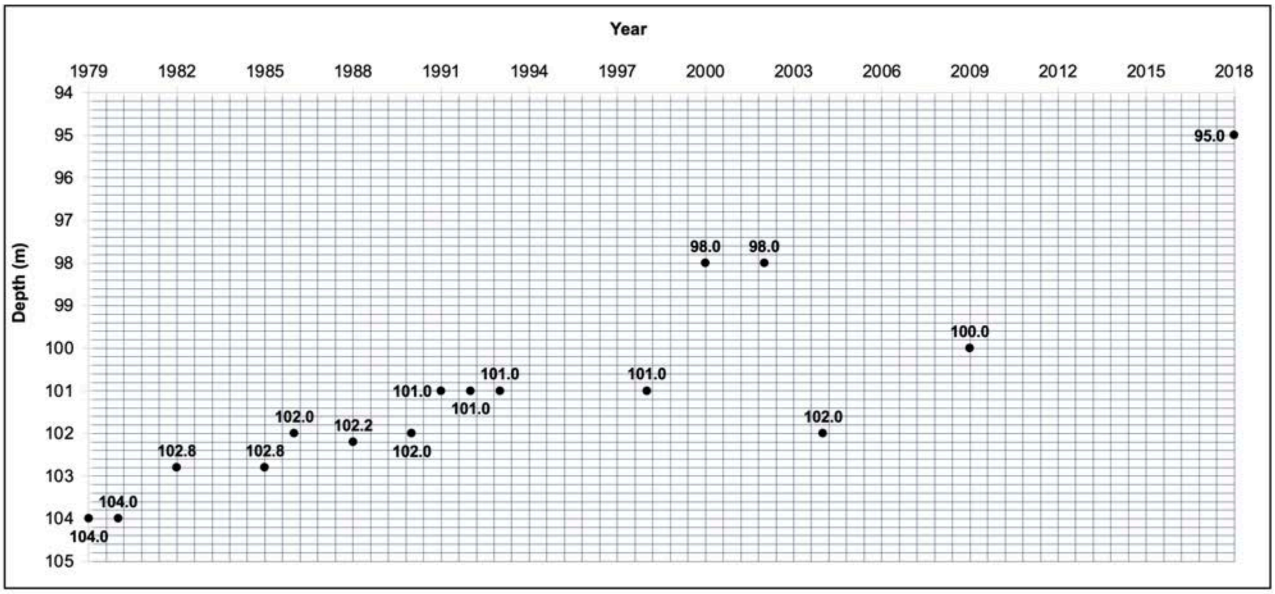

Figure 6. Graph showing the depth at which the maximum temperature zone is reached during 39 years of thermal monitoring. Note that the y-axis only shows the depth range of 94-105 m.

general cooling rate of less than 1° C per year (Fig. 5). The initial temperature measurement placed the maximum temperature of the geothermal system at about 100 m depth with values that measured up to 141.3 °C in 1980 (Fig. 5) while the maximum temperature recorded in 2018 was only as high as 123.4 °C at 95 m (Figs. 5 and 6). This accounts for an 18 °C drop in the maximum temperature in a 38-year period, giving a mean decrease of ~0.5 °C per year. Temperature profiles from 1980, 1990, 2000, 2009, and 2018 reached a maximum temperature zone at about 100 m depth (Fig. 6 and 7). Temperatures decreased below that to about 40 °C as depth reached 180 m (Fig. 7).

DISCUSSION

During the fifty years period of observations, it has not only been possible to document the evolution of the thermal activity at the surface of Surtsey, but also to follow closely the processes of consolidation and palagonitization of basaltic tephra and describe how they take place under the local physical conditions.

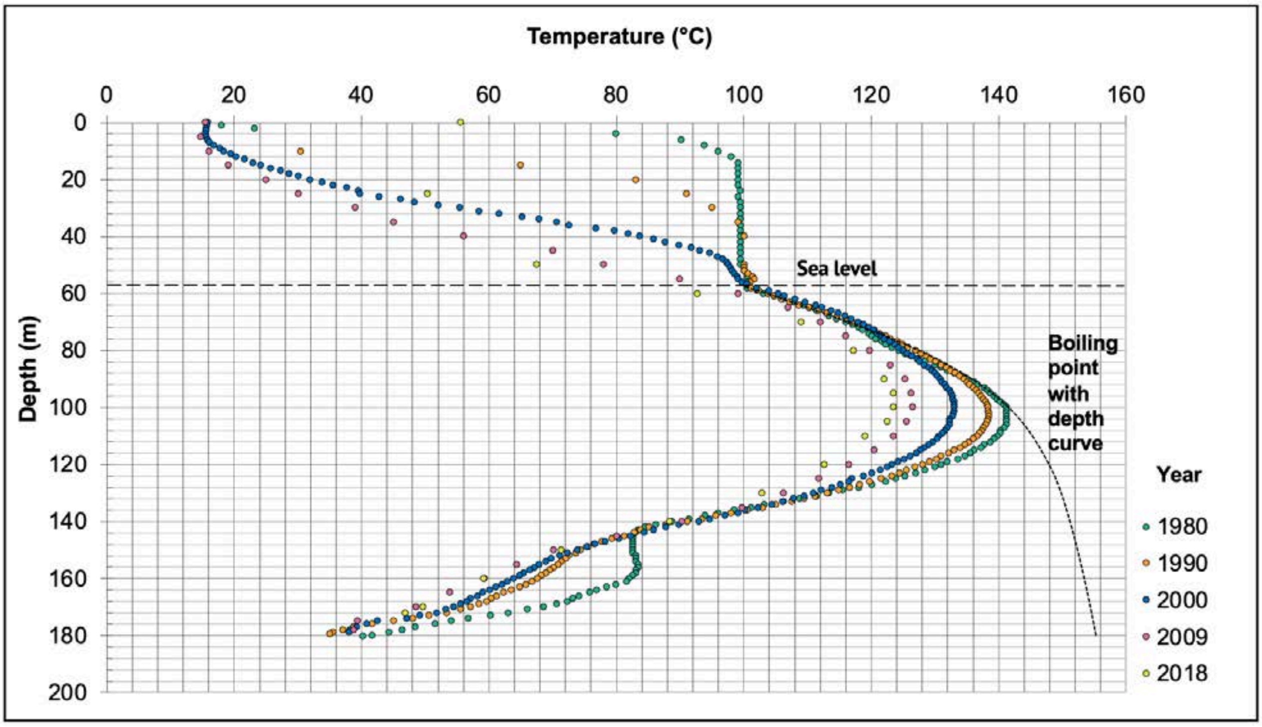

Figure 7. Temperature profiles from 1980, 1990, 2000, 2009 and 2018. The overall trend shows a decrease in temperature since 1980. The 2018 profile is from Prause et al. (2022).

The palagonitization of the Surtsey tephra

Jakobsson and Moore (1986) suggested that the geothermal system was developing as a consequence of intrusive activity at Surtur (Austurbunki), during the period of December 1966-January 1967. The record presented here supports a relationship between the intrusive activity and the early development of the Surtur geothermal manifestations, but it does not explain the gradual onset of geothermal activity in Surtungur (Vesturbunki), appearing a decade or so later. The surface temperature measurements demonstrated that the thermal area expanded within the tephra craters since the first thermal anomalies were detected in 1968, and that basalt tephra took about 1-3 years to convert to palagonite tuff at 80-100 °C (Jakobsson 1978). The observations made in this study, along with the map record analysis, conform to this link between temperature and palagonitization. They also provide a comprehensive account of the evolution of the thermal area at Surtsey during the period of 1968-2018, where it can be noted that as a result of the development of the thermal activity, the basalt tephra was altered rapidly into palagonite tuff. Moreover, the palagonitized area in 1970 had substantially increased in only one year, after the first signs of palagonitization appeared on the surface in 1969.

Thermal manifestations in the lava fields

Field observations and temperature measurements taken at the surface, reveal a distinctive variation in thermal activity within the entire thermal field on Surtsey with different time scales and intensities for different areas. The main source of thermal heat in the lava field areas was the remnant heat of the lava, as it solidified and cooled down from its estimated erupting temperature of 1150°C. Due to the volumetric and emplacement time differences between the lava fields, it is convenient to discuss separately the thermal areas in Surtur and Surtungur.

The thermal anomaly at Surtungur's lava field

Lava effusion from Surtungur's vent ceased in May 1965. The lava shield, that reached 100 m above sea level, had been cooling down for over five years before the first temperature measurements were recorded in the thermal survey of 1970. The rapid decrease in maximum temperature that was observed in the 1970-1974 record, from 460 °C to 160 °C, reflects a rapid cooling rate during this specific period. A thick lava flow can have some molten or partially molten interior parts and in the first years after full solidification of thick lava bodies, temperatures above the boiling point of water are to be expected (e.g., Turcotte & Schubert 2002). With time, as precipitation can percolate through the fully solidified lava, interior temperatures should drop fast. This may explain the rapid cooling of the lava piles compared with the tephra cones.

Following the very rapid initial cooling observed into the 1970s, the lava began to cool down slower. Subsidence of the southern part of the lava shield, along with 10-20 cm widening of fissures at the surface, are considered to account for the modest temperature increase that is observed in 1983 (Jakobsson *et al*. 2000). Despite the substantial gap in the thermal record for most of the 1990's, the ambient temperatures recorded by 2000 indicate that the thermal anomaly in the Surtungur lava field completely disappeared within 30-35 years from the end of the eruption.

The thermal anomaly at Surtur's lava field

A 70 m lava shield was formed during the effusive eruptive activity that took place in August 1966-June 1967 at Surtur (Jakobsson & Moore 1982). In addition, five very minor lava flows from five different fissures, located on the slopes of the tephra cone, erupted in December 1966-January 1967. The Surtur thermal area of the lava field comprises both eruption zones and it is worth mentioning that the thermal record does not include temperature measurements from or around the Surtur crater depression.

In 1970, when the initial maximum temperature of 63 °C was recorded, the lava that erupted at Surtur had been cooling down for three years. The substantial initial heat loss at Surtur's lava field is comparable to Surtungur's, and this was followed by a slower cooling rate. In 2008, when the last thermal survey of the lava region was recorded, Surtungur's maximum temperature was near ambient, a 55 °C maximum temperature was recorded in one of the fissures that opened up in 1966. However, a fissure that is located a few meters away only reached a maximum temperature of 27 °C. With this inference, it can still be concluded that the thermal anomaly in the Surtur lava field generally cooled down to ambient and eventually disappeared within 40-45 years.

The evolution of the thermal anomaly within the lava region

The thermal data recorded in Sveinn P. Jakobsson's thermal surveys (Fig. 3) and later data (Fig. 4) clearly showed a decrease in surface area, as the thermal manifestations that were found over an area of 0.26 km^2 in 1970, gradually decrease to ambient temperatures by 2000. This validates the source of the thermal anomaly within the lava region as the remnant heat of emplacement that is being lost by the natural process of cooling and advection of heat by water.

Thermal manifestations in the tephra cones

The thermal area of Surtsey is now confined to the tephra region of Surtur (Austurbunki) and Surtungur (Vesturbunki), and its characteristic thermal emission is steam issuing from fissures that formed in the tephra once it consolidated. As mentioned previously, the main source of thermal heat in the tephra is still up for debate but it has been hypothesized to be the intrusive activity in Surtur, during December 1966-January 1967 (Jakobsson & Moore 1986). However, as pointed out earlier, the onset of thermal activity in the Surtungur tephra cone (Vesturbunki) occurred several years after cessation of volcanic activity, suggesting that other processes may be important.

The thermal anomaly at Surtur (Austurbunki) tephra cone

The thermal values recorded in the monitoring surveys indicate that the thermal area at the surface of the Surtur tephra cone was established within 1-2 years. The area is still active with thermal manifestations concentrating along the top of the palagonite tuff rim. This concentration of thermal activity at topographic highs, that is also present at Surtungur's tephra cone, can be explained by a chimney effect that arises due to buoyancy. This is caused by the density difference between the hot fluid in the up-flow zone and the surrounding colder fluid; in the tephra cone the fluid is air (Stefánsson 1983). However, the thermal values also show that the temperature at the surface is declining slowly fifty years after its onset. The thermal activity on Surtur's tephra cone is expected to weaken and the thermal manifestations to eventually disappear in the future.

The thermal anomaly at Surtungur (Vesturbunki) tephra cone

The initial clear manifestations of thermal activity at the surface of the Surtungur tephra cone were finally observed on its western side in 1975. In contrast to Surtur, no intrusive activity was detected in the Surtungur tephra. It is therefore unlikely that the onset of geothermal activity in Surtungur can be explained by intrusions as for Surtur.

The thermal values recorded in the monitoring surveys indicate that even though the establishment of the thermal anomaly on the Surtungur tephra cone appears more gradually than that of Surtur, the latest thermal data indicates that the thermal activity on Surtsey is currently stronger within this thermal area, as the surface temperatures have stayed above 90 °C (Fig. 3). Thermal heat is expected to remain in this area for longer compared to Surtur and the intermediate zone, both of which are showing signs of weakening. Nonetheless the thermal manifestations at Surtungur are also expected to eventually diminish and disappear as the hydrothermal system in Surtsey begins to die down.

The thermal anomaly at intermediate tephra zone cone area

Overall, the intermediate zone between the well-defined Surtur and Surtungur tephra cones has shown relatively high temperatures since the first thermal survey was performed in 1969. The initial maximum temperature recorded within this area was 80 °C, and regardless of the fluctuations of the next five decades, the survey performed in 2018 still placed the maximum temperature value at 80 °C (Fig. 3). This suggests that the thermal activity at the intermediate tephra zone is still reasonably strong. Overall, the evolution of this area has resembled that of the Surtur cone. This may be related to the fact that the lower part of the tephra pile in this area is the eastern rim of Surtur, which was eventually covered by Surtungur tephra.

The evolution of the thermal anomaly within the tephra cones

The distinct difference of the evolution between the thermal region within the lava and the palagonitized tephra can be attributed to the fact that the tuff formation retains heat much better than the lava pile. This is best explained by the higher permeability of the lava that allows the sea water, as well as groundwater that accumulates due to precipitation, to easily seep through until the water reaches hot rock. At the interface, the water evaporates, effectively mining heat from the lava, with the steam generated emitted up through the lava pile until the heat is largely exhausted. In contrast, the permeability in the tephra decreases once consolidated, resulting in slow flow of groundwater through the tuff formation. This eventually allows the edifice to retain the thermal heat that is emitted by a heat source that may also lie deeper into the ground.

The thermal data from the 1979 Surtsey drill hole

The observations made during the analysis of the maximum temperature data recorded in the 1979 drill hole is essential to understand the thermal anomalies that are seen at the surface of Surtsey. Previous studies demonstrated that the heat transfer in Surtsey has been dominated by hydrothermal convection and that the system is vapor dominated above sea level (Friedman *et al*. 1976). The physical conditions found at the subsurface account for the thermal manifestations observed at the surface, which are characterized by vapor emissions that rise to 100 °C, as the water at sea level within parts of Surtsey boils and evaporates.

The hypothesis that intrusions account for the excess heat content of Surtsey has been previously favored (Friedman *et al*. 1976). The 13 m thick discontinuous intrusive complex, observed in the drill core from 1979 offered some support for this (Jakobsson & Moore 1982). However, the main source of thermal heat within the Surtur tephra cone is still up for debate, with the minor intrusions that happened from December 1966-January 1967 (Jakobsson & Moore 1986) being a contributing factor but probably not the main reason for the occurrence of a thermal area.

The difference between the onset of the thermal anomalies at the surface of the Surtur tephra cone (~1968) versus the Surtungur cone (mid 1970s) is interesting. The small intrusions in Surtur in 1966-67 presumably sped up the process and once the tephra began to consolidate, the transfer of vapor was affected. Micro cracks formed as the porosity and the micro permeability increased, and eventually the vapor was transferred to wider areas. The much later onset of visible thermal activity in the Surtungur tephra cone may be explained by the lack of late intrusive activity in that region.

The constant erosion of the island and the palagonitization of the tephra, which may have started at depth while the Surtsey eruption was still active and was eventually observed at the surface in 1969, have facilitated the formation and exposure of steaming fissures where the vapor emissions currently concentrate.

The temperature profiles of the 1979 drill hole show that the thermal heat that is concentrated within Surtsey is decreasing. As this heat dies down, it is expected that the thermal manifestations at the surface of Surtsey will also diminish and eventually disappear.

CONCLUSIONS

The monitoring of the surface thermal manifestations at Surtsey has revealed important information on the evolution of the entire thermal field. The record shows that thermal activity in the lavas and the tephra cones has followed noticeably different paths. The thermal activity on the lava fields initially exhibited very high heat loss followed by a further gradual cooling. Temperatures of up to 460 °C were recorded in fumaroles, five years after activity in the lava craters ceased. Overall, this thermal activity cooled down rapidly and the thermal anomaly disappeared in 30-40 years.

The thermal area within the tephra also exhibited a gradual onset of thermal activity, but the behavior between the two tephra cones is considerably different.

The onset of the geothermal activity at the surface of Surtur was detected in 1968. Temperatures between 80-90 °C still prevail at the surface but the size of the thermal area is now clearly declining and has been gradually doing so with time. The onset of the geothermal activity on Surtungur was detected in 1974. While there has been a significant decline in the extent of the thermal manifestations in this area, the maximum temperatures recorded have remained within the 90-100 °C range since 1979. The geothermal activity in the intermediate area, where the tephra cones of Surtur and Surtungur merge, has evolved broadly in the same way as Surtur. The 90-100 °C temperatures that were recorded there from 1979 have generally been declining since 2000.

Overall, the time series demonstrates a slow but clear trend of cooling of Surtsey with time. The record also demonstrates a clear distinction between the cooling and behavior of a pile of lava, which can cool fast as it is highly permeable, and palagonitized tuff, which has much lower permeability. The low permeability reduces the effectiveness of heat mining by convection and advection, thus retaining heat much better in the palagonitized tuff than in the lava. Additionally, temperatures measured within the 1979 drill hole also exhibit a decrease in the maximum temperature values since 1980. The drop was ca. 18 °C (141.3 to 123.4 °C) during the 38-year observation period. The abundant research on the geothermal system and the knowledge that has been gained from these studies have proven Surtsey to be an outstanding example on how post-eruptional geothermal processes can be studied under similar local physical conditions. Recent and future submarine eruptions may provide new monitoring opportunities and can benefit from programs similar to the one initiated by Sveinn P. Jakobsson, over 50 years ago on Surtsey volcano.

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REFERENCES

Baldursson, S. & A. Ingadottir, 2007. Nomination of Surtsey for the UNESCO World Heritage List. Icelandic Institute of Natural History, Reykjavik.

Bergsten, P., P. Vannier, A.M. Klonowski, S. Knobloch, M.T. Gudmundsson, M.D. Jackson & V.T. Marteinsson, 2021. Basalt-hosted microbial communities in the subsurface of the young volcanic island of Surtsey, Iceland. Frontiers in Microbiology.12, 728977. https://doi.org/10.3389/fmicb.2021.728977

Friedman, J.D. & R.S. Williams, 1970. Changing patterns of thermal emission from Surtsey, Iceland, between 1966 and 1969. US Geol. Surv. Prof. Papers 700-D, 116–124.

Friedman, J.D., D.M. Preble & S.P. Jakobsson, 1976. Geothermal flux through palagonitized tephra, Surtsey, Iceland – The Surtsey temperature data relay experiment via Landsat-1. Journ. Res. US Geol. Surv. 4(6), 645–659.

Jackson, M.D., M.T. Gudmundsson, T.B. Weisenberger, J.M. Rhodes, A. Stefánsson, B.I. Kleine, P.C. Lippert, J.M. Marquardt, H.I. Reynolds, J. Kück, V.Þ. Marteinsson, P. Vannier, W. Bach, A. Barich, P. Bergsten, J.G. Bryce, P. Cappelletti, S. Couper, M.F. Fahnestock, C.F. Gorny, C. Grimaldi, M. Groh, Á. Gudmundsson, Á.Þ. Gunnlaugsson, C. Hamlin, Þ. Högnadóttir, K. Jónasson, S.S. Jónsson, S.L. Jørgensen, A.M. Klonowski, B. Marshall, E. Massey, J. McPhie, J.G. Moore, E.S. Ólafsson, S.L. Onstag, V. Perez, S. Prause, S.P. Snorrason, A. Türke, J.D.L. White & B. Zimanowski, 2019. SUSTAIN drilling at Surtsey volcano, Iceland, tracks hydrothermal and microbiological interactions in basalt 50 years after eruption.

Scientific Drilling. 25, 35-46. https://doi.org/10.5194/sd-25-35-2019

Jakobsson, S.P., 1972. On the consolidation and palagonitization of the tephra of the Surtsey volcanic island, Iceland. Surtsey Res. Prog. Rep. VI, 121–128.

Jakobsson, S.P., 1978. Environmental factors controlling the palagonitization of the tephra of the Surtsey volcanic island, Iceland. Bull. Geol. Soc. Denmark 27, Spec. Issue: 91–105.

Jakobsson, S.P., 2006. Geological map of Surtsey, scale 1:5,000. Icelandic Institute of Natural History, Reykjavik.

Jakobsson, S.P. & J.G. Moore, 1982. The Surtsey Research Drilling Project of 1979. Surtsey Res. Prog. Rep. IX, 76–93.

Jakobsson, S.P. & J.G. Moore, 1986. Geothermal minerals and alteration rates at Surtsey volcano, Iceland. Geol. Soc. Am. Bull. 97, 648–659.

Jakobsson, S.P., G. Guðmundsson & J.G. Moore, 2000. Geological monitoring of Surtsey, Iceland, 1967–1998. Surtsey Research. XI, 99–108.

Jóhannesson, Æ., 1972. Report on geothermal observations on the island of Surtsey. Surtsey Res. Progr. Rep. VI, 129-136.

Jóhannesson, Æ., 1978. The thermal anomaly in Surtsey revisited. Surtsey Research. Prog. Rep. VII, 63-68.

Kleine, B.I., A. Stefansson, R. Kjartansdóttir, S. Prause, T.B. Weisenberger, H.I. Reynolds, A. E. Sveinbjörnsdóttir, M.D. Jackson & M.T. Gudmundsson, 2020. The Surtsey volcano geothermal system: An analogue for seawater-oceanic crust interaction with implications for the elemental budget of the oceanic crust. Chem. Geol. 550, 119702. https://doi.org/10.1016/j.chemgeo.2020.119702

McPhie, J., J.D.L. White, C.F. Gorny, M.D. Jackson, M.T. Gudmundsson, S. Couper, 2020. Lithofacies from the 1963-1967 Surtsey eruption in SUSTAIN drill cores SE-2a, SE-2b and SE-03. Surtsey Research. XIV, 19-32. https://doi.org/10.33112/surtsey.14.2

Óskarsson, B.V., K. Jónasson, G. Valsson, & J.M.C. Belart, 2020. Erosion and sedimentation in Surtsey island quantified from new DEMs. Surtsey Research. XIV, 63-77. https://doi.org/10.33112/surtsey.14.5

Prause, S., T.B. Weisenberger, B.I. Kleine, P. Monien, C. Rispoli & A. Stefánsson, 2022. Alteration of basaltic glass within the Surtsey hydrothermal system, Iceland–Implication to oceanic crust seawater interaction. JVGR, 429, 107581. https://doi.org/10.1016/j.jvolgeores.2022.107581

Prause, S., T.B. Weisenberger, P. Cappelletti, C. Grimaldi, C. Rispoli, K. Jónasson, M.D. Jackson & M.T. Gudmundsson, 2020**.** Alteration progresses within the Surtsey hydrothermal system, SW Iceland –a time-lapse alteration study of cores drilled in 1979 and 2017. JVGR 392, 106754. https://doi.org/10.1016/j.jvolgeores.2019.106754

Sayyadi, S., P. Einarsson, M.T. Gudmundsson, 2021. Seismic activity associated with the 1963-1967 Surtsey eruption off the coast of South Iceland. Bull. Volc. 83, 54. https://doi.org/10.1007/s00445-021-01481-0

Stefánsson, V., 1983. Physical Environment of Hydrothermal Systems in Iceland and on Submerged Oceanic Ridges. *In* Rona P.A., Boström K., L. Laubier, K.L. Smith (eds). Hydrothermal Processes at Seafloor Spreading Centers. NATO Conference Series (IV Marine Sciences), Vol 12, Springer, Boston, MA.

Stroncik, N.A. & Schmincke, 2002. Palagonite – a review. HU. Int J Earth Sci (GeolRundsch), 2002. 91, 680. https://doi.org/10.1007/s00531-001-0238-7

Thorarinsson, S., 1965. The Surtsey eruption. Course of events and the development of the new island. Surtsey Res. Prog. Rep. I, 51-55.

Thorarinsson, S., 1968. The Surtsey eruption. Course of events during the year 1967. Surtsey Res. Prog. Rep. IV, 143-148.

Turcotte D., & G. Schubert, 2002. Geodynamics. 3rd Edition. Cam.Uni. Press. 636 p.

Weisenberger, T.B., M.T. Gudmundsson, M.D. Jackson, C.F. Gorny, A. Türke, B.I. Kleine, B. Marshall, S.L. Jørgensen, V.Þ. Marteinsson, A. Stefánsson, J.D.L. White, A. Barich, P. Bergsten, J.G. Bryce, S. Couper, M.F. Fahnestock, H. Franzson, C. Grimaldi, M. Groh, Á. Gudmundsson, Á.Þ. Gunnlaugsson, C. Hamelin, Þ. Högnadóttir, K. Jonasson, S.S. Jónsson, A. Klonowski, J. Kück, R.L. Magnússon, E. Massey, J. McPhie, E.S. Ólafsson, S.L. Onstad, S. Prause, V. Perez, J.M. Rhodes, S.P. Snorrason, 2019**.** Operational Report for the 2017 Surtsey Underwater volcanic System for Thermophiles, Alteration processes and Innovative concretes (SUSTAIN) drilling project at Surtsey Volcano, Iceland. 98 p + appendixes. GFZ German Res. Cen. for Geosc. https://doi.org/10.2312/ICDP.5059.001