SURTSEY RESEARCH

16

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THE SURTSEY RESEARCH SOCIETY

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Cover page: Top row from left: the weevil Ceutorhynchus insularis, the orb weaver Larinioides patagiatus, ingrailed clay (Diarsia mendica). Middle row from left: red-backed cutworm (Euxoa ochrogaster), the Malaise trap in the gull colony, quensel‘s ground beetle (Amara quenseli). Bottom row from left: white-tailed bumblebee (Bombus lucorum), saddle-backed harvestman (Mitopus morio), broom moth (Melanchra pisi).

Photos: Erling Ólafsson.

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Introduction

In 2023, 60 years had passed since the volcanic eruption that created Surtsey started, an extraordinary natural event that granted Iceland, and the world, a once in a lifetime scientific laboratory. Since its birth from the sea, Surtsey has remained one of the most remarkable places on Earth for the study of primary ecological succession, geological processes, and the delicate interplay between nature and time. Its strict protection from human interference has made it uniquely valuable; Surtsey is not only a place of scientific discovery but also a powerful reminder of the importance of protecting natural environments.

The 16th volume of Surtsey Research includes 9 papers in the fields of terrestrial biology, climatology and geology. The papers are written by 24 authors taking part in the research on Surtsey. For the first time some articles in the journal are marked as “peer-reviewed articles”, when they were first sent out to anonymous reviewers in the same field before being reviewed and accepted for publication by the editorial committee. When not marked, the review was done as before, directly by the members of the editorial committee who had the closest scientific backgrounds to the article in question. Authors were given a choice for which review form they opted for.

Interest in Surtsey continues to extend beyond Iceland’s shores. Recently, The Guardian published an article highlighting the island and the ongoing research it inspires, yet another reflection of how Surtsey, despite 60 years of age, captures global interests. This enduring curiosity also underlines the importance of sharing knowledge.

The Surtsey Research Society has taken important steps to preserve our collective record. The National Archives of Iceland have classified the Society’s archival collection, as a private collection. They are unquestionably a national treasure, given the historical and scientific importance of Surtsey. Documentation related to Surtsey is currently scattered across various institutions connected to the Society’s mission. We have encouraged archivists at these institutions, and our own members, to submit their Surtsey related materials to the National Archives. This includes scientists’ and technicians’ documents such as diaries, working papers, emails, photographs, and visitor logs. By gathering these materials in one place, we ensure that they are accessible, and safeguarded for future generations.

I took on the role as Chair of the Surtsey Research Society at the Annual General Meeting in April 2025. I would like to extend my sincere thanks to our former Chair, Hallgrímur Jónasson, for his dedicated service and leadership for the past 16 years. His contributions have strengthened the Society and the mission we continue today. It is with sadness that I acknowledge the passing of Viggó Þór Marteinsson, who served on the Society’s board and the editorial committee of Surtsey Research. His work has left a lasting mark.

I wish to thank the editorial committee: Bjarni Diðrik Sigurðsson, Olga K. Vilmundardóttir, Lilja Gunnarsdóttir, Kristján Jónasson and Lovísa G. Ásbjörnsdóttir for their diligent and selfless efforts in producing the journal, which continues to be an essential platform for sharing research on Surtsey.

Thank you all for your commitment to protecting and understanding this extraordinary island. May our work continue to merit the legacy of Surtsey and the people who have dedicated themselves to its research.

On behalf of the Surtsey Society

Hólmfríður Sigurðardóttir
Chairman 2025

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CLIMATOLOGY

Reviewed research article

Weather in Surtsey 2020-2024

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ABSTRACT

The weather of Surtsey, the southernmost part of Iceland, is of great interest. Firstly, due to the location of Surtsey, the island is exposed to undisturbed southerly air masses moving towards Iceland and secondly the weather information can be vital for seafarers in the vicinity. Thirdly, the weather has great impact on the development of flora and fauna in the scientific laboratory that Surtsey is. Here we analyse the weather of the five-year period 2020–2024. The main aim is to analyse the data in such a way that it may be of use for understanding of the processes that are monitored on and around the island. The temperature and wind data are good but there were considerable failures in measurements of precipitation. A few months had unusual weather, especially the summer of 2022, which was cloudy and cool, while the winter 2022–2023 was characterized with warm and windy months as well as cold and calm months. During the analysis period a new maximum air temperature record was set on 11 July 2023 at 18.6°C, but broken on 14 July 2025 when temperature reached 22.6°C. Also, the highest and lowest mean sea level pressure records were made, 1050.4 hPa and 932.3 hPa, on 28 March and 15 February 2020, respectively.

INTRODUCTION

The weather and climate of Surtsey, the southernmost island of the Vestmannaeyjar archipelago as well as of Iceland, is of great interest. Firstly, from a meteorological standpoint, southerly air masses after having travelled great distance over open sea often impinge first up on Surtsey before impacting the rest of the country. These air masses can thus be considered undisturbed oceanic air masses when arriving in Surtsey. Secondly, as Surtsey is a small island, 1.9 km^2 in 2019 (Óskarsson *et al.* 2020), the measurements give indications of weather over the sea and are therefore vital for seafarers, especially wind information. Thirdly, since 1965 the island has been a scientific laboratory, where the colonisation by plants and animals, biotic succession and the shaping of geological formation is as natural as possible (Surtsey Research Society 2025). Many of these processes are dependent on weather, especially temperature and precipitation (e.g. Sigurdsson *et al.* 2010, 2022, Magnússon *et al.* 2023). It is therefore necessary to monitor the weather and climate of Surtsey for the purpose of better understanding these processes, their

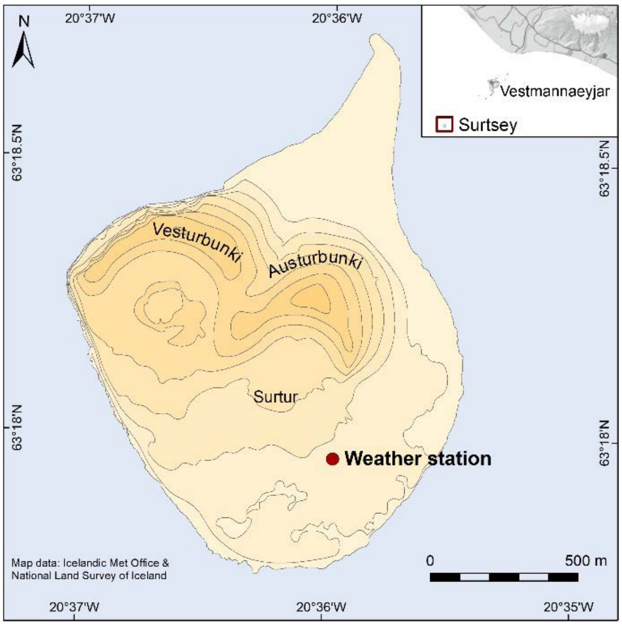

Figure 1. Map of Surtsey showing the location of the current weather station. The elevation is shown with contours, interval 20 m. Inset map shows location of Surtsey in relation to the Vestmannaeyjar archipelago as well as the southern coast of Iceland.

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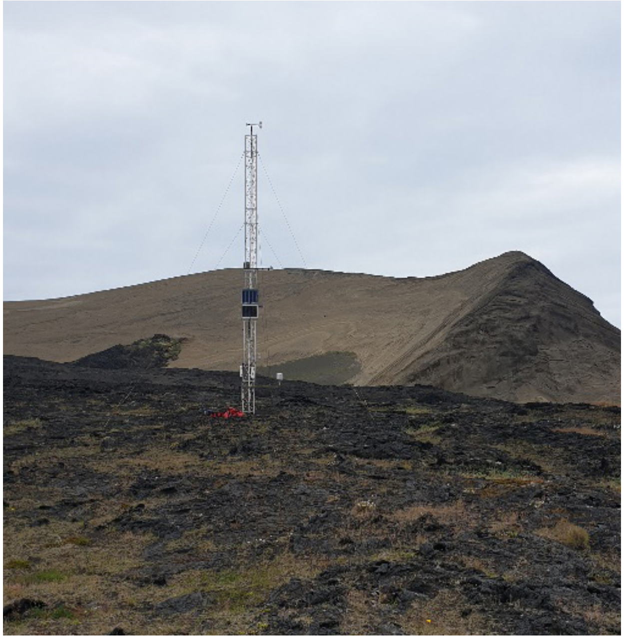

Figure 2. The automatic weather station in Surtsey with hill Austurbunki in the background. Photo: Hákon Hákonarson, 20 July 2023.

variation from year to year and how they are affected by weather and climate.

Petersen & Jónsson (2020) described the climate of Surtsey based on 10 years of data, 2009–2019, as well as documenting the meteorological measurement history of Surtsey. Here, the weather of the following five years, 2020–2024, is described and compared to measurements in Heimaey, the largest island of the Vestmannaeyjar archipelago, at Stórhöfði and in Vestmannaeyjabær. Emphasis is on identifying months with unusual weather that may impact the processes that are monitored in and around the island.

MATERIAL AND METHODS

An automatic weather station has been operating in Surtsey since 2009, station No. 6012, abbreviation surte. It is located at the southern side of the island, at 36 m a.s.l. and about 300 m from the coast, see map in Fig. 1. The surface is uneven lava with sparse vegetation, see Fig. 2. During the period 2020–2024 the station measured standard meteorological parameters as well as global solar radiation, soil temperature and humidity, see Table 1. The global radiation measurements were terminated in April 2024. The soil temperature and humidity sensors are owned by the Surtsey Research Society while the other equipment is owned by the Icelandic Meteorological Office (IMO). The measurements are recorded every 10 minutes and send in real time into the data base of the IMO.

The environment in Surtsey is harsh on the equipment as it is exposed to both sea salt and sand. During this five-year period the temperature and humidity sensor was replaced once and the anemometer twice. The station is usually only visited once every summer for regular maintenance, during annual research excursions to Surtsey. If instruments fail between these excursions, in most cases repairs/replacement will have to wait until the next summer excursion.

In this paper the meteorological conditions in Surtsey during the five years 2020–2024 are analysed. The data is put in context with automatic observations from the two stations in Heimaey, the largest island of the Vestmannaeyjar archipelago, Vestmannaeyjabær (6015, vestb) and Stórhöfði (6017, storh). These two stations are in different local environments; Vestmannaeyjabær is within the town

Table 1. The instrumentation of the automatic weather station in Surtsey, valid 2020–2024.

Parameter	Height	Instrument	
Wind speed and wind direction	10 m a.g.l.	Young wind anemometer	
Temperature & humidity	2 m a.g.l.	Rotronic temperature and humidity probe Húmi (IMO sensor)	Until 11 April 2017 From 11 April 2017
Air pressure	37.5 m a.s.l.	Vaisala Barometric pressure transmitter	
Precipitation	1.5 m a.g.l.	Lambrecht heated tipping bucket	
Solar radiation	5 m a.g.l.	Kipp & Zonen CMP3 pyranometer	Data available until 11 April 2024
Soil temperature	5 and 15 cm depth	Type unknown	Below two surfaces: sand and gras
Soil moisture	5 and 15 cm depth	Campbell CS616 water content reflectometer	Below two surfaces: sand and gras
Cloud conditions, visibility & surface conditions	3 m a.g.l.	Web camera	View direction: NE

Table 2. Information on the weather stations used in this paper.

Station	Location	Height a.s.l.	Period used	
Surtsey (6012, surte)	63.2993N 20.59947W	36 m	2020–2024 2015–2024	 Only hourly wind and relative humidity
Vestmanna-eyjabær (6015, vestb)	63.43587N 20.27578W	40 m	2020–2024	
Stórhöfði (6017, storh)	63.39957N 20.28825W	118 m	2020–2024	
Stórhöfði (815)	63.39975N 20.28832W	118 m	1981–2010	Only monthly precipitation

of the island, at 40 m a.s.l., sheltered from the sea by low mountains, vegetation and the town itself, while Stórhöfði is located at the southern tip of Heimaey on an exposed hill at 118 m a.s.l. At Stórhöfði there were manned meteorological observations for decades, from 1921 to 2014. For a climatic view the available monthly precipitation in Surtsey is compared to a 30-year time series, 1981–2010, of manned precipitation measurements at Stórhöfði. Table 2 contains information on the stations and time periods applied in the paper.

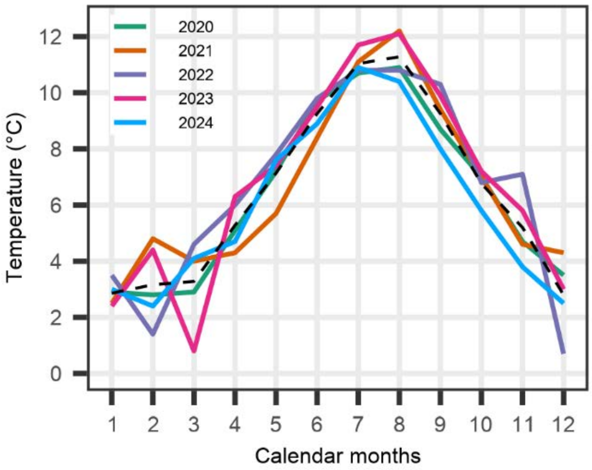

Figure 3. Annual variations in temperature (°C) in Surtsey, 2020–2024. Shown are monthly values for each year (coloured lines) and the five-year average (dashed black line).

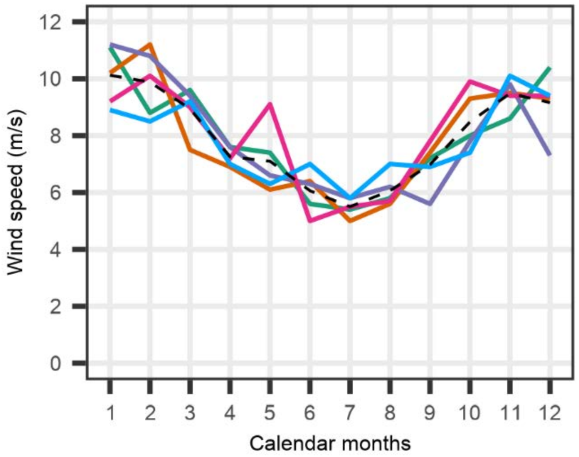

Figure 4. Annual variations in wind speed (m/s, bottom) in Surtsey, 2020–2024. Shown are monthly values for each year (coloured lines) and the five-year average (dashed black line).

Precipitation measurements are challenging in a windy country like Iceland and even more challenging when the instrument can only be maintained once a year. The precipitation gauge in Surtsey is a Lambrecht heated tipping bucket (Table 1). This means that the gauge can measure solid precipitation (e.g. snow), after melting it, but the measurements may be somewhat delayed and the precipitation intensity not reliable. Due to the nature of precipitation, missed measurements have larger impact on precipitation records than e.g. on wind speed or temperature records. In the IMO database, calculations of daily values of wind speed and temperature are considered valid if there are missing less than five hourly values while for precipitation all hourly records are needed. For monthly values three daily values are allowed to be absent for wind speed and temperature but again zero for precipitation. A significant number of precipitation records is missing for all three stations resulting in number of missing monthly values. For example, for Surtsey in July 2020 during maintenance the tipping bucket was recorded as getting stuck easily and thus all measurements from January 2020 until 13 July 2020 were not considered reliable. The gauge had other mechanical problems during the period resulting in only 25 out of total 60 months with reliable monthly precipitation. There were no reliable monthly values for July during the five-year period and for May and June there are only monthly values for the year 2024. In addition, there were several issues regarding precipitation measurements at both stations in Heimaey In fact, only during the period August 2020 until April 2021 monthly precipitation values could be calculated for all three stations. Therefore, to put the existing monthly values in Surtsey into climatic context they are compared to climatic values from the previous manned weather station at Stórhöfði, using the 30-year time period 1981–2010.

RESULTS AND DISCUSSION

Annual variations

Fig. 3 shows the annual variations of air temperature in Surtsey along with the five-year average. As has been noted before, the climate of Surtsey is in general mild and windy, with winter temperatures well above freezing level (Petersen & Jónsson 2020).

On average, the lowest monthly mean temperature occurs in January and highest in August. Interestingly, the winter 2022–2023 was characterised with both warm months (November and February) and exceptionally cold months (December and March). November 2022 was the warmest November month in Iceland since start of records, with mean temperature in Surtsey 2.3°C above the average for the last 10 years (Icelandic Meteorological Office 2022a) while the following month, December 2022, with a monthly mean temperature of 0.7°C was the coldest month in Surtsey from the start of continuous automatic observations in 2009. This was also the coldest December in Iceland since 1973 (Icelandic Meteorological Office 2022b). The year 2023 started with an average January while February was a warm month, with the temperature in Surtsey 0.9°C above the average of the last 10 years (Icelandic Meteorological Office 2023a). In contrast, the following March was cold, 2.9°C below the last 10 years (Icelandic Meteorological Office 2023b). During two of the five years analysed the August temperature was above the average of the last 10 years, in 2021 and 2023 (Icelandic Meteorological Office 2021; 2023c).

Similarly, Fig. 4 shows the annular variation in wind speed in Surtsey along with the five-year average. Surtsey is open to the North-Atlantic Ocean and thus conditions are often windy. In addition, due to the island's mostly sparse vegetation (Magnússon *et al.* 2023), the surface friction is low and therefore has little impact on the wind speed. During the five-year period the mean wind speed varied from 5.5 m/s in July to 10.1 m/s in January. May 2023 was unusually windy, with mean wind speed of 9.1 m/s. The autumn of 2023 and summer of 2024 were rather windy periods. On the other hand, March 2021, September and December 2022 were relative calm months.

Thus, during this five-year period the winter of 2022–2023 stands out due to large month-to-month variation in both temperature and wind speed, with warm and windy months as well as cold and calm.

The wind roses in Fig. 5 show the frequency of wind direction and wind speed for a 10-year period, 2015–2024, based on all observations as well as during winter months (Dec–March) and summer months (June–Sept). The top wind rose, shows that the main wind directions are easterly and east-southeasterly. These are the most dominating wind directions and from which the strongest winds are recorded. In addition, north-northeasterly winds are quite common. These winds come from the highland of Iceland and could be expected to be relatively dry and cool. The wind rose show that these winds from the highlands are often strong (up to 18–20 m/s). There is hardly any wind coming from the northeast-sector, in which the mountains at the southern coast of Iceland, e.g. Eyjafjallajökull and Mýrdalsjökull, shelter Surtsey.

The winter wind rose (centre) highlights the same dominating wind directions but also indicates that strong winds from the southwest are common during winter. Those southwesterly winter storms have been identified to be especially important in the erosion of the Surtsey island (Jakobsson & Guðmundsson 2003).

The summer wind rose (bottom) shows that during summer the main wind directions are still common but westerly winds, from southwesterly to northwesterly play a larger role. During summer most strong wind events have an easterly wind direction.

Fig. 6. shows the relative humidity as a function of wind direction for the same data set, for wind speed exceeding 10 m/s. The figure shows clearly that north-northeasterly flow is in general drier, with mean relative humidity of about 70%, while easterly flow is much moister, mean relative humidity about 90%. On the other hand, southerly to westerly flows show little correlation with relative humidity. The mean annual relative humidity ranged between 82.3% and 85.3% for 2020 to 2024. The annual variation of relative humidity is rather small, with monthly mean values ranging 71% in March 2023 and 94% in August 2021 (see Table S1 in Supplements). Interestingly March 2023 had the second lowest mean temperature and August 2021 the highest mean temperature of the period. This rather stable relative humidity of Surtsey is due to the fact that Surtsey is a small island surrounded by sea and thus a plentiful

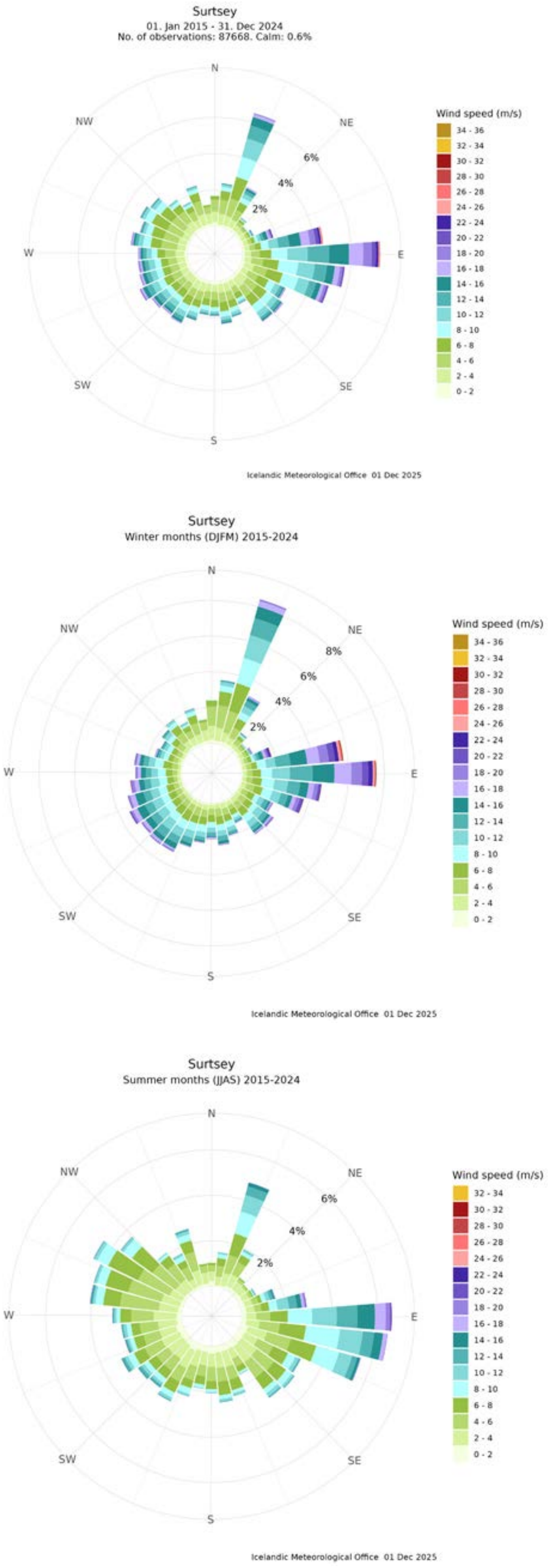

Figure 5. Wind roses showing the frequency of wind direction in Surtsey during (top) the whole year, (centre) winter months and (bottom) summer months. The wind blows towards the centre of the wind rose. The colours indicate wind speed. Hourly data from the period 2015–2024.

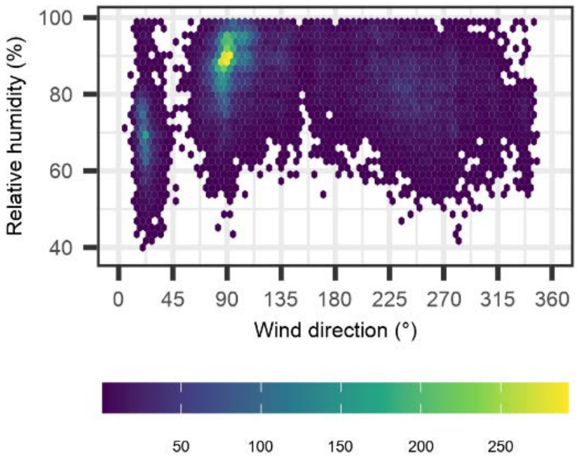

Figure 6. Relative humidity (%) as a function of wind direction (°) when wind speed exceeds 10 m/s. The hexagon cells are 5° wide and 2% high and are shaded according to number of cases. Hourly data from the period 2015–2024.

source of water vapour. The same can be said to apply to the coastal regions of Iceland.

Due to the lack of reliable monthly precipitation, both in Surtsey as well as in Vestmannaeyjabær and at Stórhöfði (see Methods), it was not possible to calculate average values or even estimate the annual precipitation. Therefore, the available monthly values from Surtsey are put into a climatic context by comparing them to 30 years of measurements at the previous manned station at Stórhöfði, see Fig. 7. In general, the precipitation in Surtsey is lower than at Stórhöfði. Previously, it has also been shown to be lower than at Vestmannaeyjabær (Petersen & Jónsson 2019). Measurements at Stórhöfði show annual variation with a maximum during autumn and winter (Sept–Feb) and a minimum during early summer (May–June). However, for Surtsey due to few values it is not possible to identify any such annual variation during this five-year period, although earlier measurements give indications of a similar pattern (Petersen & Jónsson 2019). Also, unfortunately no reliable measurements are available during the exceptionally cold February and December 2022 as well as March 2023, when one would expect less precipitation than in the milder winters of 2020–2021 and 2023–2024 where monthly precipitation in December and January was 45–95 mm. No monthly values are available for the summer of 2023 that was characterised by a cloudy and wet June followed by a warm, sunny and dry July, in fact in many places

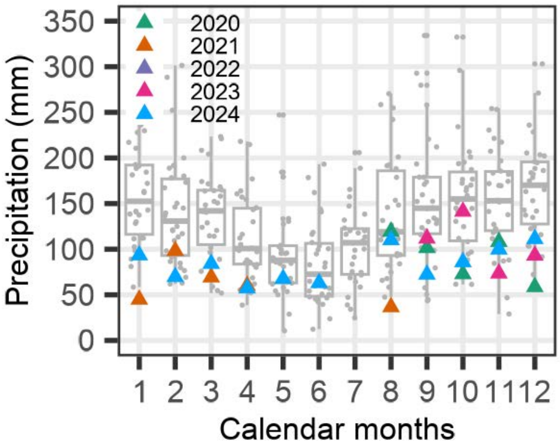

Figure 7. Available monthly precipitation in Surtsey, 2020–2024 (in coloured triangles). In the background monthly values from the manned station at Stórhöfði are shown, all values and a boxplot (in grey), 1981–2010.

this was the driest July from start of measurements (Icelandic Meteorological Office 2023e). These large fluctuations can possibly have caused stress for organisms which have colonized the island. Indeed, it was noted during the annual biological excursion in July 2023 that unusually large changes had occurred in the island’s flora compared to the previous years (Icelandic Institute of Natural History 2025).

Monthly timeseries of soil temperature and solar radiation

Fig. 8 shows the monthly time series of soil temperature at 5 and 15 cm and total solar radiation. The soil moisture data is not analysed in this paper. At both soil depths the largest difference between the two vegetation classes, “grass” and “sand” is during summer when the sand, down to at least 15 cm, warms up more than the grass. The largest difference can be found in July 2023, that was exceptionally sunny, with 241 W/m^{-2}, and air temperature was high. The impact of the solar warming on the soil temperature is also evident in that summer air temperatures in 2021 were comparable to the ones in 2023 (Fig. 3), but the summer temperature in the soil remained below 15°C as the month was cloudier, i.e. less solar radiation. The lowest soil temperature was at 5 cm in sand in December 2022 (-1.0°C), followed by January 2023 (-0.8°C) and February 2022 (-0.3°C). Interestingly, while December 2022 was a cold month in air, January 2023 was not. Thus, while the air temperature rose, the soil temperature remained low, and at 15 cm kept decreasing.

During winter, November–February, solar radiation is too low to have any impact on the surface. During this period the surface is cooled/warmed by air masses moving over the island and cooled by longwave outgoing radiation. Due to the

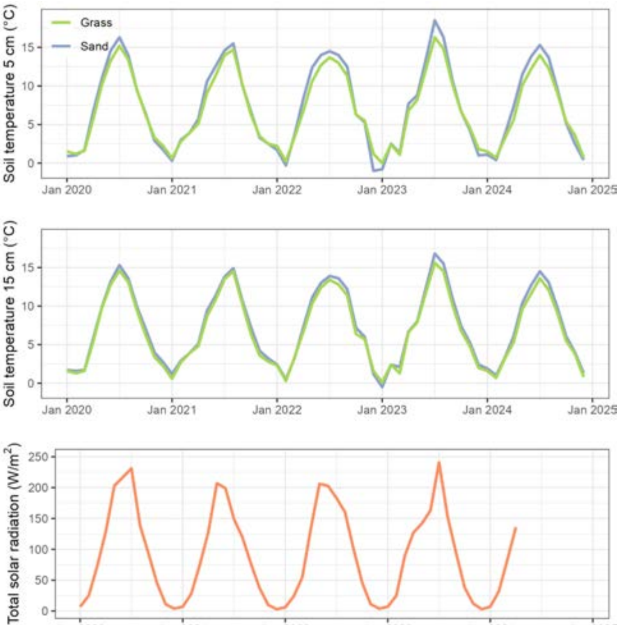

Figure 8. Monthly time series of soil temperature at 5 cm (°C, top), 15 cm (°C, centre) and total solar radiation (W/m^2, bottom).

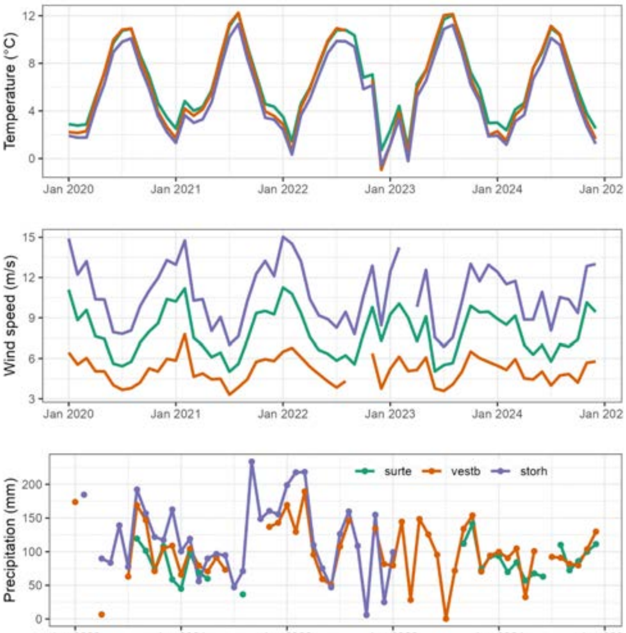

Figure 9. Monthly values of temperature (°C, top), wind speed (m/s, centre) and precipitation (mm, bottom) in Surtsey, Vestmannaeyjabær and Stórhöfði, 2020-2024.

location of Surtsey, a layer of snow rarely sits on the ground for a considerable period and therefore the insulating impact of snow has negligible impact on the temperature in the soil in Surtsey.

Table 3. Mean values during the period 2020-2024 in Surtsey, Vestmannaeyjabær and at Stórhöfði. Missing value due to missing records are shown with --.

	Surtsey	**Vestmanna-eyjabær**	**Stórhöfði**
Temperature	6.4°C	--	5.4°C
Days with minimum temperature below 0°C	52 days	77 days	80 days
Days with maximum temperature below 0°C	7 days	10 days	12 days
Length of frost-free period	219 days	167 days	193 days
Wind speed	7.9 m/s	--	--
Days with wind speed exceeding 20 m/s	32 days	5 days	118 days

Table 4. Maxima and minima during the period 2020-2024 in Surtsey, Vestmannaeyjabær and at Stórhöfði. Dates of the records are shown in parentheses and all-time records at the stations are shown in bold. Missing value due to missing records are shown with --.

	Surtsey	**Vestmanna-eyjabær**	**Stórhöfði**
Maximum temperature	**18.6°C** (11 July 2023)	19.5°C (11 July 2023)	18.8°C (11 July 2023)
Minimum temperature	-7.9°C (13 March 2023)	**-11.1°C** (12 March 2023)	-10.1°C (29 Dec 2022)
Maximum wind speed	34.7 m/s (14 Feb 2020)	**28.4 m/s** (14 Feb 2020)	45.0 m/s (14 Feb 2020)
Maximum wind gust	44.7 m/s (20 Feb 2022)	43.6 m/s (21 Feb 2022)	**58.8 m/s** (11 Nov 2022)
Maximum hourly precipitation*	8.5 mm (30 July 2020)	10.2 mm (1 Dec 2020)	14.0 mm (24 May 2020)
Maximum daily precipitation*	44.9 mm (30 July 2020)	49.4 mm (20 Oct 2023)	76.9 mm (14 Feb 2020)
Maximum monthly precipitation*	141.3 mm (Oct 2023)	189.5 mm (March 2022)	233.7 mm (Sept 2021)
Maximum sea level pressure	**1050.4 hPa** (28 March 2020)	**1050.4 hPa** (28 March 2020)	--
Minimum sea level pressure	**932.3 hPa** (15 Feb 2020)	**934.0 hPa** (15 Feb 2020)	--

*Note that the precipitation records at all stations are poor and the values not based on a full data set.

Comparison to automatic weather stations in Heimaey

The annual mean values for Surtsey, Vestmannaeyjabær and Stórhöfði are shown in Table 3 and maxima and minima in Table 4 and the continuous measurements in Fig. 9. This five-year period was slightly cooler than the preceding 10 years (Petersen & Jónsson 2020) as can be seen in lower mean temperatures, as well as more days with minimum and maximum temperature below freezing. However, at the same time the length of frost-free period is considerably longer, 20 days longer in Surtsey and 9 days at Stórhöfði. The shorter frost-free period in Vestmannaeyjabær may be related to the fact that as the station is sheltered from the sea more longwave cooling can be expected during calm and cloud free winter days and nights in all seasons. This is also evident in the monthly time series shown in Fig. 9 where summer temperatures in Surtsey are similar to the ones in Vestmannaeyjabær but winter temperatures in Surtsey are significantly higher than other stations. This suggests that Surtsey station is more impacted by the sea.

The monthly time series in Fig. 9 highlight the cool summers of 2022 and 2024 as well as the unusual temperature variations during the winter of 2022–2023. The mean wind speed could only be calculated for Surtsey as for the other two stations it was not possible to calculate monthly mean wind for all months. However, looking at the available monthly data in Fig. 9, it is clear that as expected in general wind speed is highest at Stórhöfði and lowest in Vestmannaeyjabær, where the magnitude of the annual variations is also smaller. There are indications that the winter 2023–2024 was calmer than on average.

No mean annual values could be calculated for precipitation due to lack of measurements. Fig. 9 shows the available monthly values. Where monthly values are available for the same months, in general there is correlation between the stations. There are indications that precipitation in Surtsey is closer to the one in Vestmannaeyjabær than at Stórhöfði. The autumn to winter 2021–2022 had high precipitation values, indicating especially wet winter with 150–225 mm each month at Stórhöfði. On the other hand, July 2023 was a sunny and very dry month in all of southern Iceland (Icelandic Meteorological Office 2023).

A few meteorological records were broken during this period (Table 4). On 11 July 2023 the maximum temperature at Surtsey was 18.6°C, the highest ever recorded at the station. However, it should be noted that this record was again broken on 14 July in 2025 when maximum temperature reached 22.6°C during a heatwave, where temperature records were broken at several sites in Iceland (Icelandic Meteorological Office 2025). Both the highest and lowest mean sea level pressure in Surtsey were recorded during this five-year period. A record high 1050.4 hPa mean sea level pressure was measured on 28 March 2020 when a 1052 hPa high south of Iceland controlled the weather in Iceland. The lowest pressure, 932.3 hPa, was on 15 February 2020 when a deep cyclone moved over the country with easterly winds causing one of the worst windstorms of the last few years.

Monthly means of all measured variables covered by this paper for the period 2020-2024 for Surtsey can be found in an attached Supplements at the Surtsey Research 16 folder within www.surtsey.is.

CONCLUSION

The automatic weather measurements in Surtsey, the southernmost part of Iceland, are analysed for the five-year period 2020–2024. Unfortunately, there are failures in measurements of precipitation during this period. For precipitation there are strict criteria regarding missing values; to calculate monthly or annual precipitation all daily values must be available. This results in only 25 monthly precipitation values in Surtsey, during a 60-months period. In addition, there are many monthly values missing from the two weather stations in Heimaey, Vestmannaeyjabær has the most values or 49 monthly values while Stórhöfði has 35 values. For the five-year period analysed here, only during a 9-month period in winter 2020–2021 are there monthly precipitation values from all three stations. This means that it is not possible to calculate mean precipitation and for Surtsey no annual precipitation values. The comparison of the time series and comparison of the available monthly means in Surtsey with manned observations at Stórhöfði 1981–2010, indicates that there is less precipitation in Surtsey than at Stórhöfði but there is too little data to draw any conclusions regarding annual variations. It would be of interest to retrieve precipitation data from a reanalysis, e.g. the Copernicus Arctic Regionald Reanalysis (CARRA, Schyberg *et al.* 2020), compare to observations when possible and thus assess the usability, especially when measurements fail. Such work is outside of the scope of this paper but would be a worthy investigation, given how important reliable weather data is for analysing other data from Surtsey.

The impact of the solar radiation on the summer temperature in the soil is evident by comparing summer of 2021 and 2023, where mean air temperatures where similar but the first summer cloudier, resulting in lower soil temperatures.

Weatherwise, especially two periods had rather unusual weather. The summer of 2022 was cloudy and cool and during the winter 2022–2023 there were periods of warm and windy weather as well as very cold and calm.

Most weather observations from Surtsey are publicly available on www.athuganir.vedur.is, as 10-minutes, hourly, daily and yearly values. Soil measurements are at two locations and two depths, and it remains to find a way to publish them automatically. In the meantime, those data are available on request.

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TERRESTRIAL BIOLOGY

On fungi collected on Surtsey kept in the fungarium of the Natural Science Institute of Iceland, AMNH

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ABSTRACT

In the fungarium of the Natural Science Institute of Iceland in Akureyri, AMNH, are samples of many of the fungi collected on Surtsey. Some have been identified to species while other only to the genus level. The first author had collected macrofungi and overwintered plant parts with microfungi. Macrofungi collected in 2008 have been reported but those from 2010 were introduced in a lecture in 2013 but not in print until now. This summer the second author examined microfungi on the dried plant material from 2008 and the results are presented here. Eleven species of microfungi new to Surtsey and two reported earlier were identified. A list of fungi on goose dung from Surtsey in 2008 where all eight species were new records for the island is included. Those results were part of a larger study of coprophilous fungi of Iceland. The macrofungi reported here new to Surtsey are seven plus one myxomycete identified. Four additional unidentified species of three genera are also new to the island.

INTRODUCTION

In the first investigation on macrofungi on Surtsey in early July 2008 no agarics were found but overwintered plant material and plant-parasitic microfungi on their host and microfungi on driftwood were collected. In August 2008, during the second investigation, sporocarps of ectomycorrhizal fungi of the three *Salix* L. species growing on the island were collected. Other fungi and fungal-like organisms were also collected and the species found were presented (Eyjólfsdóttir 2009) listing six agaric species that were identifed and two additional species which were identified to the genus level growing with *Salix* spp. plants.

Four of the agaric species listed in Eyjólfsdóttir (2009) were *Hebeloma* P. Kumm. species, of which *H. vaccinum* Romagn. and *H. velatum* (Peck) Peck (first identified as *H. collariatum* Bruchet) are very rare in Iceland. While the saprophytic *Entoloma sericeum* Quél. was present in large areas of the older part of the gull colony, in the forb rich grassland vegetation type (Magnússon *et al.* 2022). Hence, the species was well established in that habitat, where it was first observed in 2005 (Baldursson & Ingadóttir 2007) now its sporocarps were in long lines and rings indicating the growing edge of its mycelia in the grassland.

In sparse vegetation at the edge of the gull colony a small agaric identified as *Arrhenia rustica* (Fr.) Redhead, Lutzoni, Moncalvo & Vilgalys *s.l.* has been growing from around 1990, when it was first collected. Later its occurrence has moved with the edge of the expanding gull colony, in primarily the *Cochlearia* sea-cliff vegetation (Magnússon *et al.* 2022).

The third saprophytic agaric, *Deconica subviscida* Peck (first identified as *Psilocybe inquilinus* (Fr.) Bres.), produced its sporocarps among dead parts of the grass *Leymus arenarius* L. where it grew in

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a sheltered area that retained moisture longer than the typical sandy soil of the island. In 2007 there had been 26 species of fungi and fungal-like organisms reported from Surtsey (Eyjólfsdóttir 2009) and in 2009 their number had increased to 33 (species identified to the genus level not included).

In 2008 three samples of goose dung were collected in July and two in August. Those samples were sent to Mike Richardson who incubated the goose dung in moist chambers and identified the fungi which fruited on the dung. Total of 8 species which all were new records for Surtsey, seven ascomycetes and one basidiomycete, and the findings were published by Richardson (2011) (Table 1).

Some fungi which have been found on Surtsey by other researchers and sent to the Natural Science Institute of Iceland are kept in the fungarium (AMNH). There is a table listing those seven received before 2008 in Eyjólfsdóttir (2009) with AMNH as reference.

In the culture collection of CBS of fungi and yeasts (Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands) is an isolate of the fungus *Talaromyces aerugineus* (Samson) Yilmaz, Frisvad & Samson from soil on Surtsey deposited by A. Sponring in 1996, CBS 176.97. This species is presumed to be from Klamer *et al.* (2000) research on microbial biomass and community composition in soils collected near a crevice between the craters Surtur and Surtungur in 1996. They reported the number of colony forming units, CFU, from four samples from bare soil, one from soil covered by moss and six from area with *Honkenya peploides* (L.) Ehrh. This fungus could be from the sample from warm soil with moss with the highest CFU number.

The third investigation of macrofungi on Surtsey took place on 18-20 of August 2010, when all the 10 *Salix* spp. plants known at the time were checked for sporocarps of ectomycorrhizal fungi. Sporocarps of other fungi were also collected on the island. The macrofungi collected on Surtsey during this investigation and are kept in the fungarium (AMNH) are the main subjects of this article.

The results of the investigations on macrofungi 2008 and 2010 were presented at the Surtsey 50th anniversary Conference (Eyjólfsdóttir 2013). Then the fungi that had been reported on Surtsey from 1965 to 2013 were 51 including 1 basidiolichen and three fungus-like organisms. The updated results on species of fungi and fungal-like organisms that are presented in this article were first presented as a list of species, habitat or substrate and the year of sampling at a seminar in 2025 (Eyjólfsdóttir & Lipiński 2025).

Recently, Almeida *et al.* (2022) published their results from a sequence-based identification of soil samples taken from 23 permanent study plots on Surtsey in 2014. They reported 18 new genera and 56 new species for Surtsey, not listed in the Eyjólfsdóttir (2009) survey. They, however, noted that such sequence-based methods on soil samples may also pick up species which stem from wind-borne spores that have accumulated in the soil, forming a dormant propagule bank, but would not be truly established. For this reason, we choose to focus on those species which were identified based on their sporophores collected on Surtsey or cultivated in the laboratory from material from Surtsey. In the checklist of Icelandic fungi and fungal-like organisms (Hallgrímsson & Eyjólfsdóttir in preparation) the species Almeida *et al.* (2022) listed are included and all fungi from Surtsey have Surtsey specified in the distribution of the species.

Table 1. Coprophilous fungi on goose dung collected on Surtsey in 2008, a species list extracted from Richardson (2011).

	Specimen no. in the article	**26/08**	**27/08**	**28/08**	**29/08**	**30/08**
	Surtsey grid system	**D16**	**D16**	**B16**	**P11**	**O11**
Species	**Collected on**	**8 Jul**	**8 Jul**	**8 Jul**	**11 Au**	**13 Au**
Ascobolus crenulatus P. Karst.		x				
Ascobolus stictoideus Speg.		x	x	x	x	x
Laetisaria fuciformis (Berk.) Burds.						x
Stemphylium vesicarium (Wallr.) E.G. Simmons					x	
Schizothecium vesticola (Berk. & Broome) N. Lundq.		x			x	
Sordaria fimicola (Roberge ex Desm.) Ces. & De Not.		x				
Sordaria minima Sacc. & Speg.			x			
Thelebolus stercoreus Tode		x	x	x	x	

METHODS

In 2008 fungi were collected in situ on Surtsey on July 7 to 10 and August 11 to 14. In 2010 fungi were collected August 19 to 20. Earlier that summer the known *Salix* sp. plants had been labelled with wooden pegs painted yellow and red and given numbers by a member of the biological expedition. *Salix herbacea L.*, two plants (no. 2; 11) were first found in 1995 estimated as two years old and additional two young plants (no. 5; 6) were present in 2010, increasing the total number of *S. herbacea* to four in 2010. *Salix phylicifolia* L. was first found in 1998, one plant (no. 1), but in 2010 there were in total three known plants (no. 7; 8). *Salix lanata* L. was first found in 1999 as one plant and in 2010 there were three *S. lanata* plants labelled (no. 3; 4; 9) (the first plant was then presumed dead).

The same methods as described in Eyjólfsdóttir (2009) were used in 2010 collecting, photographing, describing and drying the fungi and recording coordinates for each site and placing those in the 100 x 100 m grid system for Surtsey (Fig. 1).

In 2025 dried plant material collected on Surtsey in 2008 was examined by Maciej Lipiński and some of the microfungi identified. Those are reported in this article.

Dried plant material was examined using a dissecting microscope to locate fungi. Small slices of the plant tissue with what could be fungi were cut and placed on a microscope slide in a drop of water, allowed to soak, arranged on the slide and examined using a light microscope. If the fungus could be identified its name and plant host were listed and usually some spores were photographed through the lens of the microscope. Some of the samples did not include any useful fungal material for identification purposed.

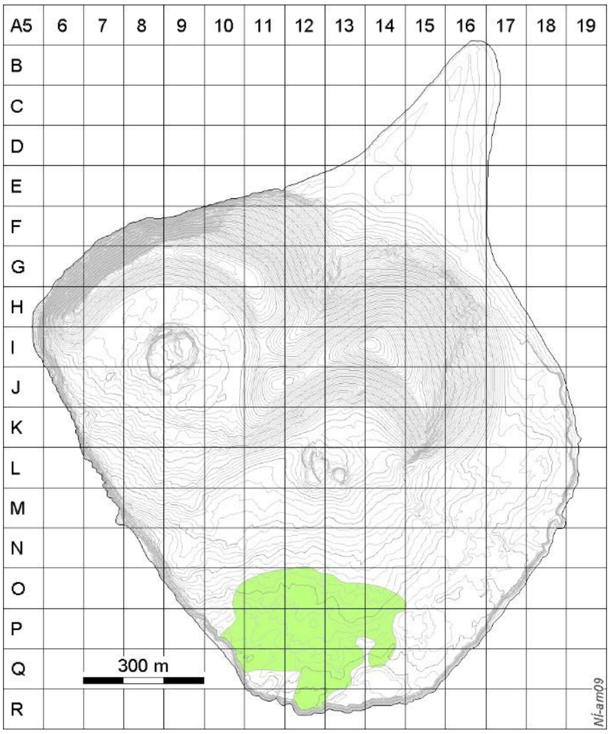

Figure 1. Surtsey in 2007 with the area of dense vegetation shown in green and the 100 x 100 m grid system for mapping distribution of plants and fungi on Surtsey. The names of quadrats of the grid e.g. (I8) or (O14), are used in the text to indicate the site where the fungus was collected.

Figure 2. The uredinia of *Puccinia festucae* infecting living leaves of *Festuca richardsonii* which show yellow bands where yellowish brown uredinia form. Surtsey, 9.07.2008 (Photo: GGE).

Figure 3. The growth of *Blumeria graminis*, a powdery mildew on living leaves of *Poa pratensis* on Surtsey on 11.08.2008 (Photo: GGE).

RESULTS AND DISCUSSION

From the dried plant material collected in 2008 one rust fungus and one powdery mildew, both parasitic fungi of grasses, were identified. It was *Puccinia festucae* Plowr. urediniospores II, in a living *Festuca richardsonii* Hook. within yellow bands in the leaves with yellowish brown uredinia (P14 on Fig. 1) (Fig. 2) and *Blumeria graminis* (DC.) Speer, a powdery mildew making the surface of living leaves of *Poa pratensis* L. white where mycelium and chains of conidia cover their surface (O13) (Fig. 3).

Two fungal-like organisms, oomycetes, were found. The former on recently dead shoots of *Stellaria media* (L.) Vill. and the other on still living but yellow shoots of a *Honckenya peploides* plant, making the surface of the infected area appear mealy. These were identified as *Peronospora alsinearum* Casp. on dead shoots of *Stellaria media* (P14) (Fig. 4) and *Peronospora honckenyae* (Syd.) Syd. parasitic on a living *Honckenya peploides* plant (C16) turning its leaves yellow and mealy (Fig. 5).

Ascomycetes either their sexual state or anamorphic state were identified on overwintered plant parts. The species found included the ascomycetes *Alternaria alternata* (Fr.) Keissl., *Lophodermium alpinum* (Rehm) Weese in (N16) (Fig. 6) and in (L17) *Leptosphaeria elymi* P. Larsen found on overwintered leaves or other parts of the grass *Leymus arenarius*. Further, *Cladosporium cladosporioides* (Fresen.) G.A. de Vries and *Cladosporium macrocarpum* Preuss grew on dead shoots of *Honckenya peploides* (I18) (Fig. 7). The latter had previously been found in soil on Surtsey. *Pleospora junci* Pass. & Beltrani that was found on overwintered parts of *Juncus arcticus* Willd. in sandy soil (N15), *Pleospora eleocharidis* P. Karst. was found on overwintered *Poa pratensis* in the oldest part of the gull colony (P12) (Fig. 8) and *Stemphylium botryosum* Wallr. on dead leaves of *Cochlearia islandica* Pobed. in sparse vegetation on smooth lava, *Cochlearia* sea-cliff vegetation (O14) (Fig. 9).

Figure 4. Dead shoots of *Stellaria media* and a few still living on Surtsey on 9.07.2008. The plant parasitic *Peronospora alsinearum* was present on the dead leaves (Photo: GGE).

Figure 5. A *Honckenya peploides* plant with yellow shoots infected by *Peronospora honckenyae* while green shoots are next to them. Surtsey, 8.07.2008 (Photo:GGE).

Species found in other dead organic habitats included *Corniculantispora psalliotae* (Treschew) Khons., Thanakitp. & Luangsa-ard growing on a mouldy sporocarp of *Deconica subviscida* Peck amongst a *Penicillium* sp. (M16-M17) (Fig. 10). This finding in 2010 was the third occurrence of this fungcolous species on Surtsey. *Ceriporia reticulata* (Hoffm.) Domański is a basidiomycete found growing on decaying driftwood (D15), forming soft,

Figure 6. In overwintered parts of this *Leymus arenarius* plant, two microfungi, *Alternaria alternata* and *Lophodermium alpinum* had formed their spores. Surtsey, 9.07.2008 (Photo: GGE).

Figure 7. In recently dead shoots of *Honckenya peploides* the fungi *Cladosporium cladosporioides* and *C. macrocarpon* produced their conidiophores. Surtsey, 9.07.2008 (Photo: GGE).

Figure 8. In overwintered parts of this *Poa pratensis* the ascomycete *Pleospora eleocharidis* was found on Surtsey, 9.07.2008 (Photo: GGE).

Figure 9. *Cochlearia islandica* plant where spores of *Stemphylium botryosum* were found on dead parts on Surtsey, 9.07.2008 (Photo: GGE).

Figure 10. Three fungi, the agaric *Deconica subviscida* which is covered in growth of an unidentified *Penicillium* sp. but the third species, *Corniculantispora psalliotae*, grew mixed with the *Penicillium* sp. and was found when its conidia were seen during examination of the specimen with a microscope. Surtsey, 19.08.2010 (Photo: GGE).

white, reticulate sporocarps in gaps inside the wood (Fig. 11). This was its first occurrence on Surtsey in 2008.

The fungal-like organism *Didymium spongiosum* (Leyss.) J.M. García-Martín, J.C. Zamora & Ladó, a myxomycete previously known as *Mucilago crustacea* P. Micheli ex F.H. Wigg., was present in four places in the lush grass in the oldest part of the gull colony (P12) in 2010 (Fig. 12).

One myxomycete (Fig. 12) and six saprophytic basidiomycetes were collected on Surtsey for the first time and two saprophytic basidiomycetes additional two ectomycorrhizal species of *Cortinarius* were indentified to the genus level in 2010 (Eyjólfsdóttir 2013). Thus adding ten agaric species (thereof four only identified to a genus) to the known funga of Surtsey (Table 3).

Figure 11. White sporocarps of *Ceriporia reticulata* on decaying driftwood on Surtsey. 8.07.2008 (Photo: GGE).

Figure 12. The myxomycete *Didymium spongiosum* having crawled up the grass before turning into a sporocarp which resembles bird droppings. Surtsey. 20.08.2010 (Photo: GGE).

The ten species of agarics treated below were found for the first time on Surtsey in 2010, thereof six were identified to species and four only to the genus level. The first two in the lush grass of the oldest part of the gull colony (P11), which both are presumed to be nitrophilous fungi growing in fertile soils (Gerhardt 2012). *Panaeolus fimicola* (Pers.) Quél. its sporocarps bigger and darker than those of *Panaeolus olivaceus* F.H. Møller growing in the same spot (Fig.13). The *Panaeolus* sp. collected in 1994 by Hörður Kristinsson in a *Puccinella* grassland (P12) in the gull colony also fits the description of *P. fimicola*.

Figure 13. *Panaeolus fimicola* and *P. olivaceus* growing together in the grassland on the fertile soil of the oldest part of the gull colony in Surtsey. 20.08.2010 (Photo: GGE).

At the edge of the oldest part of the gull colony on a lava ridge (P13) a tall, 20 cm tall and with 14 cm wide cap, a whitish mushroom grew in grass, *Agaricus arvensis* Schaeff., three sporocarps were found in 2010 (Fig. 14). The sporocarps have been found repeatedly since, and in July 2025, nine groups of *A. arvensins* were recorded inside a 37 x 15 m (555 m^2) area where *A. arvensis* was originally found in 2010. In total the groups contained 43 sporocarps (B.D. Sigurdsson, pers. comm.). Assuming that all are linked to the same hyphal network and the distance between sporocarp groups are representing its area, the average increase is size has coarsely been 37 m^2 per year, since 2010.

Just outside the oldest part of the gull colony (P13) in less dense grass where the vegetation resembles that of the heathland type, three agarics were found growing: *Hygrocybe conica* (Schaeff.) P. Kumm. (Fig. 15), *Entoloma sericellum* (Fr.) P. Kumm. (Fig. 16) and the third that has finally been identified as a *Gamundia* Raithelh. species based on its verruculose spores, probably *Gamundia xerophila* (Luthi & Röllin) Raithelh. ex P.A. Moreau & Courtec. (Fig. 17).

In 2010 there were ten known *Salix* spp. plants on Surtsey and only one of them had not produced any sporocarps present at the time of the investigations in August of 2008 or 2010 (Table 2).

Figure 14. *Agaricus arvensis* growing in a lush grassland on Surtsey. Two mature sporocarps and one younger with the partial veil in the process of becoming a ring. 19.08.2010 (Photo: GGE).

Figure 15. *Hygrocybe conica*, three sporocarps, blackening at the base of stipe. Surtsey, 19.08.2010 (Photo: GGE).

Figure 16. *Entoloma sericellum*, its gills becoming pinkish as the spores mature. Surtsey, 19.08.2010 (Photo: GGE).

Figure 17. *Gamundia xerophila*, two photographs of its single slender sporocarp on Surtsey. 19.08.2010 (Photo: GGE).

Figure 18. Small reddish brown sporocarps of *Cortinarius* sp. with squamulose cap, which could belong in the *C. comatus* complex, close to *C. sagarum*. Growing with *Salix herbacea* no. 5 in Table 2. Surtsey. 19.08.2010 (Photo: GGE).

While less production of sporocarps was observed in 2010 around some of the older *Salix* sp. plants than in August 2008, two young *S. herbacea* L. where no sporocarps had been seen in 2008 now each had one agaric species producing its sporocarp(s) within the plant. Furthermore, a *Salix lanata* plant which had not been found in 2008 now had one unidentified *Cortinarius* sp. amongst its short shoots in the lush grassland of the oldest part of the gull colony.

In 2010 two unidentified *Cortinarius* species were found, one at young *Salix herbacea* no. 5 (O14) where no fungi had been found in 2008, and the other at *Salix lanata* no. 9 (O12) a plant that had not been found in 2008 as the grass probably covered it (Table 2). The former (Fig. 18) resembles species in the *Cortinarius comatus* complex, having squamulose cap and small reddish brown sporocarps, close to *C. sagarum* Kokkonen (Kokkonen 2020). The latter *Cortinarius* species had pale reddish brown cap with pointed umbo and very pale brown stipe (Fig. 19) and might be the species *C. fulvescens* Fr. which Almeida *et al.* (2022) found in soil from this area using ITS2 metabarcode sequensing of fungi.

Bjarni Diðrik Sigurðsson found the large

Table 2. Fungi present in 2008 and 2010 around the 10 individual *Salix* plants on Surtsey in 2010. Grid points refer to Fig. 1.

***Salix* species**	**No.**	**Grid plot**	**Ectomycorrhizal fungi 2010**	**Ectomycorrhizal fungi 2008**
Salix herbacea	2	I8	*Hebeloma mesophaeum*	*Hebeloma mesophaeum*
Salix herbacea	11	O12	*Entoloma sp.* (beige cap)	*Entoloma* sp (beige cap), *Hebeloma velatum,* *Laccaria laccata,* *Cortinarius* sp. (*Telamonia* dark brown cap)
Salix herbacea	5	O14	*Cortinarius* sp. (*Telamonia* reddish brown squamulose cap)	No fungi
Salix herbacea	6	O13	*Hebeloma* sp. (young)	No fungi
Salix phylicifolia	1	I9	*Hebeloma mesophaeum* (young)	*Hebeloma marginatulum*
Salix phylicifolia	7	O13	*Inocybe lacera*	*Inocybe lacera,* *Hebeloma vaccinum*
Salix phylicifolia	8	O13	*Hebeloma mesophaeum*	*Hebeloma mesophaeum*
Salix lanata	3	N14	No fungi	No fungi
Salix lanata	4	O14	*Hebeloma mesophaeum*	*Hebeloma mesophaeum*
Salix lanata	9	O12	*Cortinarius* sp. (reddish brown, conical cap)	Plant not found 2008

Figure 19. *Cortinarius* sp. growing with *Salix lanata* number 9 in rich grassland in the oldest part of the gull colony on Surtsey. Surtsey. 20.08.2010 (Photo: GGE).

Figure 21 Unidentified grayish brown *Arrhenia* sp. in a depression in the lava at the edge of the gull colony on Surtsey. 19.08.2010 (Photo: GGE).

sporocarps of *Neolentinus lepideus* (Fr.) Redhead & Ginns on driftwood in 2012 (Fig. 20).

There are agarics which have only been identified to the genus level in the fungarium. One of those is a grayish brown *Arrhenia* species (Fig. 21) collected amongst lichenes, in moss and sparse grass sheltered in a depression in the lava at the edge of the gull colony (O14) in 2010. Another is a rather small *Galerina* species in a strong reddish-brown colour (Fig. 22) growing in moss in a depression in the crater Surtungur (I8). Young and small sporocarps of a *Galerina* sp. were found amongst low moss and lichens in two places (O14). These may or may not be the same species.

Figure 20. Sporocarp of *Neolentinus lepideus* on driftwood. Surtsey. 16.07.2012 (Photo: Bjarni Diðrik Sigurðsson).

Figure 22. *Galerina* sp. on moss carpet in the sheltered Surtungur crater on Surtsey. 20.08.2010 (Photo: GGE).

The only *Galerina* species on Surtsey which has been identified was collected in 2015 by Bjarni Diðrik Sigurðsson, growing on wet dead leaves of *Leymus arenarius* (Fig. 23). It was much larger than the sporocarps from the crater (Fig. 22) and was identified as *Galerina pseudomycenopsis* Pilát. It grows in the same habitat as *Deconica subviscida* and both species are brown but *G. pseudomycenopsis* has longer spores. In 2010 *D. subviscida* was found in three sites, thereof two new sites (M16/M17, M17,

Figure 23. *Galerina pseudomycenopsis* on dead parts of *Leymus arenarius*. 17.07.2015 (Photo: Bjarni Diðrik Sigurðsson).

M18).

Further, some *Entoloma* specimens kept in the AMNH fungarium, other than those of *E. sericeum* and *E. sericellum*, have not been identified to the species level yet. Based on the different habitats where those specimens were collected they could belong to different species.

In the future, more focused collection of overwintered plant material would allow recording of more of the saprophytic microfungi of different plants on Surtsey. We identified one rust species, one powdery mildew and two *Peronospora* spp. on living plants or plants which had died the summer the material was collected. There are probably more plant parasitic fungi on the island.

In summary, the preliminary results from the 2008 and 2010 investigations were first presented at the Surtsey 50th Anniversary Conference (Eyjólfsdóttir 2013), then the fungi known from Surtsey were 51 including 1 basidiolichen and three fungus-like

Table 3. A list of fungi and fungal-like organisms collected on Surtsey or isolated from soil samples or other material from the island 1965 to 2024. Species in AMNH fungarium are marked (x).The year collected refers to when samples were collected with reference to the results. A question mark in the gridplot column for marine fungi refers to the beach of the island but to an old *Leymus arenarius* dune for the Glomeromycota.

Species of fungi or fungal-like organisms[j]	Year collected	Gridplot	Habitat or substrate	AMNH
Fungi Ascomycota				
*Alternaria alternata (*Fr.) Keissl.	2008 [a]	N16	*Leymus arenarius*, overwintered	x
Alternaria botrytis (Preuss) Woudenb. & Crous	1972 [d]	B15	From 14°C sand near driftwood	
Ascobolus crenulatus P. Karst.	2008 [h]	D16	Goose dung	x
Ascobolus stictoideus Speg.	2008 [h]	B16; D16; O11; P11	Goose dung	x
Blumeria graminis (DC.) Speer	2008 [a]	O13	*Poa pratensis*, parasitic on living leaves	x
Cadophora fastigiata Lagerb. & Melin	1972 [d]	B15; F10	14°C sand near driftwood; 22°C tephra	
Cadophora malorum (Kidd & Beaumont) W. Gams	1972 [d]	D11	From 14°C black sand near driftwood	
Ceriosporopsis halima Linder	1965 [c]	?	On driftwood, marine fungus	
Cladosporium cladosporioides (Fresen.) G.A. de Vries	2008 [a]	I18	*Honckenya peploides*, on a dead plant	x
Cladosporium macrocarpum Preuss	1972 [d] 2008 [a]	I18; G16	14°C tephra; in *H. pepl.* dead shoots	x
Corniculantispora psalliotae (Treschew) Khons., Thanakitp., & Luangsa-ard	1968 [b] 1972 [d] 2010 [a]	M16-M17; G16; L11-L12; I8-I9	From 14°C light-colored tephra; soil from craters; on a mouldy agaric	x

Table 3, continued

Dinemasporium marinum Sv. Nilsson	1965[c]	?	On driftwood, marine fungus	
Epicoccum nigrum Link	1972[d]	H12	42°C tephra with green surface	
Halokirschsteiniothelia maritima (Linder) Boonmee & K. D. Hyde	1965[c]	?	On driftwood, marine fungus	
Lamprospora miniata De Not.	1990[i]	J13	On short moss on palagonite	x
Leptosphaeria elymi P. Larsen	2008[a]	L17	*Leymus arenarius*, overwintered	x
Lophodermium alpinum (Rehm) Weese	2008[a]	N16	*Leymus arenarius*, overwintered	x
Lulworthia medusa (Ellis & Everh.) Cribb & J.W. Cribb	1965[c]	?	On driftwood, marine fungus	
Octospora axillaris (Nees) M.M. Moser	1990[i]	O17	At *Bryum* moss by some fishbones	x
Onygena corvina Alb. & Schwein.	1994[i]	L12	Regurgitated pellet f. predat. bird	x
Paraboeremia putaminum (Speg.) Qian Chen & L. Cai	1968[b]	L11-L12; I8-I9	From soil in craters	
Penicillium citrinum Thom	1968[b]	L11-L12; I8-I9	From soil in craters	
Penicillium palitans Westling	1972[d]	E13	From 17°C soil of a dry pond	
Peziza varia (Hedw.) Röhl.	1990[i]	M15	On concrete foundations of Pálsbær hut	x
Pleospora eleocharidis P. Karst.	2008[a]	P12	*Poa pratensis*, overwintered	x
Pleospora junci Pass. & Beltrani	2008[a]	N15	*Juncus arcticus*, overwintered	x
Schizothecium vesticola (Berk. & Broome) N. Lundq.	2008[h]	D16; P11	Goose dung	x
Sordaria fimicola (Roberge ex Desm.) Ces. & De Not.	2008[h]	D16	Goose dung	x
Sordaria minima Sacc. & Speg.	2008[h]	D16	Goose dung	x
Stemphylium botryosum Wallr.	2008[a]	O14	*Cochlearia officinalis*, overwintered	x
Stemphylium vesicarium (Wallr.) E.G. Simmons	2008[h]	P11	Goose dung	x
Talaromyces aerugineus (Samson) Yilmaz, Frisvad & Samson	1996[e]	?	From soil	
Thelebolus stercoreus Tode	2008[h]	B16; D16; P11	Goose dung	x
Trichoderma harzianum Rifai	1972[d]	I9; M13	42°C soil, crat. edge; 24°C red lava	
Trichoderma viride Pers.	1972[d]	I9; E14	42°C soil, crat. edge; driftwood	
Fungi Basidiomycota				
Agaricus arvensis Schaeff.	2010[a]	P13	In grass on lava ridge	x
Arrhenia rustica (Fr.) Redhead, Lutzoni, Moncalvo & Vilgalys	1990[i] 2008[g]	O14; P14; J13; I8; K12; M11	In biological crust at edge of gull colony	x
Ceriporia reticulata (Hoffm.) Domański	2008[a]	D15	On driftwood, decay fungus	x
Deconica subviscida Peck	2008[g]	M16-M17; M18	*Leym. aren.*, dead, saproph. fungus	x
Entoloma sericellum (Fr.) P. Kumm.	2010[a]	P13	Heathland veg. in gull colony	x
Entoloma sericeum Quél.	2005[i] 2008[g]	O11; O13; P11; P12	In grassland in the gull colony	x
Galerina pseudomycenopsis Pilát	2015[a]	O12	*Leym. aren.*, dead, saproph. fungus	x
Gamundia xerophila (Luthi & Röllin) Raithelh. ex P.A. Moreau & Courtec.	2010[a]	P13	In heathland-like vegetation in gull colony	x
Hebeloma marginatulum (J. Favre) Bruchet	2008[g]	I9	Ectomycorrhizal with *Salix*	x
Hebeloma mesophaeum (Pers.) Quél.	2005 2008[g]	I8; I9; O14	Ectomycorrhizal with *Salix*	x
Hebeloma vaccinum Romagn.	2008[g]	O13	Ectomycorrhizal with *Salix*	x
Hebeloma velatum (Peck) Peck	2008[g]	O12	Ectomycorrhizal with *Salix*	x
Hygrocybe conica (Schaeff.) P. Kumm.	2010[a]	P13	In heathland veg. in gull colony	x
Inocybe lacera (Fr.) P. Kumm.	2008[g]	O13	Ectomycorrhizal with *Salix*	x
Laccaria laccata (Scop.) Cooke	2005 2008[g]	I8; O12	Ectomycorrhizal with *Salix*	x
Laetisaria fuciformis (Berk.) Burds.	2008[h]	O11	Goose dung	x

Table 3, continued

Lichenomphalia cf. *velutina* (Quél.) Redhead, Lutzoni, Moncalvo & Vilgalys	1971[i]	I9	A lichen	x
Neolentinus lepideus (Fr.) Redhead & Ginns	2012[a]	E16	On driftwood, decay fungus	x
Panaeolus fimicola (Pers.) Quél.	2010[a]	P11; P12	Lush grassland, oldest part of gull col.	x
Panaeolus olivaceus F.H. Møller	2010[a]	P11	Lush grassland, oldest part of gull col.	x
Puccinia festucae Plowr.	2008[a]	P14	*Fest. rich.*, parasitic on living plant	x
Fungi Glomeromycota				
Glomus hoi S.M. Berch & Trappe	1997[f]	?	AM mycorrhiz. fungus of *L. aren.*	
Scutellospora dipurpurescens J.B. Morton & Koske	1997[f]	?	AM mycorrhiz. fungus of *L. aren.*	
Fungi Mucoromycota				
Lichtheimia corymbifera (Cohn) Vuill.	1972[d]	J8	From 24°C black soil at crater border	
Mucor hiemalis Wehmer	1972[d]	M13	24°C moss-covered red lava stones	
Chromista Oomycota				
Aphanomycopsis bacillariacearum Scherff.	1965[c]	?	On an algae on beach	
Peronospora alsinearum Casp.	2008[a]	P14	On *Stellaria media*, dead plant parts	x
Peronospora honckenyae (Syd.) Syd.	2008[a]	C16	Living *H. pepl.*, parasitic fungus	x
Protozoa Myxomycota				
Didymium spongiosum (Leyss.) J.M. García-Martín, J.C. Zamora & Ladó	2010[a]	P12	In lush grassland in oldest part of gull colony	x

[a] Eyjólfsdóttir & Lipiński, 2025; [b] Schwabe, 1970; [c] Johnson & Cavaliere, 1968; [d] Henriksson & Henriksson, 1974;
[e] Klamer *et al.*, 2000; [f] Greipsson *et al.* 2002; [g] Eyjólfsdóttir 2008; [h] Richardson, 2011; [i] Baldursson & Ingadóttir (eds), 2007; [j] MycoBank Database.

organisms. This article adds some microfungi on overwintered plants and parasitic fungi on plants, bringing the total to 64 species of fungi and fungal-like organisms 45 of which are stored in the AMNH fungarium (Table 3). In addition at least seven species of macrofungi have not been identified to species.

From the more recent sequencing work of Almeida *et al.* (2022) it is clear that there are numerous other fungi on Surtsey some of which might produce sporocarps above ground. Documenting the development of the funga of Surtsey is a project that should continue for many years to come.

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Reviewed research article

Chromosome number, genome size and spore morphology of the Iceland-endemic fern *Struthiopteris fallax* in comparison with its related taxa

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ABSTRACT

Struthiopteris fallax (isl, *tunguskollakambur*) is an Iceland-endemic deer fern species known from a single geothermal site by the hot spring Deildartunguhver in Borgarfjörður, western Iceland. It is closely related to *Struthiopteris spicant* var. *spicant* (isl, *skollakambur*), a widespread species in northern Icelandic lowlands, typically found in areas with persistent snow cover. The present study investigated taxonomically relevant characteristics of *S. fallax*, including chromosome number, genome size and spore characteristics, in comparison with *S. spicant* var. *spicant* from Iceland and the Iberian Peninsula. Field-collected samples included fiddleheads or young frond tips for chromosome analysis with light/fluorescence microscopy (LM), and genome size estimation using flow cytometry (FCM). Fertile fronds were used for spore size measurement and morphological analysis via scanning electron microscopy (SEM). Spore size data were statistically evaluated. The LM results indicated that *S. fallax* is most likely diploid ($2n=2x=68$), like *S. spicant*. The present study is the first to document meiotic chromosomes in *S. fallax*, inferring its haploid gametic number of 34. The FCM results showed average 1C genome sizes of 6.96 pg for *S. fallax* and 6.91 pg for Icelandic *S. spicant*, with a combined average of 6.94 pg, only a 1.02% deviation from the single existing record for *S. spicant* in the Plant DNA C-values Database. The spore analysis by SEM showed that spores of *S. fallax* (mean equatorial length: 41.70 µm) are not statistically different in size from those of *S. s.* var. *spicant* from Iceland and Spain (means: 43.58 and 42.32 µm, respectively). On the other hand, the spore of *S. fallax* is clearly different in morphology from *S. spicant* in that it is oblate/elliptic in shape with smooth outline and filamentous pattern of perispore ornamentation, whereas the spore of *S. s.* var. *spicant* appears more rounded and angular in shape with irregular outline and rugulate/reticulate pattern of perispore ornamentation. These findings highlight the diagnostic value of spore morphology in fern taxonomy.

INTRODUCTION

The genus *Struthiopteris* Scop., which belongs to the leptosporangiate fern family Blechnaceae, comprises five temperate species, mostly from China and Japan, with *Struthiopteris spicant* (L.) Weiss (type species) having a circumboreal distribution (de Gasper *et al*. 2016; PPG I 2016). Recently, one new species was added to the list, that is, the Iceland-endemic *Struthiopteris fallax* (Lange) S. Molino, Gabriel y Galán & Wasowicz, upgraded from the variety status *S. spicant* var. *fallax* (Lange) Wasowicz & Gabriel y

Galán (Molino *et al*. 2019). Species investigated in the present study are *S. spicant* and *S. fallax*.

The fern species *Struthiopteris spicant*, or the deer fern, is distributed across northern temperate and arctic regions, but concentrated in two major clusters, in western N-America (Cousens 1981; Soltis & Soltis 1988; Nauman 2025a) and western Europe (Molino *et al*. 2019; POWO 2025). Previously, *S. spicant* was placed in the genus *Blechnum* L., as *Blechnum spicant* (L.) Roth, but a series of molecular and phylogenetic studies have indicated that *Blechnum* in the traditional sense is not a monophyletic group and this has led to the transfer of the species from *Blechnum* to *Struthiopteris*, as *S. spicant* (Gabriel y Galán *et al*. 2013; Perrie *et al*. 2014; de Gasper *et al*. 2016; Wasowicz *et al*. 2017a).

Struthiopteris spicant has a compact erect stem with frond rosettes growing from the apex, creeping rhizomes and dimorphic fronds (de Gasper *et al*. 2016). The sterile fronds are pinnate, lanceolate in the proportions 1:5 and form a rosette. The fertile fronds are longer than the sterile fronds, erect with narrower and more dispersed pinnae which bear sporangia on the underside in continuous bands. This widely distributed *S. spicant* is quite variable in its taxonomic circumscription for which several varieties have been proposed. Three varieties are recognized to date: *Struthiopteris spicant* (L.) Weiss var. *spicant* (hereon referred to as *S. s.* var. *spicant*); *Struthiopteris spicant* var. *homophyllum* (Merino) Gabriel y Galán & R. Pino (hereon referred to as *S. s.* var. *homophyllum*); and *S. spicant* var. *pradae* S. Molino & Gabriel y Galán (Molino *et al*. 2019, 2020). The present study includes two of these varieties, *S. s.* var. *spicant* and *S. s.* var. *homophyllum*. The latter variety is only included in a small part of this study. The variety *homophyllum* comprises smaller plants than the variety *spicant*, with erect fronds up to 20 cm, usually all sporogenous, monomorphic or subdimorphic, but has several morphoanatomical features overlapping with those of the variety *spicant* (Merino *et al*. 2019). *S. s.* var. *homophyllum* is endemic to the northwest of the Iberian Peninsula, in both Spain and Portugal (Molino *et al*. 2019).

There are two species of *Struthiopteris* in Iceland: *S. s.* var. *spicant* (isl, *skollakambur*) and *S. fallax* (isl, *tunguskollakambur*) (Kristinsson *et al*. 2018; Wasowicz *et al*. 2017b; Wasowicz 2021). The former, *S. s.* var. *spicant*, is by far the dominant species found mostly in the northern part of Iceland. It generally grows to 10-50 cm (Kristinsson *et al*. 2018), in lowland areas below 200 m, often in basins or crevices frequented by heavy snows (Wasowicz 2021). Globally, *S. s.* var. *spicant* is considered LC- least concern according to the IUCN Red List Categories and Criteria. It has, however, not been evaluated regionally for Iceland.

In contrast, the latter species, *S. fallax*, has the status of EN- endangered according to the IUCN Red List Categories and Criteria regionally, and is protected nationally (Wasowicz & Heiðmarsson 2019). This species is Iceland-endemic and has very limited distribution. It has so far been found only at one location in western Iceland, that is, by the hot spring Deildartunguhver in Reykholtsdalur (Fig. 1), where the soil temperatures reach about 30°C, in mosses or on bare ground at an altitude of 34 MASL (Wasowicz 2021). *S. fallax* differs from the common variety *S. s.* var. *spicant* in many ways (Kristinsson *et al*. 2018; Wasowicz *et al*. 2017b; Molino *et al*.

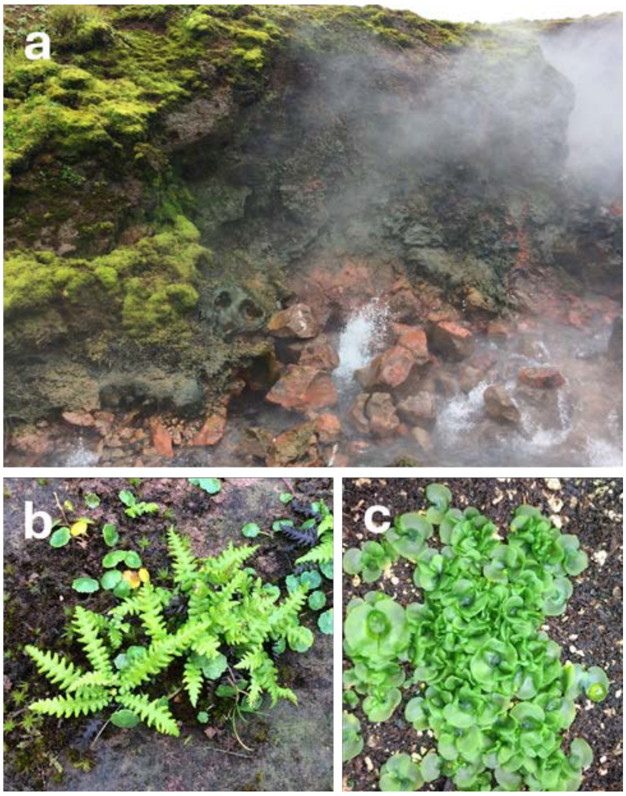

Figure 1. (**a**): Deildartunguhver geothermal hot spring in Reykholtsdalur, western Iceland. (**b**): *Struthopteris fallax* growing in the warm soil above Deildartunguhver. Diameter of the plant on the left is around 12 cm. (**c**): Gametophytes of *S. fallax* growing in a pot at Reykjavík Botanic Garden. Average size of the gametophytes is about 4 mm. They were germinated from spores collected in the field. These gametophytes later produced *S. fallax* sporophytes.

2019). Firstly, the environments in which the two species thrive are the opposite of one another, that is, in warm ground versus snow basins. Secondly, *S. fallax* is minuscule, measuring merely 2-8 cm. Thirdly, the fronds of *S. fallax* are prostrate but those of *S. s.* var. *spicant* have raised and slightly draping leaves. Fourthly and probably the most important, characteristic of *S. fallax* is its monomorphism. Instead of having architecturally different fertile and sterile fronds (dimorphism) like *S. s.* var. *spicant*, *S. fallax* has only one type of leaves, where the spore bearing leaves are morphologically the same as sterile leaves.

The present study investigated microscopical characteristics, including chromosome number, genome size and spore morphology and size, of *S. fallax* in comparison with *S. s.* var. *spicant* from Iceland and with reference to *S. s.* var. *spicant* and *S. s.* var. *homophyllum* from the Iberian Peninsula. The aim was to see if there would be any of such characters that can further differentiate between *S. fallax* and *S. s. var. spicant*. This could strengthen the species delineation, which so far has been based on macro- and micro-morphology, together with certain ecological and geographical preferences.

Chromosome number is the karyotypic feature most used in cytotaxonomical analyses (Guerra 2008). The chromosome base number (*x*), in particular, when constant confirms evolutionary relatedness among closely related species, but when variable can reflect evolutionary changes among species. In the traditional genus *Blechnum*, base chromosome numbers are variable, x = 28, 29, 31, 32, 34, 36 (Nauman 2025b). This is expected, however, as *Blechnum* is not monophyletic. Based on the Chromosome Counts Database (CCDB; Rice *et al*. 2015), existing records of chromosome number in *Struthiopteris* are extremely limited with only two records for *S. spicant*, one of *S. s*. var. *homophyllum* and no records on *S. fallax*. An additional reference on chromosome number of *S. spicant* from Iceland (Löve & Löve 1961) showed the same sporophytic number as in CCBD, which is diploid with $2n=2x=68$, implying $x=34$ gametic number (base number). Records on genome sizes of *Blechnum* are even more limited, i.e., with only one reference for *S. spicant*, which reported the DNA amount 1C as 6.44 pg (Pustahija *et al.* 2013). In the present study, we measured genome size and attempted chromosome extraction from leaf samples of both *S. fallax* and *S. s.* var. *spicant*. The mega analysis of genome size data by Clark *et al*. (2016) revealed strong correlation between genome size and chromosome number across all ferns. Thus, in the case of our study, genome size may be used to infer chromosome number, and vice versa. To the best of our knowledge, the present study is the first report of genome size of *S. fallax* and the first showing meiotic chromosomes from the monomorphic frond of *Struthiopteris*.

Recently, fern spores have been emphasized as a diagnostic feature of homosporous ferns, even at species specific level, in particular spore size and ornamentation (Passarelli *et al*. 2010). In the present study, we examined spores of *S. fallax* in comparison with its related taxa, using Scanning Electron Microscopy (SEM). We described morphological appearance of the spores from SEM images and statistically analysed spore sizes. The aim was to compare our data with those of Molino *et al*. (2020), the study that also included *S. fallax*. The knowledge of spores is important in understanding the taxonomy and evolutionary history of a species.

MATERIALS AND METHODS

Plant material

Plant species and varieties examined in the present study are listed in Table 1, together with their place of origin, sample identification numbers and the investigations performed. The Icelandic samples were collected during field trips in June and July 2016 and again in 2017. The *Struthiopteris* samples used in this study came from the only one location of *S. fallax*, Deildartunguhver (four samples from the field and three from RBG- Reykjavík Botanic Garden), five populations of *S. s.* var. *spicant* from diverse regions in Iceland (total nine field samples and two samples from RBG), two locations of *S. s.* var. *spicant* from Spain (one sample each) and one location of *S. s.* var. *homophyllum* also from Spain (one sample). Field samples from Iceland were collected by JBUT, KAJ and HÞ, authors of this manuscript, and they were identified by HÞ, Director of RBG. The samples for Spain were provided by JM Gabriel y Galán (University Complutense Madrid, Spain) and corroborated by P. Wasowicz (Icelandic Institute of Natural History, Akureyri, Iceland).

The Iceland-endemic species *S. fallax* was found growing on the warm ground just above the hot spring Deildartunguhver (Fig. 1). Deildartunguhver

Table 1. Samples used in this study.

Species of *Struthiopteris*	**Location**	**Origin GPS-Coordinates**	**Sample ID**	**Chromo-somes**	**Genome size**	**Spores by SEM**
S. fallax (Lange) S. Molino, Gabriel y Galán & Wasowicz	Deildartunguhver Borgarfjörður W-Iceland	64.66348°N 21.41075°W	DE 03	X		X
			DE-01, DE-02 & DE-04	X		
			RBG- Pot1S & Pot2S Sporophyte		X	
			RBG- Pot1G Gametophyte		X	
S. spicant (L.) Weiss var. *spicant*	Svanshóll Bjarnarfjörður NW-Iceland	65.78971°N 21.55871°W	BJ-02 (Bjarn 02)	X		X
			BJ-01, BJ-05 & BJ-06	X		
	Landmannalaugar (Brennisteinsalda) S-Iceland	63.98264°N 19.08941°W	LA-01	X		
	Héðinsfjörður (Grundarkot) E-Iceland	66.10055°N 18.81422°W	HE-01 & HE-02	X		
	Reykjanes (Trölladyngja) SW-Iceland	63.94981°N 22.09039°W	RE-01 & RE-03	X		
	Skútudalur Siglufjörður N-Iceland	66.123611°N 18.885556°W	ISL-03-2018-pl.1 & pl.2		X	
	Valdés, Paladeperre Spain	~43.783331°N 6.56667°W	AS JND09			X
	San Miguel de Valera, Salamanca Spain	~40.55000°N 5.91667°W	SA JND03			X
S. spicant var. *homophyllum* (Merino) Gabriel y Galán & R. Pino	Tabagón/Tomiño, Pontevedra Spain	~41.93333°N 8.78333°W	GA JND04	X		X

is a hot spring in the valley Reykholtsdalur in Borgarfjöður, western Iceland. Deildartunguhver is considered Europe’s most powerful hot spring, providing around 180 L/sec of 97°C hot water. It provides hot water for central heating in the nearby towns of Borgarnes and Akranes. Geothermal soil is usually a few to several degrees warmer than the ground in nearby areas, due to radiated heating from geothermal water channels that are present in the bedrock. In the case of Deildartunguhver, the soil temperatures that support *S. fallax* could be up to 30°C (Wasowicz 2021). Moderate soil warming promotes plant growth through an active root system and a healthy underground network of microorganisms. It is therefore expected that many plants growing on geothermal soil are either not able to grow in colder environments or they are species particularly adapted to a geothermal habitat, so-called thermophilic species. The geothermal area around this hot spring supports a relatively rich herbaceous vegetation that is typical of moist habitats such as bogs and marshes. In this hot spring area, mosses are the most prevalent component of the vegetation. According to the survey commissioned by the Icelandic Institute of Natural History (Kristinsson *et al*. 2007), mosses and bryophytes together formed 50 – 84 % of the total vegetation. This survey recorded population size of the fern *S. fallax* as comprising 200-300 plants essentially in the main area of about 10 m^2, the area of the Deildartunguhver site where *S. fallax* is most abundant.

Chromosome preparation

Developing fiddleheads, or small pieces of frond tips, were collected in the field. The fresh samples were placed immediately in ice water and kept in there at 4°C for 24-27 hours to arrest metaphases. The samples were then transferred into freshly made fixative composed of a 3:1 ratio of 96% ethanol and glacial acetic acid.

Chromosomes were prepared from these fixed samples using the protoplast-dropping method described in Anamthawat-Jónsson (2004). The fixed samples were first rinsed off fixative with distilled water and kept in water for 20 min. An individual sample was then prepared by trimming away older tissue with forceps leaving behind the youngest part about 1–2 mm in size. For each sample, 2–3 such pieces were placed in 100 µL of cellulase/pectinase enzyme mixture and incubated at 37°C for 16 h. The enzyme mixture contained Pectinase (30 units/mL, Merck no. 1.06021) and Cellulase Onozuka R10 (80 units/mL, Merck no. 1.02321) in buffer containing 75 mM KCl and 7.5 mM EDTA. The digested leaf tissue was then minced in its enzyme mixture into suspension using a 200-µL pipette tip. The suspension was filtered through a nylon mesh. The filtered cell/protoplast suspension was then hypotonically treated with 1.5 mL of cold 75 mM KCl solution for 15–20 min at room temperature. The suspension was spun down in a microfuge at 7,000 rpm for 5 min and the supernatant discarded. The cell/protoplast pellet was then cleaned with 1 mL of ice-cold fixative by resuspending and spinning down pellet, twice. The final, cleaned pellet was resuspended in 50-100 µL of fresh and cold fixative. The protoplast suspension was then dropped onto an ice-cold and water-wet microscopic slide from 10–20 cm height, one drop on each slide. When the drop just dried up, the slide was dipped briefly in 96% ethanol and air-dried. The slides were kept at 4 °C in a dry place until use.

The chromosomes were then stained for 1 min with a 1 µg/mL solution of blue-fluorescing DAPI (4,6-Diamidino-2-phenylindole), the fluorochrome that binds specifically to chromosomes (to the double-stranded DNA in chromosomes), not to cytoplasmic artefacts. The DAPI-stained cells were examined under 1000x magnification in the Nikon Eclipse E800 epifluorescence microscope. The images were captured with Nikon Digital Camera DXM1200F.

Flow cytometry

For genome size measurement by flow cytometry, fresh samples of fiddleheads or pieces of young fronds and gametophyte plants were sent by an express delivery to Vienna and kept in the meanwhile on wet tissue to avoid dehydration. Fresh sporophyte leaves (or fresh gametophyte tissue in one case) were co-chopped (Galbraith *et al*. 1983) together with an appropriate internal standard organism (*Pisum sativum*, 4.42 pg/1C, Greilhuber & Ebert 1994; *Solanum pseudocapsicum*, 1.295 pg DNA/1C, Temsch *et al*. 2010) in Otto´ buffer I (Otto *et al*. 1981) using a sharp razor blade. Subsequently, the nuclei isolate was filtered through a 30 µm nylon mesh and treated for 30 min with RNase A (0.15mg/mL, Sigma, USA) at 37°C in the water bath. For fluorescence staining, propidium iodide (PI, 50µg/ml, AppliChem GmbH, Germany) containing Otto´s buffer II (Otto *et al*. 1981) was added.

After incubation in the refrigerator, measurement was conducted on a CyFlow ML flow cytometer (Partec, Münster, Germany) equipped with a green laser (100 mW, 532 nm, Cobolt Samba, Cobolt AB, Stockholm, Sweden). Finally, genome size calculation followed the equation: ($G_{0/1}$ FI peak position$_{\text{Object}}$ / $G_{0/1}$ FI peak position$_{\text{Standard}}$)* 1C-value$_{\text{Standard}}$ = 1C-value$_{\text{Object}}$ (where FI is the mean fluorescence intensity).

Spore analysis

For spore analysis, whole leaves or pinnae were collected and dried in an envelope until use. In the present study, the spores were examined in SEM (Scanning Electron Microscope), model JEOL JSM 6610LA, located at the Institute of Life and environmental Sciences, University of Iceland. Spore samples were prepared by pouring loose spores from the drying envelope and carefully scraping them from the underside of dried leaf of each sample onto a sample plate, a double-sided adhesive carbon-dot (from Agar Scientific Ltd. UK). The cardon-dot with spores was placed on the specimen stub. Each set of stubs accommodated seven dots, or seven samples. They were then loaded into the SEM specimen chamber. All samples were imaged using BEIW (back-scattered electron imaging) mode with compositional contrast, low vacuum mode with pressure setting at 20 Pa (Pascal units), relatively high accelerating voltage of 10 kV, very short working distance of 8 mm between sample and detectors, zero tilt range and 45 mm spot size. For each sample, images at ×500, ×900 and ×1000 magnifications were taken from different areas on the sample dot.

SEM images were used for observing perispore patterns and for measurements of the spores. Description of the perispore pattern followed the terminology used in Passarelli *et al*. (2010). Spore size was measured from SEM images in a computer by using pixel coordinates and Pythagoras' theorem to calculate the length of the spores. In all samples the perispore (the outermost layer of the spore) was measured. The equatorial axis was measured as in Gómez-Noguez *et al*. (2016). The equatorial axis for irregularly shaped spores was defined as the length of the spore parallel to the laesura. For statistical purposes spores were on occasion pooled into four groups: *S. fallax*, *S. s*. var. *spicant* from Iceland, *S. s*. var. *spicant* from Spain and *S. s.* var. *homophyllum* from Spain. Statistics were performed in R version 4.5.1 using RStudio version 2025.05.1+513 for Windows.

RESULTS

Chromosome number by fluorescence microscopy

The *Struthiopteris* chromosome analysis is summarized in Table 2 and selected DAPI-stained cells are shown in Fig. 2. The aim of this part of the study was to obtain 2*n* mitotic chromosome number of each of the species and varieties investigated (Table 1). We adopted the protoplast dropping method developed for trees to prepare chromosomes from shoot-tips collected in the field (Anamthawat-Jónsson 2004). Although the method was successfully applied for diverse groups of plants, such as *Betula* L. (Thórsson *et al*. 2007), *Curcuma* L. (Puangpairote *et al*. 2016) and *Sorbus* L. (Anamthawat-Jónsson & Þorbjörnsson 2016), it was not tested in ferns. As it turned out, the chromosome preparation from leaf cells of the *Struthiopteris* ferns did not yield well-spread metaphases usable for chromosome counting. The problem was likely technical, for example, the hypotonic treatment was insufficient. Some of the samples were not good either. While fiddleheads were suitable as they contained active mitosis, mature leaves/ fronds were not. They contained differentiated cells, mostly, for example, RE-03 (*S. s.* var. *spicant* from Reykjanes) was dominated by spores. Leaf pieces of GA JND04 (*S. s.* var. *homophyllum* from Spain) only contained interphase cells. The sample was probably not ice-water treated, or chemically treated, to arrest metaphases.

In some samples that were prepared from fiddleheads, metaphases were present, but they were mostly too compact to allow chromosome counting. As the mitotic chromosomes were long and slender, they tended to overlap vastly. Nevertheless, rough estimates of chromosome number were

Table 2. Microscopic evidence for ploidy levels of *S. fallax* and *S. spicant* samples assorted by their origin, based on CCBD (Chromosome Counts Database, Rice *et al*. 2015), whereby *S. spicant* is mitotic diploid (2*n*=2*x*=68). N/A= Not applicable (due to either the leaf sample was too mature, hence no mitosis, or some technical reasons of the chromosome preparation).

Species	Origin	Sample ID	Ploidy	Microscopic evidence
S. fallax	Deildartunguhver Reykholtsdalur Borgarfjörður W-Iceland	DE-01	Fronds diploid containing some gametic haploid cells	Small cells, with 1-2 nucleoli. Larger cells, with 3-4 nucleoli.
		DE-02	Meiotic I	Metaphase with ≥30 chromosome pairs (Fig. 2a).
		DE-03	N/A	Numerous nucleoli
		DE-04	Gametic haploid included	Small cells mostly. Compact metaphases.
S. spicant var. *spicant*	Landmannalaugar S-Iceland	LA-01	Likely diploid	Long, slender (mitotitc) chromosomes. Large, compact metaphases (Fig. 2b). Nucleoli 2-4.
S. spicant var. *spicant*	Bjarnarfjörður NW-Iceland	BJ-01	Likely diploid	Chromosomes similar to other samples. Compact metaphases (Fig. 3c). Numerous nucleoli.
		BJ-02	N/A	Compact metaphases.
		BJ-05	Likely diploid	Compact metaphases.
		BJ-06	Likely diploid	Chromosome number >50 (Fig. 2d). At least 3 nucleoli.
S. spicant var. *spicant*	Héðinsfjörður E-Iceland	HE-01	Likely diploid	Large, compact metaphase. Nucleoli 2-4.
		HE-02	Likely diploid	Chromosome number >50 (Fig. 2e). Nucleoli 2-4.
S. spicant var. *spicant*	Reykjanes SW-Iceland	RE-01	Likely diploid	Metaphases similar to other samples. Nucleoli 2-4.
		RE-03	N/A	N/A Spores abundant.
S. spicant var. *homophyllum*	Tabagón Spain	GA JND04	Probably diploid	At least 3 nucleoli.

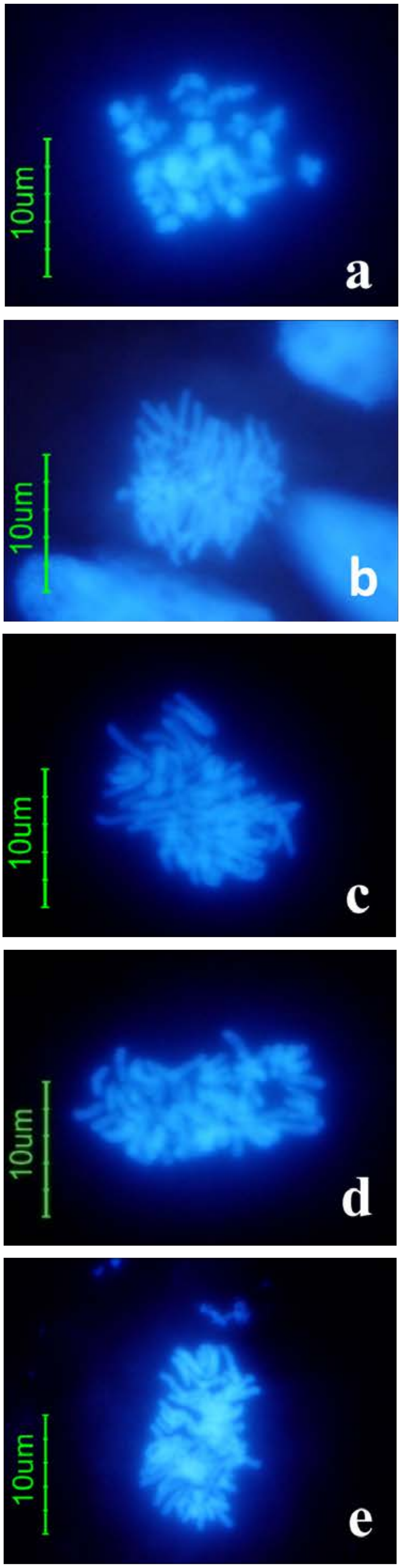

Figure 2. Results of the chromosome preparation from leaf tissues or fiddleheads of *Struthiopteris* sporophytes showing DAPI-stained metaphase chromosomes.

(**a**): *S. fallax* from Deildartunguhver, Iceland. Meiotic metaphase cell from sample DE-02 showing at least 30 pairs of chromosomes, which is not far from the expected gametic (1*n*) number of 34 for this species.

(**b**): *S. spicant* var. *spicant* from Landmannalaugar, S-Iceland. Mitotic metaphase cell from sample LA-01 showing a cluster of >50 chromosomes, which is the typical size and shape observed in this species/variety. It is most likely diploid with 2*n*=2*x*=68, rather than being any other ploidies.

(**c-d**): *S. spicant* var. *spicant* from Bjarnarfjörður, NW-Iceland. Mitotic metaphases from both samples, BJ-01 (**c**) and BJ-06 (**d**), are identical in both chromosome shape and cluster size, that is comprising well over 50 chromosomes. This variety/accession is most likely diploid with 2n=2x=68.

(**e**): *S. spicant* var. *spicant* from Héðinsfjörður, E-Iceland. Mitotic metaphase cell from sample HE-02 showing a cluster of >50 chromosomes, as with other accessions from Iceland, supporting that this species/variety is most likely diploid.

possible in some cases (Table 2). For example, BJ-06 and HE-02, both *S. s.* var. *spicant* from Iceland, each appeared to contain many more than 50 chromosomes. It is therefore likely that this variety is diploid (expected 2*n*=2*x*=68, as in CCDB, Rice *et al*. 2015), rather than being in other ploidy levels, as each level increases the 2*n* number by 34. One feature that is shared among all samples in the present study is that all metaphases, even partially analysable, are of the same overall size and the chromosomes are very similar in shape (see for example, Fig. 2b/ LA-01, Fig. 2c/ BJ-01, Fig. 2d/ BJ-06 and Fig. 2e/ HE-02). Furthermore, interphase nuclei, which were found abundant in all samples, are of the similar shape and size. They also showed similar number of nucleoli, 3-4 in each nucleus. It is therefore likely that all samples in the present study have the same ploidy level, which in this case is diploid with 2*n*=2*x*=68.

An interesting result coming out of this study is the discovery of cells undergoing meiosis in leaf tissues of *S. fallax* (Table 2). This is only possible because we isolated chromosomes from shoot-tips (fiddleheads or young fronds), not from root-tips. In the *S. fallax* plant DE-02, the first meiosis (meiosis I) was evident, whereby chromosomes were seen in pairs, and in this case showing at least 30 pairs (Fig. 2a). This means the gametic chromosome number of *S. fallax* is most likely 34, half of the diploid somatic number of 68. For other *S. fallax* plants investigated, such as DE-01 and DE-04, their leaf tissues contained both large and small cells. The large ones are presumably diploid sporophytic cells (before meiosis), and these nuclei tend to have 3-4 nuclei in each, like those of *S. spicant*. The small ones are presumably haploid gametic cells (after meiosis) and these cells showed 1-2 nucleoli in each. In conclusion, the sporophytic stage of *S. fallax* is most likely diploid with 2*n*=2*x*=68, just like *S. s.* var. *spicant*. The gametic stage of *S. fallax* is haploid with 1*n*=1*x*=34.

Genome size by flow cytometry (FCM)

The results of FCM (Table 3) show that there is no notable difference in genome size between the Iceland-endemic species *Struthiopteris fallax* (as measured from two transplanted sporophyte plants, twice, and from one gametophytic plant) and *S. spicant* var. *spicant* (two sporophytic plants) from Iceland. The results here are considered preliminary, however, given low replication and small sample size.

The earlier measurements (January 2018) produced almost the same 1C values for *S. fallax*. The average value of the two sporophytic samples was 6.94 pg, whereas the value from the gametophytic sample was 6.90 pg. Theoretically, the 1C-values of sporophyte- and gametophyte- derived genome size measurement must be the same (Temsch *et al.* 2021). The 1C-value refers to the DNA content of an unreplicated haplophasic nucleus (one chromatid per chromosome, one chromosome set per nucleus, i.e., as in a gamete). This is irrespective of the tissue types used for measurement.

The later measurements of sporophytic samples from Iceland (autumn 2018) included *S. fallax* (the same two samples measured before in January) and *S. spicant* var. *spicant* (two plants originally from Siglufjörður, northern Iceland). The former had the average 1C value of 7.00 pg and the latter had the average 1C value of 6.92 pg. The values of the two taxa are similar. It can be interpreted that *S. fallax* and *S. s.* var. *spicant* from Iceland are in the same ploidy level, that is both are diploid.

The results conform well with the author EMT's own measurement in 2014 of sample from an unknown subspecies of *S. spicant* from Rettenegg, Styria, Austria, whereby 1C value was 7.17 pg (unpublished results), only 3% higher when compared to the final average 1C value in the present study (that is 6.96 pg considering taxa together). One record of 1C DNA amount in the Kew C-values database (Pustahija *et al*. 2013) shows the value for *S. spicant* to be 6.44 pg, which seems different from the average value of 6.94 pg of *S. s.* var. *spicant* from Iceland (7.7% variation). In fact, the *Pisum sativum* standard C-value used by Pustahija *et al*. (2013) was lower (4.185pg/1C) than we used for our measurements (4.42pg/1C, Greilhuber & Ebert 1994). The resulting variance was therefore only 1.02-fold.

The difference in mean 1Cx values between the two measurement periods (January vs. September/October) is insignificant. Compared to the measurement in January, there is a higher variation among the recent samples (Table 3). This is probably due to the preparations and is not a true variation between the taxa. The peak-CV% were higher in the later measurements than in the measurements in January. The variation between the two taxa is low, only 1.0061-fold (*S. s. var. spicant*: mean = 6.9173 pg, CV% = 2.88%; *S. fallax*: mean = 6.9594 pg, CV% = 1.47%) when the January measurements of *S. fallax* samples were included, but 1.012-fold when only the autumn measurements were considered.

Table 3. Results of genome size measurements.

Sample	Species/ Variety	Generation	Date of measurement	1C value (pg)	1C average
Fallax RGB-Pot1S	*S. fallax*	Sporophyte	January 2018	6.99	6.94
Fallax RGB-Pot2S	*S. fallax*	Sporophyte	January 2018	6.90	
Fallax RGB-Pot1G	*S. fallax*	Gametophyte	January 2018	6.90	
Mean (January)				**6.93**	
Fallax RBG-Pot1S	*S. fallax*	Sporophyte	October 2018	7.1243	7.00
Fallax RBG-Pot2S	*S. fallax*	Sporophyte	September 2018	6.8761	
ISL-03-2018-pl.1	*S. s. var. spicant*	Sporophyte	October 2018	7.0584	6.92
ISL-03-2018-pl.2	*S. s. var. spicant*	Sporophyte	September 2018	6.7762	
Mean (autumn)				**6.9588**	
Standard deviation (autumn)				**0.1607**	
Coefficient of variation (autumn)				**2.3097**	

Spore morphology and size by Scanning Electron Microscopy (SEM)

Spore ornamentation and morphological appearance by SEM are summarized in Table 4 and representative images are shown in Fig. 3. Spores of *S. fallax* differ from other taxa in the present study in that they were oblate/elliptic with smooth outline and the perispore ornamentation was no obvious rugate, but instead a filamentous pattern resembling non-anastomosing veins (Fig. 3a-3b). Another difference encountered between *S. fallax* and other taxa under study was that *S. fallax* spores were more concave as if having a reduced or absent protoplast (Fig. 3c). The severity of this deformity differed among spores but was noticed in a large part of the spores examined. Spore samples of *S. s.* var. *spicant*, both from Iceland and from Spain, had more rounded and full appearance (not concave), angular in shape, and the outline was irregular with rugulate/reticulate pattern of perispore ornamentation (Fig. 3d-3f and Fig. 3g-3h). The pattern varied in intensity among samples, with most having an apparently thick perispore, as compared to the *S. fallax* samples, with consistent and obvious rugate ornamentation on the perispore. The spores of *S. s.* var. *homophyllum* from Spain (GA-JND04, Fig. 3i-3j) had the same appearance as *S. s.* var. *spicant*.

Exospores of *S. s.* var *spicant* were smooth, with long laesura (images not shown). The perispore appeared thick and were easily fragmented or cracked, exposing its smooth exospore. In contrast, the perispore of *S. fallax* appeared thinner and when ripped exposing its exospore (Fig. 3b).

Spore sizes, as measured in equatorial length of spores, are summarized in Table 4. The average equatorial length of spores in this study was 43.27 µm, which ranged between groups, from 41.7 to 47.09 µm. Spore equatorial lengths were normally distributed in all sample groups, as designated by a Shapiro-Wilk test, with $p > 0.05$ for all groups (Sokal & Rohlf 2012). The Levene's test for homogeneity of variances resulted in $p = 0.983$. A one-way analysis of variance (ANOVA) of equatorial spore length was performed on four groups of *Struthiopteris* sampling origins: *S. fallax* from Deildartunguhver, Iceland (n = 40, mean 41.7 µm, median 41.82 µm); *S. s.* var. *spicant* from Svanshóll in Bjarnarfjörður, Iceland (n = 16, mean 43.58 µm, median 43.48 µm); *S. s.* var. *spicant* from Spain, one sample from Paladeperre and one from Salamanca combined (n = 30, mean 42.32 µm, median 42.84 µm); and *S. s.* var. *homophyllum* from Pontevedra, Spain (n = 12, mean 47.09 µm, median 45.02 µm). The ANOVA analysis revealed a significant difference among the means of these four groups ($p < 0.05$). The follow up Tukey's test (Table 5) showed that the *homophyllum* variety had significantly larger spores than *S. fallax* ($p < 0.05$) and *S. s.* var *spicant* from Spain ($p < 0.05$).

Table 5. Results of a Tukey's honest significance test for equatorial spore length presented as a pairwise comparison in relation to the sample groups. Bold numbers with asterisk denote significant differences ($p < 0.05$). The four groups tested are (1) *S. fallax* (*Struthiopteris fallax*, (2) Var. *spicant* IS (*Struthiopteris spicant* var. *spicant*, Iceland), (3) Var. *spicant* ES (*S. s.* var. *spicant*, Spain), and (4) Var. *homophyllum* (*S. s.* var. *homophyllum*, Spain).

Group A	Group B	Mean Difference (µm)	p-value
Var. *homophyllum*	*S. fallax*	4.25	**0.03***
Var. *spicant* ES	*S. fallax*	-0.19	0.10
Var. *spicant* IS	*S. fallax*	1.00	0.09
Var. *spicant* ES	Var. *homophyllum*	-4.44	**0.04***
Var. *spicant* IS	Var. *homophyllum*	-3.25	0.26
Var. *spicant* IS	Var. *spicant* ES	1.19	0.86

Table 4. Spore morphology and size, where n stands for the number of spores examined. Spore ornamentational patterns were based on descriptions by Passarelli et al. (2010). The four groups examined are (1) *S. fallax* (*Struthiopteris fallax*, Deildartunguhver), (2) Var. *spicant* IS (*S. spicant* var. *spicant*, Bjarnafjörður, Iceland), (3) Var. *spicant* ES (S. s. var. *spicant*, Spain, SA JND03 and AS JND09), and (4) Var. *homophyllum* (S. s. var. *homophyllum*, Spain, GA JND04).

Sample group	n	Spore size Mean µm	Spore size Median µm	Spore outline	Perispore pattern	Concave
S. *fallax*	40	41.70	41.82	Smooth	Filamentous	Yes
Var. *spicant* IS	16	43.58	43.48	Irregular	Rugulate	No
Var. *spicant* ES	30	42.32	42.84	Irregular	Rugulate	No
Var. *homophyllum*	12	47.09	45.02	Irregular	Rugulate	No

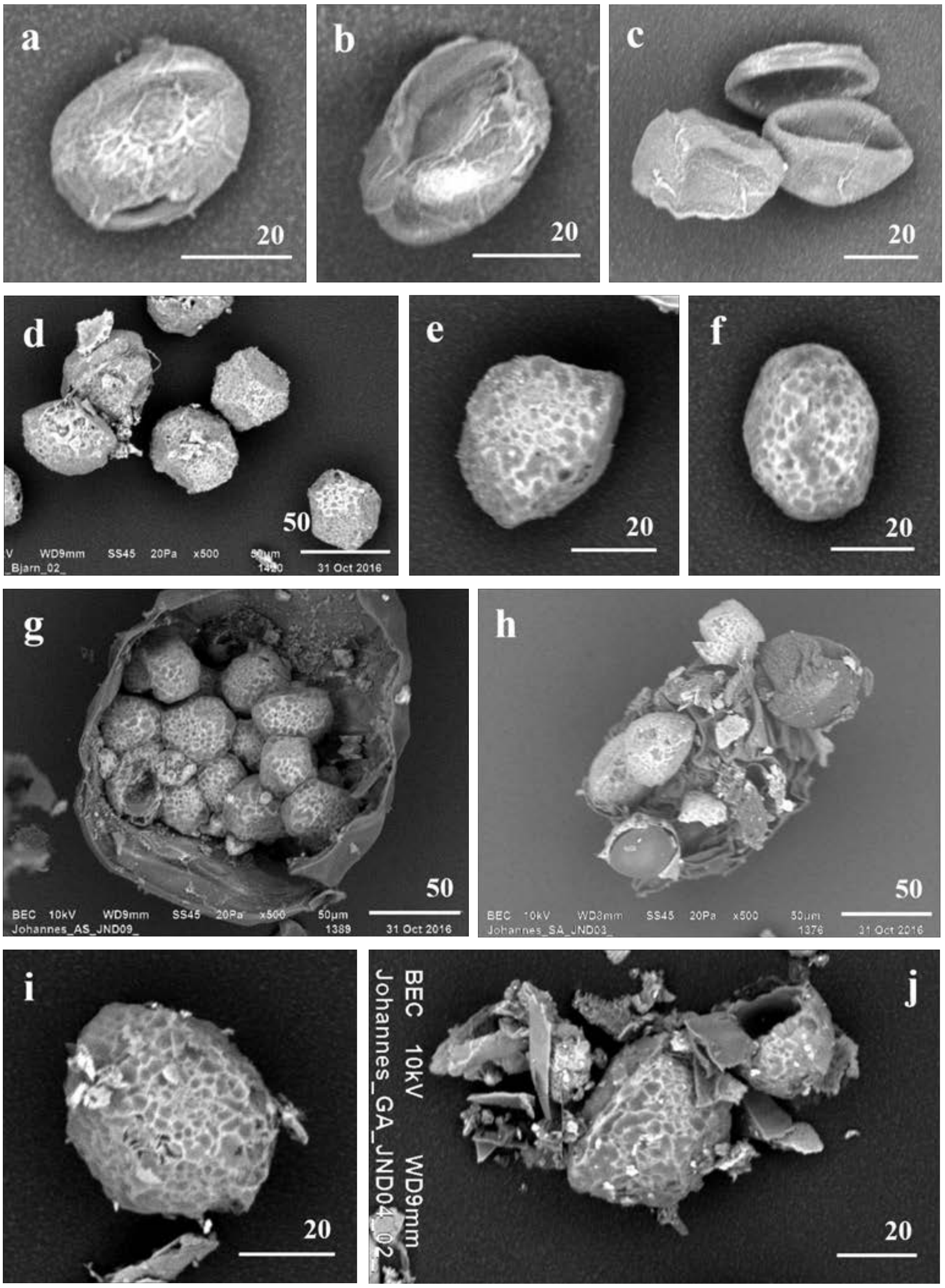

Figure 3. Representative SEM-images of spores from *Struthiopteris fallax* and *S. spicant*. Note different scales in µm.

(**a** – **c**): *S. fallax* from Deildartunguhver, Iceland: sample DE-03. The spores are oblate/elliptic, with relatively smooth outline and filamentous pattern of the perispore ornamentation, resembling non-anastomosing veins (**a**, **b**). The perispore appears thin and when ripped exposing its exospore (**b**). *S. fallax* spores tend to be strongly concave as if having a reduced or absent protoplast, resembling aborted spores (**c**).

(**d** – **f**): *S. spicant* var. *spicant* from Bjarnarfjörður, NW-Iceland: sample BJ-02. The spores are angular in shape but overall, they are more rounded than those of *S. fallax*. The perispore outline is irregular with rugulate or reticulate pattern of ornamentation. The perispore appears thick and brittle.

(**g** – **h**): *S. spicant* var. *spicant* from Spain: sample AS-JND09 from Paladeperre (**g**) and sample SA-JND03 from Salamanca (**h**). The spores shown here are contained in a sporangium (**g**). Spores from both accessions have similar morphology as those of *S. s.* var. *spicant* from Iceland (Bjarnarfjörður), that is, they are angular and with rugulate pattern of ornamentation. The perispore is clearly thick and when cracked exposing its smooth and filled exospore (**h**).

(**i** – **j**): *S. spicant* var. *homophyllum* from Spain: sample GA-JND04 from Pontevedra. The spores have the same morphology as those from *S. s.* var. *spicant*, both from Iceland and Spain. The perispore is also thick and brittle.

In summary, spores of *S. s. var. homophyllum* were relatively larger than spores of two of the other sample groups in the present study, but *S. fallax* had a unique appearance and ornamentation pattern of perispore compared to *S. spicant*.

DISCUSSION

The main subject of this study is the Iceland-endemic fern species *Struthiopteris fallax*. We investigated its chromosome number and measured genome size in comparison with its closely related species *S. spicant* var. *spicant* widely distributed in Iceland. We examined spores of these ferns, described spore morphology and evaluated spore size, in comparison to the Iberian varieties of *S. spicant*, i.e., *S. s.* var. *spicant* and *S. s.* var. *homophyllum*.

Struthiopteris fallax has the same genome size and chromosome number as S. spicant.

This paper is the first report of genome size of *S. fallax* and of *S. spicant* var. *spicant* from Iceland. The average genome size (1C value) of *S. fallax* is 6.96 pg, calculated from four measurements of two sporophytic samples and one measurement of gametophytic sample, whereas the average of *S. s.* var. *spicant* is 6.91 pg based on two sporophytic samples. We therefore interpret that these two taxa have the same genome size. One record of 1C DNA amount in the Plant DNA C-values Database (Leitch *et al*. 2019) shows the value of 6.44 pg for *S. spicant* (unknown variety), which is not far from the average value of *S. s*. var. *spicant* from Iceland or from that of *S. fallax*.

Current Pteridophyte genome size database covers about 2.8% of extant fern diversity (Clark *et al*. 2016; Pellicer & Leitch 2020), a significant increase from the previously low <1% taxonomic coverage by Bennett & Leitch (2012). In this new analysis (Clark *et al*. 2016), Blechnaceae (unknown number of species) has the mean ancestral a1C value of 12.06 pg, whereas Polypodiales (7192 taxa) has the mean extant 1C value of 12.19 pg. The Plant C-DNA Database (PC-DD, 2025) shows genome size of three *Blechnum*/ *Struthiopteris* species, *S. spicant* (6.44 pg, mentioned earlier), *B. microphyllum* (8.95 pg) and *B. numdum* (12.89 pg) (Leitch *et al*. 2019). This is all that is published regarding genome sizes in the polyphyletic genus *Blechnum*, far too little information to make any inference in the evolutionary context. But the most important point from the analysis is the confirmation of the positive relationship between holoploid genome size (1C) and chromosome number across all ferns (Clark *et al*. 2016), which is not the case with angiosperms or gymnosperms. Ferns are considered to have shown considerably greater stability in their chromosome structure over the last 400 million years (Haufler 2014), compared with the seed plants (Leitch & Leitch 2012). Based on this direct correlation between genome size and chromosome number among ferns, we assume that, as *S. fallax* has the same genome size as *S. spicant*, *S. fallax* also has the same chromosome number as *S. spicant*, that is, $2n=2x=68$.

Results from karyotyping in the present study were unclear as few cells from the samples taken were actively dividing and samples with visible chromosomes usually had a large and tight metaphase (see examples in Fig. 2). Precise chromosome count was therefore not possible but rough estimates could be made in some cases. As described in the result section, all the rough estimates indicated diploidy with $2n=2x=68$. This is the case of *S. spicant* var. *spicant* from all four different locations in Iceland, i.e., BJ- Bjarnafjörður (NW), HE- Héðinfjörður (E), LA- Landmannalaugar (S) and RE- Reykjanes (SW). In conclusion, *S. s.* var. *spicant* from Iceland is also diploid having 68 chromosomes like all other *S. spicant* elsewhere. All 27 records of chromosome number of *S. spicant* (registered as *Blechnum spicant*, no identification to varieties) in the CCBD-Chromosome Count Database show the sporophytic number $2n=2x=68$, where the base number x for this species is 34 (Rice *et al.* 2015).

Chromosome numbers in ferns, both $2n$ and x numbers, are generally higher than those among the seed plants (Leitch & Leitch 2012). The range of 2n chromosome numbers in all ferns (9118 taxa) is 18-1440, mean 121, whereas in Polypodiales (7192 taxa) the 2n range is 22-576, mean 114 (Clark *et al.* 2016). Blechnaceae of North America comprises six species in two genera, *Blechnum* (including *B. spicant* with $2n=68$) and *Woodwardia* Smith, all together the 2n numbers reported for this family are 56-72 (Nauman 2025b). For China and Asia, Blechnaceae comprises 14 species in eight genera (including *Blechnum* and *Struthiopteris*), all together the 2n numbers reported for this family are 66, 68, 74 and 136 (eFlora 2025). This 2n=136 (or 2x 68) is unique – it is *Woodwardia orientalis* Swartz, growing at relatively high altitudes in China, Taiwan, Japan and the Philippines. Overall, the most common 2n number from these two references is 2*n*=68, the number of *Struthiopteris* species in the present study. It is considered a diploid number, 2*n*=2*x*=68, where *x*= 34, as the ferns behave as genetic diploids.

Struthiopteris fallax undergoes meiosis early on at the fiddlehead stage.

The present paper shows for the first time meiotic cell division in young leaf tissue (fiddlehead) of *S. fallax*. We encountered metaphase cells in an unfurling leaf, which showed the chromosome count of ≥30 (sample DE-02). The chromosomes were condensed and appeared in pairs, typical of those in meiotic metaphase I, in contrast to the long and slender mitotic chromosomes of *Struthiopteris*. We interpret this as diploid spore mother cells undergoing meiosis to produce spores. We also found that older frond tissue (sample DE-03) comprised differentiated cells and mature spores, with no meristematic cells left among them. Spores collected for SEM imaging also came from this plant DE-03. The other samples studied (DE-01 and DE-04) showed a mixed cell diversity, comprising large interphase nuclei with 3-4 nucleoli and small nuclei with 1-2 nucleoli, presumably sporophytic diploid and gametophytic haploid cells, respectively. As proposed earlier, *S. fallax* is comparatively diploid with the sporophytic chromosome number 2*n*=2*x*=68, like *S. spicant*, the discovery of meiosis here means that the gametic (and gametophytic) chromosome number of *S. fallax* is haploid with 1*n*=1*x*=34. The same gametophytic count was found in the Iberian variety *S. s.* var. *homophyllum* (Horjales et al. 1990). Eight out of 27 records of chromosome number of *S. spicant* (no identification to varieties) in the CCBD also show the gametophytic number *n*=34 (Rice *et al*. 2015). These records, however, might simply be the sporophytic number 68 divided by two, or it is the number from gametophyte plants. We believe we are the first to report the gametic number from a fertile frond.

Struthiopteris fallax is a monomorphic fern, that is, sterile (vegetative) frond and fertile (soriferous, spore producing) frond are architecturally the same (Wasowicz *et al*. 2017b). But are they two separate fronds? All four plants of *S. fallax* in the present study held evidence of meiosis or spore production, although the samples collected for chromosome analysis were at a very young stage (such as in the fiddlehead stage). These young fronds may have been considered non-reproductive (sterile) simply because spores are not visible to the naked eye. Microscopically, all fronds of *S. fallax* appear to be fertile. As noted by Molino et al. (2019), most fronds of *S. fallax* are fertile. This could be considered as an extreme case of fern monomorphy, whereby the frond has dual functions, both photosynthesis and reproduction. The photosynthesis is to build up energy and the reproduction spends it.

Fertile–sterile dimorphy in ferns appears to come at considerable carbon cost in dimorhic species (Watkins Jr. et al. 2016), as carbohydrates must be transported to the sori from other leaves or other parts of the plant. This same study also found that for dimorphic species there were approximately 80% more sterile fronds produced than fertile fronds, a consistent pattern both within and across individuals, but in the monomorphic taxa this phenomenon was reversed. It means that to support the expensive reproduction system, dimorphic species produce prolific vegetative growth, and that requires rich environment both above ground (light and CO2) and below ground (water and minerals). In the case of the Iceland-endemic fern *S. fallax*, the dual-functioning monomorphy must have ecological and physiological advantages, that is, it can survive limited resources. The plant study by Raven & Griffiths (2015) suggested possible evolutionary benefits of photosynthesis in reproductive structures to include decreasing the carbon cost of reproduction (due to short distance between photosynthesis and reproduction) and using transpiratory loss of water to deliver phloem-immobile minerals via the xylem (more effective transport system within plant).

Struthiopteris fallax differs in its spore morphology from that of S. spicant.

Although preliminarily, cytotaxonomic analysis in the present study does not differentiate *Struthiopteris fallax* from *S. spicant*. But morphologically and ecogeographically, *S. fallax* stands out, thus it received the species status (Molino *et al*. 2019). The question left is whether spore morphology can differentiate the two closely related species. Our study shows that it does. Spores have been used to separate fern taxonomic groups, thus becoming an extremely important source of character traits with taxonomic relevance, mainly the spore dimensions, the model of laesura, and the perispore ornamentation and structures (e.g., Passarelli *et al*. 2010).

Results from the measurement of spore size, based on equatorial length of perispore from SEM images, do not indicate that there is a considerable difference between the spores of *S. fallax* (mean size 41.7 µm) and spores of *S. spicant* var. *spicant* (Iceland: mean size 43.58 µm; Spain: mean size two accessions combined 42.32 µm) (Table 4). The difference is not statistically significant either (Tables 5). Molino *et al.* (2020) measured spore size (equatorial length of exospore) under light microscope (LM) and found that *S. fallax* from Iceland had larger spore size (43.33 µm, n=20-30) than *S. s.* var. *spicant* from Spain (40.37 µm, n=20-30), but the difference was not statistically tested. In our study, we measured perispore, not the exospore, which placed the *S. fallax* on the smaller, rather than larger, end of the spectrum of our spore samples. In our results, we note that the perispore of *S. fallax* appeared thinner than that of the other taxa. Furthermore, spore sizes from different studies, using different microscopies, e.g. LM vs. SEM, cannot be compared directly.

As stated in the results, the mean spore size of all taxa in the present study combined is 44.27 µm. The measurements in this study were performed with the perispore intact, therefore 2-3 µm (estimated from SEM images) should be subtracted from the values given here, thus the mean exospore size in the present study becomes 42-43 µm. This fits well within the exospore size range of 35-50 µm reported by Passarelli *et al*. (2010) for *S. spicant*. Another paper describes *S. spicant* spores from Poland as ranging within 34-48 µm, although it is not clear whether that applies to the exospore or perispore length (Zenkteler 2012).

We also measured spore size of *S. s.* var. *homophyllum* from Spain and found mean perispore size of this variety to be 47.09 µm (Table 4), which is significantly larger than that of *S. s.* var. *spicant* from Spain and *S. fallax* (Table 5). Molino *et al.* (2020) reported the opposite, that is, the exospore size of *S. s.* var. *homophyllum* from Portugal (38.01 µm) was smaller than that of *S. s.* var. *spicant* (40.37 µm). The pattern of ornamentation on perispore is also quite different. In our study, the rugulate/reticulate pattern of this variety is the same as that of *S. s.* var. *spicant* from Spain (Fig. 3). In Molino *et al.* (2020), the spore of *S. s.* var. *homophyllum* appears less rugulate and more filamentous than that of *S. s.* var. *spicant*, somewhat similar to the spore of *S. fallax* in their study. We have no explanation for this discrepancy, but as *S. s.* var. *homophyllum* is not the focus of this paper we just leave it at that.

The most important point of the spore analysis in our study is that the spores of *S. fallax* exhibit certain differences in spore morphology and ornamental pattern from the spores of other taxa (Table 4, Fig. 3). Ornamentation on the perispore is an important diagnostic tool in fern taxonomy. *Struthiopteis spicant* s.l. has rugulate spores (Zenkteler 2012; Mazooji & Salimpour 2014; Molino *et al*. 2020), which is the predominant ornamentation pattern in Blechnaceae (Passarelli *et al*. 2010), and so do all samples in the present study with one exception. The spores of *S. fallax* are ornamented bearing filamentous and smooth pattern. This pattern appeared on the perispore of spores obtained from nature and from transplanted plants kept in a greenhouse sampled at different times. We therefore regard this perispore pattern to be consistent for *S. fallax*. Possibly, the pattern observed on the perispore of *S. fallax* is a less intense expression of the typical *S. spicant* pattern rather than a novel ornamentation. Interestingly, the perispore ornamentation of *S. fallax* shown in Molino *et al*. (2020) is also rugulate/filamentous like that discovered in our study.

Struthiopteris fallax also show different spore morphology from that of *S. spicant* var. *spicant*. Spores of *S. fallax* are oblate/elliptic in an overall shape, whereas spores of *S. s.* var. *spicant* are more rounded and angular in shape (Fig. 3). The angular spore shape of *S. spicant* is illustrated in Passarelli *et al*. (2010, Fig. 3D) and Molino et al (2020, Fig. 6f). Furthermore, spores of *S. fallax* often appear concave as if having a reduced protoplast. This characteristic was also consistent throughout repeated sampling of *S. fallax* over time and was not found in *S. spicant* varieties in the present study. The reason for this morphology is unknown. Wagner Jr. *et al.* (1986) mentioned that concave structure of spores is a symptom of spore abortion or that spores could have been immature when collected. While this may be the case, other symptoms of spore abortion and of immature spores are either incompatible or contrary to the morphology of the samples, for example, abortive and immature spores show great variability in spore size, perispore thickness and size and shape of the laesura (Wagner Jr. *et al*. 1986), but our samples appeared consistent in all of these traits, and even showed less variability than samples of *S. s.* var. *spicant*. We have obtained numerous gametophytes from spores of *S. fallax* in a greenhouse (e.g. Fig. 1c), clearly indicating that *S. fallax* is fertile. We have further obtained a few sporophyte plants belonging to *S. fallax* from these gametophytes.

Nevertheless, say that the *S. fallax* spores are often abortive, the fertility of the sporophytes may not be as much compromised if the species is highly spore productive. Indeed, *S. fallax* is most likely a spore productive species. Peck *et al*. (1990) evaluated several life history attributes of temperate North American ferns, including estimating annual spore production of several species. They found a clear difference in annual spore production across dimorphic species: the monomorphic taxa in their study produced an average of 151,000 million spores per plant per year, followed by 29,000 million in holodimorphic and 7,500 million in their hemidimorphic species. Such differences are dramatic. For *S. fallax*, being a monomorphic fern gives the species the advantage of producing huge quantity of spores compared to dimorphic ferns such as *S. spicant*, hence *S. fallax* should be able to afford spore abortion due to environmental stresses. Clearly as *S. fallax* thrives in an extreme environment, i.e. warm geothermal soil and cold air above ground, the species may not be able to support full spore production, that is the production of high-quality spores. There are several examples of flowering plants that when under stress during seed development stages, such as drought, heat, salt or nutrient stress, they allocate their limited resources (due to low photosynthetic rates) to produce low number of good seeds and leave the rest empty or aborted, rather than filling all seeds halfway (e.g. Contreras *et al*. 2008 for lettuce; Farahani *et al*. 2010 for barley; Cohen *et al*. 2021 for soybean).

The diagnostic value of fern spores has been acknowledged in the taxonomic classification at the genus or species levels. Spore ornamentation has distinct diagnostic value even at specific level for *Blechnum* species (Passarelli *et al*. 2010) and novel *Blechnum* species from Brazil, such as *B. areolatum* Dittrich & Salino and *B. longipilosum* Dittrich & Salino, have been assorted into groups based on perispore ornamentation and their spore size. Their spore ornamentation was also used to support their distinction as separate species (de Oliveira Dittrich *et al*. 2012). Although *Struthiopteris* has recently been segregated from *Blechnum* (de Gasper *et al*. 2016), there are indications that spore ornamentation could also be a useful complementary tool in *Struthiopteris* taxonomy since *S. spicant* appears to have unique spores when size and ornamentation are considered together (Passarelli *et al*. 2010). The above results of *S. fallax* spore ornamentation are therefore interesting as they indicate that the spore ornamentation of *S. fallax* is not the same as that of its closely related *S. spicant* var. *spicant*. Our results of the spore analysis could thus support the species status of the Iceland-endemic *Struthiopteris fallax*.

CONCLUSION

The aim of this paper was to investigate the spores, chromosome number and genome size of the Iceland-endemic fern *Struthiopteris fallax* and to compare it with its closely relates species *S. spicant* var. *spicant*. The results are that although the chromosome number and genome size are most likely to be the same between the two, *S. fallax* spores differ significantly in appearance. Our results are consistent with the current recognition of *S. fallax* as a distinct species, based on previously established morphological and ecological differences.

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ETHICAL STATEMENT

Not applicable

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Variation in the chlorophyll content index (CCI) in pioneer plants on Surtsey

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ABSTRACT

A plant community, dominated by *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa*, has formed a relatively stable successional sere on most of the Surtsey island. A handheld instrument for measuring Chlorophyll Content Index (CCI) was tested in July 2012 on both species at 23 permanent study plots found on all the main surface types of the island. By grouping the plots based on the conditions of their surroundings, it could be derived how differences in water availability, nutrient availability and soil depth affected the CCI of those two species. Both had significantly higher CCI values ($p = 0.004$) when they grew on plots that received additional runoff water from nearby impermeable palagonite tuff surfaces, indicating that water availability could be an important limiting factor. Increased depth of the rooting substrate also significantly enhanced the CCI values for both species ($p = 0.001$), indicating again that soil resources (water and nutrients) were indeed limiting for both species. Plots with allochthonous nutrient inputs (located within a seagull colony) also had a strong interaction with the depth of the rooting substrate (<0.001), yielding the highest CCI values where both conditions were met. It is concluded that chlorophyll content meters have the potential to enable rapid assessment of the relative resource acquisition of pioneer plant species, giving valuable insights into their adaptations to different environmental conditions.

INTRODUCTION

Surtsey is the youngest island of the Vestmannaeyjar archipelago, which is located on an insular shelf 32 km off the south coast of Iceland. The island surfaced during an eruption in 1963-1967 and was protected already by 1965 to serve as a laboratory of how life establishes on an isolated volcanic island. With time it has become one of most studied ecosystems in Iceland (Baldursson & Ingadóttir 2007).

A plant community, dominated by *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa*, has formed a relatively stable successional sere on most of the Surtsey island (Magnússon & Magnússon 2020, Magnússon 2022). It is only less dominant within a seabird colony on its southern part, where it has been partly replaced by different heathland and grassland species and on the palagonite tuff surfaces, where no vascular plants can colonize due to a lack of loose substrate for root growth.

Most terrestrial biology studies on Surtsey have focused on the colonization and community changes in flora, fauna and microbes (e.g. Fridriksson 1992, Ilieva-Makulec *et al.* 2015, Marteinsson *et al.* 2015, Magnússon S. *et al.* 2022, Magnússon B. *et al.* 2023, Ólafsson & Alfreðsson 2025) and only a few have been on the underlying ecophysiological and ecosystem processes (*e.g.* Sigurdsson 2009, Leblans *et al.* 2014, Sigurdsson & Stefánsdóttir 2015, Sigurdsson *et al.* 2022).

The Chlorophyll Content Index (CCI) is a non-destructive, relative measure of the amount of chlorophyll in a plant tissue, often used to explain variations in plant nutrient status or aboveground net primary production (Liu *et al.* 2019). It is calculated using a device that measures the ratio of light transmittance at a near-infrared wavelength (around 930 nm) to that in the red region (around 653 nm). Higher CCI values indicate greater chlorophyll content (Cate & Perkins 2003, Parry *et al.* 2014). The

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CCI is a unitless value, usually within the range of 1.0 (no pigment) to about 70.0 (very high pigment content), depending on instrument make and model (Cate & Perkins 2003).

The Chlorophyll Content Index has not been studied before on Surtsey, but Sigurdsson *et al.* (2022) did a study on three other vegetation indices and related them to variation in soil water availability, net photosynthesis rates and vegetation cover. Those were Normalized Difference Vegetation Index (NDVI), Photochemical Reflectance Index (PRI) and Clorophyll/Carotenoid Index (CCI). The last index mentioned is not the same as studied in this paper, albeit the same abbreviation (CCI), which here will only be applied to the Chlorophyll Content Index. The Clorophyll/Carotenoid Index uses different reflected wavelengths (around 532 nm and 630 nm) than the CCI.

The following hypotheses were put forward when the study was designed:

I. *Morphological differences*. Many plant species growing where light availability is a limiting factor, such as within mixed canopies of different species, distribute chlorophyll unevenly in space, and increase its contents where it is more likely that the leaf will receive higher light levels (top of canopy and upper surface of thicker leaves) (Chapin *et al.* 2011). As both studied species are pioneer species where light competition is normally not strong, I did not expect CCI to differ much between upper and lower leaf surfaces.

II. *Water availability:* There are certain permanent study plots located next to the impermeable palagonite tuff craters in Surtsey which receive lateral rainwater discharges and a significant increase in net photosynthesis per surface area has been documented there for the two pioneer species (Sigurdsson 2009, Sigurdsson & Stefánsdóttir 2015). If water is a strong limiting factor for the pioneer plants on the island I expected CCI to be higher on those plots for both species.

III. *Species differences.* Both species are pioneer species that invest mainly in belowground root growth, while maintaining relatively small but physiologically active aboveground parts (Leblans *et al.* 2014, Stefansdóttir *et al.* 2014). Therefore, I did not expect much difference in the CCI values for the two species, and that both would have relatively high CCI per unit leaf area.

IV. *Nutrient availability.* Many studies have documented how nutrient availability has increased within the seagull colony on the south part of Surtsey because of allochthonous nutrient inputs the birds have transferred from sea to land (Magnusson *et al.* 2000, Leblans *et al.* 2014, Aerts *et al.* 2020) and both photosynthetic rates per surface area and NDVI have been found to be significantly higher there (Sigurdsson *et al.* 2022). I expected that both species would invest in more chlorophyll content per leaf area on plots within the seagull colony.

V. *Depth of rooting media.* Leblans *et al.* (2014) showed that vegetation biomass accumulation and accumulation of soil organic matter (SOM) and nitrogen (N) was significantly different between plots established on lava with shallow depths of substrate for root growth, compared to plots established on deeper tephra sand areas. The reasons for this are likely partly related to H_{II} and H_{IV}. I expected that this would also be mirrored in the CCI of the plants growing on plots with contrasting "soil depth".

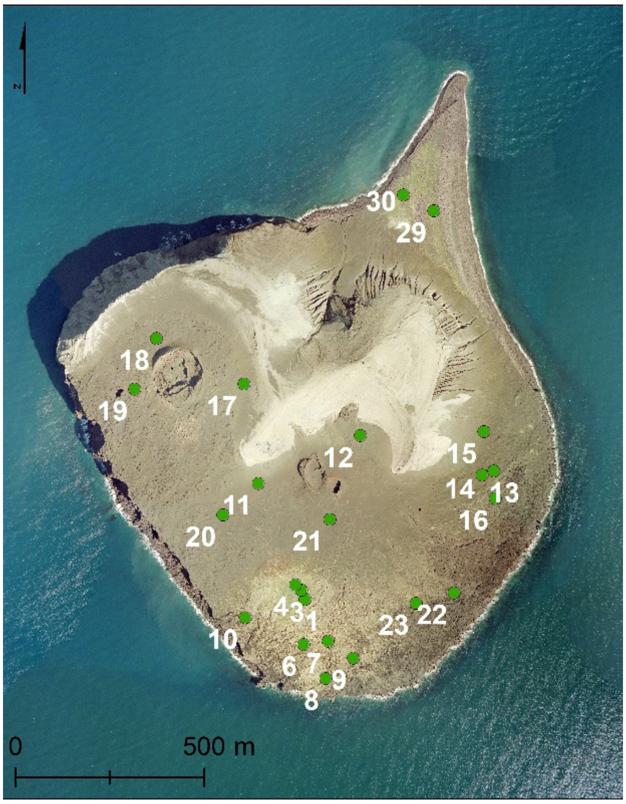

Figure 1. Location of the permanent study plots (dots and numbers) relevant to this study on Surtsey, shown on an aerial image from 2012 (© Surtsey Research Society)

VI. *Interactions between factors*. *L. arenarius* net photosynthesis has been shown to be less sensitive to drought than *H. peploides* (Sigurdsson 2009). Nutrient availability and "soil depth" has also been shown to strongly interact in its effects on vegetation growth (Leblans *et al.* 2014). I therefore expected that this would be the case for CCI in both species.

METHODS

Site description

Samples were collected on Surtsey (63°18´11 N, 20°36´17W) during 17-19 July 2012. The island has cool maritime climate, i.e. the annual temperature variation is dampened by the sea that cools the climate during summer and warms it during winter (Petersen & Jónsson 2020). During 2009-2019, the mean annual temperature was +6.6°C, with January (+3.2°C) and August (+11.3°C) as the coldest and warmest months, respectively. Total annual precipitation during the same period was on average 1009 mm, with Jun being driest (ca. 30 mm), while Sep-Feb typically receive >100 mm each (Petersen & Jónsson 2020). More information on the island's climate can be found in Petersen (2025).

The surface of the higher parts of Surtsey consists of palagonite tuff, whereas in lower parts it is made of basaltic lava or covered by deep tephra sands (Baldursson & Ingadóttir 2007). The island is still young and does not have well-developed soils (Möckel & Sigurdsson 2025). The lava is partly filled with tephra sand and silt, which originate from the eruption, erosion of the bedrock material and aeolian transport. The vegetation on these sandy areas is dominated by *Honckenya peploides* ssp. *diffusa* (Hornem.) Hultén ex V.V. Petrovsky and *Leymus arenarius* (L.) Hochst (Stefansdottir *et al.* 2014; Magnússon *et al.* 2022; plant nomenclature according to Wąsowicz 2020). Those two pioneer species were among the first vascular plants to successfully colonize Surtsey (Fridriksson 1992) and are now widely distributed all over the island (Magnússon *et al.* 2022), where they have formed a relatively stable successional sere.

In 1985, a seabird colony of lesser black-backed gulls (*Larus fuscus* L.) was established in an area on the south part of the island (Petersen 2009) and has been expanding in size ever since. Within the seagull colony, most pioneer plant species are gradually replaced by grasses, especially *Poa pratensis* L. and *Festuca richardsonii* Hook., except for the *L. arenarius* which continues to co-exist on deeper tephra sands (Magnússon *et al.* 2023).

Between 1990 and 2014, 37 permanent 10×10 m study plots were established on Surtsey to monitor the ongoing ecosystem changes at all the main occurring surface types found on the island. Today, 29 remain in the vegetation monitoring programme (Fig. 1). I selected 23 plots of those (Table 1), 9 inside and 14 outside the seabird colony. Both groups were placed

Table 1. Permanent study plots on Surtsey that were included in this work and how the basic environmental conditions vary among them. The conditions were if plots were located within the borders of the seagull colony on south and southwest Surtsey (Seagull), if they had deep (>30cm) tephra sand for rooting (Deep) and if they were located where they were likely to receive additional lateral rainwater discharges (Water).

Plot	Seagull	Deep	Water
01	1	1	0
03	1	1	0
04	1	1	0
06	1	0	0
07	1	0	0
08	1	0	0
09	1	0	0
22	1	0	0
23	1	0	0
10	0	0	0
11	0	1	0
12	0	1	1
13	0	0	0
14	0	0	0
15	0	1	1
16	0	0	0
17	0	1	0
18	0	0	0
19	0	0	0
20	0	1	0
21	0	1	0
29	0	1	1
30	0	1	1

on lava surfaces which most had some shallow tephra sand or on deep (≥30 cm) tephra sands.

Chlorophyll Content Index measurements

A portable, non-destructive and lightweight instrument (CCM-200 Chlorophyll Concentration Meter, Opti-Sciences, Hudson, NH, USA) was used to measure Chlorophyll Content Index (CCI) for six randomly chosen individuals of *L. arenarius* and *H. peploides* within or adjacent to each permanent plot. The measurements were done *in situ* on both above and below surfaces of the 3rd-4th and the 7th-8th leaf from the youngest emerging leaf of each plant for *L. arenarius* and *H. peploides*, respectively.

Data analysis

All analyses were done on average values for the six individuals measured at or adjacent to each plot, which were randomly selected. Distributions were first checked visually for normality before ANOVAs were used to test for differences in CCI between upward and downward sides of leaves of the two species (Two-Way), plots with additional lateral rainwater discharge inputs (Two-Way) and between the two species growing and on plots with contrasting soil depth (Deep) inside and outside the seagull colony (Three-Way).

RESULTS

There were no significant differences in CCI values between upward and downward facing leaf surfaces of either species (p = 0.99). The average CCI value across both leaf sides, both species and all plots was 16.1 (data now shown).

The average CCI values increased across both species from 14.1 to 19.2, or 37%, on permanent plots that received additional lateral rainwater discharges (Fig. 2; p = 0.004). There were no significant differences between the two species in this respect (Fig. 2).

The average CCI across all the plots for *L. arenarius* and *H. peploides*, was 16.4 and 15.7, respectively. This difference was not significant (S, p = 0.62; Table 2), and neither was there a significant interaction in how *L. arenarius* and *H. peploides* responded at plots at different environmental conditions (S×D, p = 0.22; S×G, p = 0.52; Table 2). When, however, the CCI values of both species together were compared across all plots, a significant 40% positive effect was found if they were located on deep tephra sands (18.8 vs. 13.4; D, p = <0.001; Table 2).

Figure 2. The CCM-200 Chlorophyll Content Meter next to *Leymus arenarius* (straws) and *Honckenya peploides* ssp. *diffusa* (forbs) next to Plot 13 on Surtsey in July 2012. Photo: B.D. Sigurdsson.

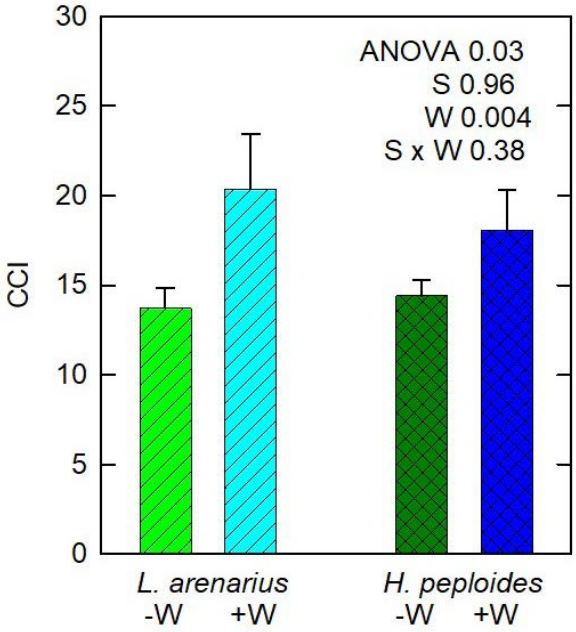

Figure 3. Mean (±SE) values of Chlorophyll Content Index (CCI) of *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa* plants without (green colours) and with additional rainwater inputs by lateral rainwater discharges (blue colours) on Surtsey. Also shown are p-values of 2-Way ANOVA on species (S) and plots with additional water (W) and their interaction (S x W).

When the CCI values of both species were compared on plots inside the seagull colony compared to outside, only a weakly significant 20% increase was observed (17.6 vs 14.6; G, p = 0.03; Table 2). However, plants that grew on plots within the seabird colony on deep tephra sands had 40%

Table 2. Mean (±SE) values of Chlorophyll Content Index (CCI) of the two species (S), *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa*, on permanent study plots on lava or on deep (>30cm) tephra sands (D) inside and outside the seagull colony (G) on Surtsey. Also shown are the p-values for 3-Way ANOVA on those three factors. Significant values are shown in bold format.

Outside seagull colony		Inside seagull colony	
Shallow	Deep	Shallow	Deep
L. arenarius			
14.4 ±1.1	14.5 ±2.1	11.3 ±1.0	25.5±1.8
H. peploides			
13.9 ±1.1	15.5 ±1.7	13.9 ±1.5	19.7 ±2.5
3-Way ANOVA p-values			
Model	**<0.001**		
S	0.62		
G	**0.03**		
D	**<0.001**		
S × G	0.52		
S × D	0.22		
G × D	**0.001**		
G × D × S	0.07		

and significantly higher CCI values across the two species (G×D, p = 0.001; Table 2). It was noteworthy that *L. arenarius* had somewhat stronger positive G×D reaction than *H. peploides*, or +125% (11.3 vs 25.4 CCI) compared to +41% for *H. peploides* (13.9 vs. 19.6 CCI), but the species, gull colony and depth interaction was not quite significant (S×G×D p = 0.07; Table 2).

DISCUSSION

The H_{I} was confirmed, the CCI values did not vary between upper and lower leaf surfaces of the *L. arenarius* and *H. peploides* plants. As both species are pioneers and commonly grow on sandy areas with low vegetation cover along coasts in Iceland (Kristinsson *et al.* 2018), where light competition is not strong, this was expected. They also both form a relatively sparse single layer canopy, where leaves are typically not placed fully laterally (Figs. 2 and 4), so an even distribution of chlorophyll along all leaf surfaces can receive some solar light and yield higher total net photosynthesis per surface area.

The H_{II} was confirmed, that CCI would be higher on plots adjacent to palagonite tuff surfaces. Sigurdsson (2009) and Sigurdsson and Stefánsdóttir (2015) had already shown that soil water availability and net-photosynthesis rates were higher in such plots. However, the summer 2012 when this study took place had a long dry-spell which severely affected the island's vegetation (Schrenk *et al.* 2022), and the apparent "drought response" may therefore have been especially strong this year.

The CCI values did not significantly differ between *L. arenarius* and *H. peploides* per unit leaf area, so H_{III} was also confirmed. Neither were the S×G, S×D or S×G×D interactions significant, indicating that both species responded similarly to changes in nutrient availability and "soil depth". The H_{VI} was therefore not confirmed. Sigurdsson (2009) found that *L. arenarius* maintained higher net photosynthesis rates per surface area than *H. peploides* on drier plots. There, it was hypothesized that this was due to the *L. arenarius*' deeper and more extensive root systems which could then partly alleviate water stress. Higher soil water contents were also measured later in those same plots (Stefánsdóttir *et al.* 2014). Plants with the same chlorophyll content can have different

Figure 4. *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa* plants close to Plot 30 in July 2012, where lateral rainwater discharges from the palagonie tuff craters on Surtsey increases soil moisture. Photo: B.D. Sigurdsson.

photosynthetic rates during water stress, if stomates partly close for the species which experiences more water stress (Chapin *et al.* 2011). These contrasting findings may therefore not contradict each other.

It has been observed that *L. arenarius* is less sensitive to competition from other vascular plants when nutrient availability has improved after it had colonized than *H. peploides* (Magnússon 2023). *L. arenarius*, with its long straws and leaves, can form taller canopy and more leaf area per unit surface area than *H. peploides* can (Fig. 4). That is probably why it persists longer in competition with other species on deeper soils.

The CCI averaged as 16.1 across both species on Surtsey. It was highest for both species on deep soils within the seagull colony, 19.6 and 25.4 for *H. peploides* and *L. arenarius*, respectively. Parry *et al.* (2014) stated that the highest CCI values recorded are ca. 70 for vascular plants with exceptionally thin leaves with high chlorophyll contents. However, Cate and Perkins (2003) found maximum CCI of 25 in fertilization experiments on sugar maple (*Acer saccharum* Marsh.) and Rex Immanuel and Miruna (2024) found it to vary between 10 and 33 in rice leaves (*Oryza sativa* L.) with contrasting N contents. Values of 20-25 in the present study may therefore be relatively high, especially for plant species with thick leaves, as both *L. arenarius* and *H. peploides* have. More measurements of CCI need to be done for different plant species in Iceland to get a good comparison for what is “normal”.

It came as a surprise that the higher CCI values per unit leaf area inside and outside the seagull colony were only weakly significantly different across both species. The higher net photosynthesis and NDVI that have been found within the seagull colony for surfaces where these two species are at least co-dominating (Sigurdsson *et al.* 2022) may therefore rather be a product of denser canopies (more leaf area) per surface area rather than more activity per unit leaf area. However, the dry summer of 2012 (Schrenk *et al.* 2022), may also have reduced the difference between plots inside and outside the gull colony on the shallower soils, which would have reduced the overall difference (see later). The H_{IV} was still confirmed as the difference was still significant ($p = 0.03$; Table 2).

The CCI was significantly higher across both species on deeper tephra sands than on plots on lava with shallow depths of substrate for root growth (Table 2), and H_V was therefore confirmed. Leblans *et al.* (2014) also found that plant productivity and SOC accumulation was higher in plots with deeper rooting substrates, both inside and outside the seagull colony. However, the strongly significant G×D interaction in Table 2 was also noteworthy, caused by plants on plots within the seagull colony growing on “deep soil” having the highest CCI values recorded. It is possible that this strong G×D interaction was also partly caused by the exceptionally dry 2012 summer (Schrenk *et al.* 2022), so the expected strong positive impact of enhanced nutrient availability within the seagull colony (H_{IV}) was only realized where soils were deeper with higher water availability.

Chlorophyll content meters have the potential to enable rapid assessment of the relative condition of leaf chlorophyll in a variety of plant species, giving valuable insights into their adaptations to different environmental conditions.

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Survey on the terrestrial invertebrate fauna of Surtsey with special emphasis on 2007–2021

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ABSTRACT

This paper summarises the results of standardised studies on the colonisation and succession of terrestrial invertebrate communities on Surtsey during 2007–2021, continuing from the previously published results from 2002–2006. Sampling has been carried out annually in mid-July using pitfall traps placed in permanent plots, supported by a Malaise trap in the gull colony and manual collection in various habitats. The aim has been to follow changes in the terrestrial invertebrate fauna and provide evaluation of species establishment in relation to habitat succession. In total, 410 species or species-equivalent taxa have been identified on Surtsey since the beginning of research there in 1965. Of these, 198 were regarded as settled, 33 of uncertain status and 179 not settled. Species composition and community structure were analysed by TWINSPAN and DCA ordination of material from 30 permanent plots. The results showed clear faunal differences between the well vegetated gull colony, the sand-filled lava areas, and the northern spit. The gull colony represented the most diverse habitat in terms of both specimens and species, strongly influenced by nutrient input from the breeding birds. Dipterans and hymenopterans represented the greatest diversity and specimen abundance, while staphylinid beetles and spiders were among the most successful colonisers. The succession of the terrestrial invertebrate communities followed the gradual formation of organic soil and denser vegetation cover, showing slow but steady change. This research was of great importance for understanding the colonisation of terrestrial invertebrate species and the development of their communities on newly formed volcanic islands.

INTRODUCTION

A submarine eruption started off the south coast of Iceland in November 1963, eventually lasting until June 1967 and leading to the formation of a new island that soon rose above the ocean surface (Þórarinsson 1968). As the eruption progressed, scientists gradually reached the conclusion that the island being formed had a good change to last. The eruption, and an island building up from the ocean bottom 130 m below sea level, provided a remarkable opportunity for geological studies. Biologists also recognised it as a unique chance to study how a sterile, isolated landmass would become invaded and colonised by living organisms. To ensure that the colonisation and succession of flora and fauna would remain as undisturbed by humans as possible, the island was protected by law in 1965 and reserved exclusively for scientific research, with media granted occasional access to document and communicate the ongoing succession of life on Surtsey (Svavarsdóttir & Walker 2009).

Surtsey is the southernmost offshore island of Iceland, located 32 km off the south coast and 4.8 km from the nearest small island of the Vestmannaeyjar archipelago. From the very beginning, the island has been continuously shaped by coastal erosion, with, heavy surf and severe winter storms gradually reducing its size. In 2019, the area of the island was estimated 1.2 km^2 (Óskarsson *et al.* 2020), remaining from the maximum area of 2.7 km^2 when the eruption stopped in 1967 (Jakobsson *et al.* 2000).

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Surtsey´s volcanic surface can be divided into three main types (Fig. 1). Firstly, the consolidated palagonite tuff core formed from two central tephra craters, partly mantled by mobile ash that is actively reworked by wind erosion (Óskarsson *et al.* 2020). Secondly, a southern basaltic lava field, continuously eroded by open-ocean surf, especially during winter storms, forming steep sea cliffs. Thirdly, a northern boulder-based spit, built by wave driven transport of cliff material from the south, which remains highly unstable and is still periodically submerged during winter storm tides.

There have been fast and dramatic changes in vegetation cover and succession of plant communities for terrestrial invertebrates to colonise (Friðriksson 1994, Magnússon *et al.* 2009, 2014). The pace of ecological succession changed when seagulls started to breed and form a colony in the centre of the lava field in 1985 (Friðriksson 1994, Magnússon & Ólafsson 2003, Petersen 2009). Until then, plant succession was slow and relatively stable (Baldursson & Ingadottir 2007). The fertilising effect of the breeding gulls (Leblans *et al.* 2014), along with their import of nesting materials from neighbouring islands, marked a turning point in the succession of both flora (Magnússon & Magnússon 2000) and the terrestrial invertebrate fauna (Ólafsson & Ingimarsdóttir 2009). New plant species were recorded regularly thereafter, some of which did not persist for long. By 2021, 79 species of vascular plants had been recorded on the island, 66 of which were confirmed alive that year (Magnússon *et al.* 2023). Several plant species are rare and appear unable to sustain viable populations on the island. Consequently, they contribute minimally to the plant community composition and have little influence on the settlements of invertebrate species (Magnússon *et al.* 2023).

Organic soil is gradually being formed which is the essential foundation for colonisation of soil invertebrates and maintaining the humidity required by most species (Magnússon & Magnússon 2000, Sigurdsson & Leblans 2020, Möckel & Sigurdsson 2025). Sparsely vegetated lava surfaces and sand plains are generally too dry for invertebrate communities to form and develop. These substrates are porous and dry quickly on sunny days (Sigurdsson 2009, Sigurdsson & Stefánsdóttir 2015).

The terrestrial invertebrate survey on Surtsey was initiated as early as 1965, under the direction of Prof. Carl H. Lindroth and his team (Lindroth *et al.* 1973). The first author of this article, Erling Ólafsson, first visited the island in 1970 for a summer long stay to prepare for Lindroth´s fifth expedition to the island that summer. Lindroth´s final visit to Surtsey took place two years later. From then on, the first author grabbed the baton and secured the continuation of the studies. Summer long studies by author were repeated in 1971, and by biology student Jón Eldon in 1972, followed by the first author´s visits in 1974, 1976, 1981 and 1984. A gap in his research followed until 2002. Since that time, the island has been visited annually for terrestrial invertebrate monitoring, in connection with other terrestrial ecology research.

Results of terrestrial invertebrate studies up to 2006 have been reported by several authors in multiple publications. References are made here to the most important works. As mentioned earlier, Lindroth´s original project was followed by his student Ólafsson (1978, 1982). H. Bödvarsson (1982) presented the results of his collembolan studies, Gjelstrup (2000) reported on soil mites and collembolans collected in 1995, and Sigurdardóttir (2000) published her collembolan studies from the same year. Ólafsson´s studies have been carried out annually since 2002, with assistance from M. Ingimarsdóttir from 2003 to 2006. Their 2002–2006 results were published in Ólafsson and Ingimarsdóttir (2009), including a comprehensive species list covering all recorded terrestrial invertebrate taxa with assessments of species status (settled, unsettled or uncertain) and habitat-based presentations derived from DCA ordinations of pitfall trap samples.

In this paper the emphasis is on results from the standardised studies of the colonisation of terrestrial invertebrates, and on how their communities have formed and developed across different habitats during 2007–2021, in continuation of the earlier five years series from 2002–2006. In 2015, M. Alfredsson (second author) joined the project and took over the research after 2020, when the first author retired after 50 years of service.

For this publication, new species recorded during 2007–2021 have been added to the list, and all species statuses have been revised. The paper further provides updated analyses of terrestrial invertebrate community succession across habitats, derived from four successive five-year datasets covering the period 2002–2021.

METHODS

In 2002 the re-initiated terrestrial invertebrate research program was standardised. The work focused on: 1) collecting invertebrates in permanent research plots previously established for botanical studies using pitfall traps; 2) sweep netting in vegetation and across sparsely vegetated surfaces; and 3) manual searches beneath lava stones, driftwood and carcasses on the ground. This collecting program has been repeated annually since 2002, and sampling has been carried out each year over continuous four-day period in mid-July. In 2008, a Malaise trap was first installed in the gull colony to obtain better information on that most important habitat.

These standardised data collection methods were meant to give comparable results as the studies progressed, to indicate the succession of the terrestrial invertebrate fauna, to track new settlers, and to document how communities form and evolve.

Weather conditions prior to and during fieldwork can influence sampling efficiency; for example, rainy or windy days may prevent sweep netting and reduce the accessibility of invertebrates sheltering in vegetation or soil. As a result, short sampling periods can be affected by such variability.

Figure 1. Locations of the 30 permanent terrestrial invertebrate pitfall trapping sites on Surtsey 2002–2021. Dense vegetation appears in green colour showing the gull breeding colony in a Worldview 2 image from 8 August 2021 (Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community).

Pitfall trapping

In 2002, pitfall traps were placed in 21 square plots (10 x 10 m) used by botanists to monitor vegetation succession and biomass in different habitats (Fig. 1). One plot, located at the northern foothills of the palagonite hills (R25), which no longer is used in the botanical studies due to its unstable surface, has continued to be included in this study. Three additional trap sites, not associated with the permanent plots, were established in 2002 to detect potential human effects. They are traps R27 and R28. adjacent to the research hut and trap R26 at the edge of the helicopter platform (Fig. 1). No trapping was conducted on the hard tuff surfaces on the hills where pitfall traps cannot be installed effectively.

In 2005, two new plots were added on the northern spit (R29 and R30), followed by a third in 2015 (R37). In 2008, two additional plots (R31 and R32) were established in an AA-lava flow, an area with very slow vegetation succession. A total of 30 traps have been operated for varying length of time up to 2021 (Fig. 1).

To summarise, five categories of trap sites were defined: 1) bare and sand-filled lava with an active breeding colony of large gulls; 2) sand-filled lava without breeding gulls; 3) mostly bare lava outside the gull colony; 4) the sandy northern spit, periodically under overflowing conditions during wintertime; and 5) areas possibly influenced by human activity around the research hut (Fig. 1).

Each pitfall trap consisted of a plastic container with 6.3 cm diameter opening and depth of 6.5 cm, filled up to one quarter of its volume with 4% formaldehyde as well as a drop of soap to break the surface tension. The trap was covered with a round plastic lid to prevent rain from entering and was kept approximately 4 cm above the surface using 6 inches nails. Within the gull colony the traps were shielded with wire mesh screens to protected them from curious gulls. To minimise the impact on the fauna within the permanent plots, a single trap was placed near the centre of each plot during each field visit and left running for approximately 70 hours (Fig. 2).

Figure 2. A pitfall trap in Plot 22. Photo Erling Ólafsson.

Malaise trap

Malaise traps are designed to capture flying insects and operate automatically once deployed. On Surtsey, this device was first set up in 2008 and has been operated continuously since then. It was located within the oldest part of the gull colony, at a fixed position next to plot R3 (Fig. 1), set up for approximately 70 hours, weather permitting (Fig. 3). Operation of the Malaise trap can be restricted by adverse weather conditions, particularly heavy rainfall and strong wind.

Figure 3. The Malaise trap in oldest part of gull colony. Photo Erling Ólafsson.

Manual sampling

Manual collecting was performed to sample invertebrates that might escape the trapping methods. This was mainly based on sweep netting conducted in vegetation in the gull colony and areas of lush vegetation elsewhere, for instance from lyme grass stands (*Leymus arenarius*) and sea sandwort (*Honckenya peploides*) on the northern spit and inside the larger crater, Surtungur. Secondly, direct picking was performed where conditions allowed, from beneath lava stones and driftwood, carcasses and among roots of plants. Thirdly, on top of the eastern palagonite tuff crater, Austurbunki, the ruins of a lighthouse were regularly checked as newly windblown insects often accumulate there, both inside and around cracks emitting hot steam.

Storage of material

Specimens collected by pitfall traps were fixed in formaldehyde (4%) on site and subsequently preserved in 80% ethanol for long-term storage. Malaise trap specimens were collected directly into ethanol. Most manually collected specimens were also placed directly in ethanol, except for lepidopterans and coleopterans, which were pinned; A small number of dipteran and hymenopteran specimens were likewise pinned. All research material is housed in the scientific collections of the Natural Science Institute of Iceland.

Identifications

Identifications of the collected material were carried out in the laboratory. Most insect orders were determined to species level except for certain families within the Diptera and Hymenoptera, for which taxonomic expertise is limited, (e.g., Sciaridae and Cecidomyiidae within Diptera, several families or species groups within Hymenoptera, and aphids and coccoids within Hemiptera). In such cases, specimens were assigned to unnamed morphospecies or grouped at the genus level and listed accordingly to obtain an approximate estimate of species diversity. Springtails (Collembola) and mites (Acari) were treated in the same manner as in Ólafsson and Ingimarsdóttir (2009), and new specimens were extracted, counted and stored.

Data analysis

The assessment of terrestrial invertebrate communities is based on data obtained from pitfall traps placed in permanent plots across multiple locations on Surtsey between 2002 and 2021. Species in individual samples were identified and specimens counted, giving numerical values allowing neutral comparison of invertebrate faunas under different environmental conditions. The data were analysed using, firstly, Two-Way Indicator Species Analysis (TWINSPAN), secondly, Detrended Correspondence Analysis (DCA) in PC-ORD version 6.08 (McCune and Mefford 2011).

A data matrix of 30 samples, including 160 arthropod species or species equivalent taxa was used for analysis. The dataset also included an unidentified Pseudococcidae species, presumably with species status. Species groups comprising more than one species, such as Aphididae, were omitted, as were all Colembola and Acari, except for the bdellid species *Neomolgus littoralis*, a habitat describing species on the northern spit. Prior to analysis, species abundances data were standardised by trap days and number of years and finally log(x+1) transformed. Rare species were downweighted.

TWINSPAN was run with user defined cut levels of 0, 0.2, 0.5, 1.0, and 2.0 to define pseudo-species categories. Axis scores were generated using pseudocanonical correspondence analysis. The resulting classification was used to identify distinct arthropod assemblages and their indicator species.

For the analysis of pitfall trap data, DECORANA ordination (Hill 1979) was used to assess similarities between sampling plots. As the four-day annual samples were regarded too small for meaningful ordination, five-year data sets were combined to trace successional changes over time. Accordingly, the material from 2002–2021 was divided into four data sets prior to analysis (2002–2006, 2007–2011, 2012–2016, and 2017–2021). The small annual samples are sometimes affected by unfavourable weather during the sampling days. The impact of a single defective sample among five years should therefore be reduced. Species and taxa treated equivalent to species were included, and the number of individuals captured was standardised as catch per day (24 hours). Rare species, and those of minor significance in the plot-fauna were down weighted to avoid unrealistic influence on the results. Rare species are not necessarily important elements in describing the functional composition of the plot fauna, as they may represent unsettled, randomly windborne stragglers.

RESULTS

The species list

A revised species list (1965–2021) was compiled, including all terrestrial Arthropoda, Mollusca and Annelida i.e. including revised earlier data together with new additions from 2007–2021 (Supplement S1). In the new list, seven species from previous version have been omitted, species originally found dead in drift material on the shore during the early years and not rediscovered since. The updated species list comprises 410 species or species equivalent taxa, including 136 new records from 2007–2021.

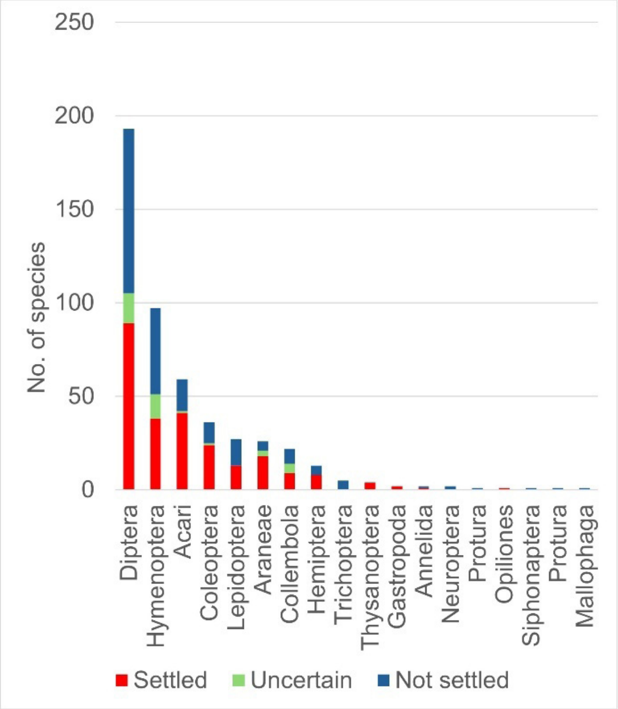

Figure 4. Terrestrial invertebrates, orders and higher taxa, collected on Surtsey during the 2002–2021 survey, no. of species and status evaluations; red: settled; green: status uncertain; blue: not settled. For further information on status evaliations reference is made to Appendix 1.

Species were evaluated as either settled, unsettled or of uncertain status (Fig. 4). With new data some of the previous evaluations have changed. The annual standardised samplings have provided the basis for these evaluations. In many cases, there is little or no doubt about stable settlement, species collected every year, often in considerable numbers. Many species are not easily detected in the field yet were collected in certain years and habitat conditions suggest they should be regarded as settled. In total, 198 species are considered settled. Thirty-three species are currently of uncertain status, but continued annual sampling may confirm settlement for many of them. The remaining 179 species are certainly, or most likely, not settled, although some of them may deserve reclassification to the uncertain category (Fig. 4).

TWINSPAN results

The TWINSPAN resulted in a clear first division of the 30 plots into two groups (Fig. 5). Ten plots

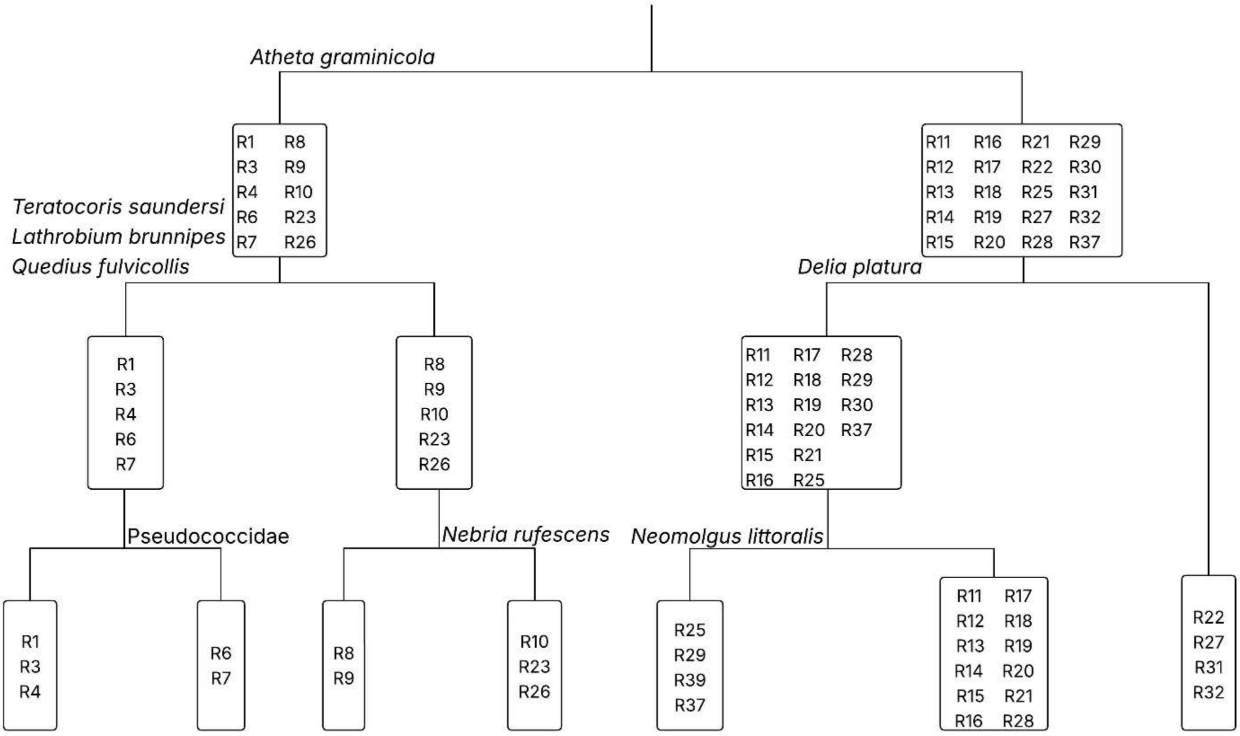

Figure 5. TWINSPAN results from 30 pitfall trap plots on Surtsey 2002–2021 with terrestrial invertebrate species directing divisions. Rxx stands for the trap number on Fig. 1.

fell within the gull colony that began to develop in 1986 in the centre of the lava field south of the main craters. The presence of the breeding gulls, together with their nutrient rich droppings and food remains, led to a quick succession of the vegetation cover and the development of luxuriant plant growth. The remaining twenty plots are located on less vegetated sand-filled lava and the sandy surface of the northern spit, areas largely unaffected by breeding gulls, except perhaps to minor degree in recent years. This division is directed by the staphylinid beetle, *Atheta graminicola*, common within the colony but absent on the less vegetated dry sandy grounds.

A subdivision within the gull colony separates plots located in the oldest part of the colony (R1, R3, R4, R6, R7), characterised by dominating grasses leaving other plants limited possibilities to grow, and marginal plots (R8, R9, R10, R23, R26) still under marked succession where grasses have not taken over completely. The species primarily responsible for this division are the hemipteran bug *Teratocorix saundersi* and the staphylinid beetles *Lathrobius brunnipes* and *Quedius fulvicollis*, which are associated with the more developed side. It is worth mentioning that an unidentified pseuducoccid species, expected to feed on grass roots, separates two plots within the oldest part dominated by the grasses *Festuca richardsonii* (R6, R7) and *Poa pratensis* and *Leymus arenarius* (R1, R3, R4) all of which are omnipotent in that area. The other branch also subdivides. The first group (R8, R9) comprises two plots that, given the ongoing succession, will likely converge with the most advanced plots. The second subgroup represents true marginal plots (R10, R23, R26), characterised by more open surface and diverse flora. The relatively recently established carabid beetle *Nebria rufescens*

Figure 6. The carabid beetle *Nebria rufescens*, a relatively new settler on Surtsey. Photo Erling Ólafsson.

Figure 7. The dbellid mite *Neomolgus littoralis*, characteristic for the bolder beaches of northern spit. Photo Erling Ólafsson.

(Fig. 6), which prefers open surface for its quick movements, is responsible for this division. In fact, one of these plots (R26) lies beyond the colony boundaries, it is located at the edge of the helicopter platform near the research hut. Gulls tend to bathe in temporary rainwater pools on the concrete platform, leading to rich fertilisation round the edges.

The remaining 20 plots are all situated on sandy grounds, spread widely over the island, mostly unaffected by breeding gulls (Fig. 5). A second split, driven by the common anthomyiid fly *Delia platura*, whose larvae develop on plant roots, groups 16 plots together while separating four plots (R22, R27, R31, R32) from the rest. Three of these plots are situated in lava that gulls appear to regard as future breeding grounds. The fourth plot (R27) is quite anomalous. It is sheltered under a terrace at the research hut and was originally established to assess possible effects of the hut and human activity. This assemblage of four plots is stabilised in the Twinspan graph. The other branch splits convincingly. The low-lying spit on the northern side of the island is extremely unstable and is regularly submerged by seawater during fierce winter storms. In autumn, this area is also affected by a large grey seal (*Halichoerus grypus*) rookery, which contributes notable amounts of marine-derived nutrients to the northern spit (Magnússon *et al*. 2020). A cluster of four coastal plots (R25, R29, R30, R37) is caused by the halophilic bdellid mite *Neomolgus littoralis* (Fig. 7).

DCA-ordination

The results of the DCA ordination revealed substantial variation in community structure (Fig. 8). Axis 1 had a gradient length of 3.11 standard deviation (SD) units and an eigenvalue of 0.645, indicating strong species turnover and supporting the use of a unimodal ordination method. Axes 2 and 3 had gradient lengths of 2.34 and 1.98 SD units, respectively, with corresponding eigenvalues 0.208 and 0.110.

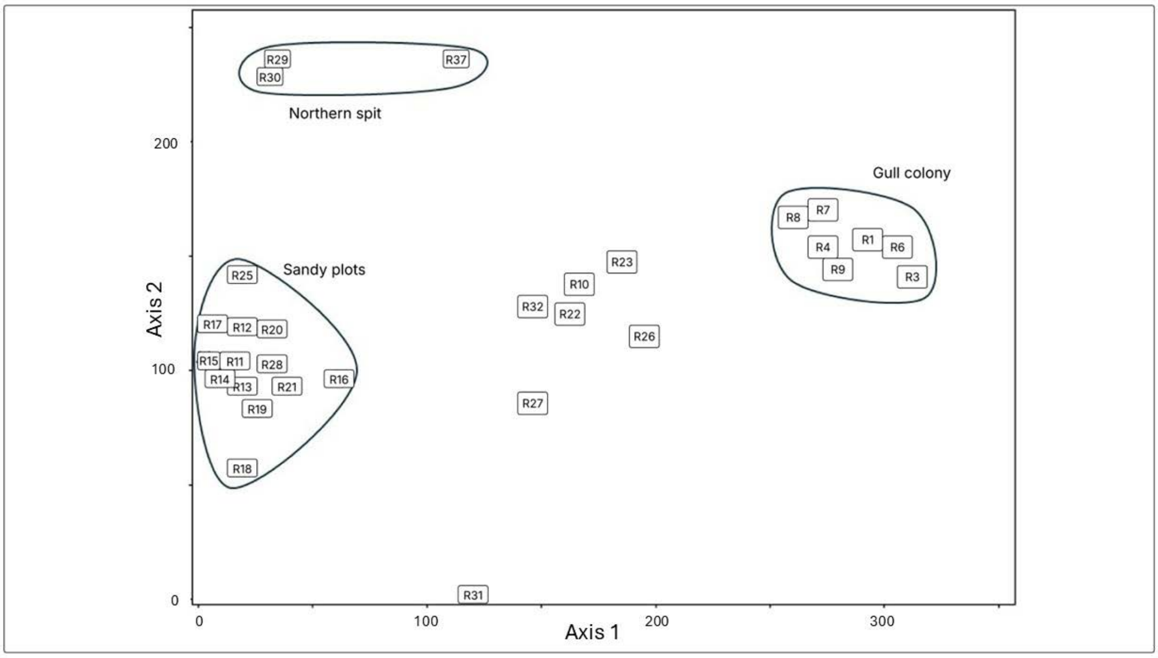

Figure 8. DCA-ordination results from permanent pitfall trap plots on Surtsey 2002–2021. Encircled upper left: northern low spit (3 plots); lower left: sandy ground (13 plots); far right: gull colony (7 plots); outside circles: marginal plots near gull colony (R10, R22, R23), human effect study traps near hut (R26, R27), recent plots in AA-lava (R31, R32). See Fig. 1 for locations.

The DCA ordination diagram shows a clear separation of plots and great variation along Axis 1 (Fig. 8). Three clusters of plots will be considered specially. On the right side are plots within the oldest part of the gull colony and on the left side two clusters of plots on less affected sandy grounds, firstly on sand-filled lava, secondly plots on the northern spit. The decided cluster of plots on sand-filled lava indicates a stable situation in a habitat with limited vegetation succession. In the middle of the diagram are plots some of which with uncertain future. There are two marginal plots in the gull colony (R10, R23) expected by time to move further towards the left side. To mention, R10 will fall into the ocean within few years. Two of the plots established to trace possible human effects around the hut are located there in the diagram, a plot at the helicopter platform (R26) affected by gulls attracted by incidental rain pools on the platform is grouped with the gull colony marginal plots. The second plot under the terrace at the hut (R27) shows that the location is affected by human activity. A third plot (R28) on the opposite side 6m away from the hut shows that human effect round the hut does not reach that far, the plot being placed with other sand-filled lava plots on the left side of Fig. 8.

Pitfall traps results

There are three main types of habitats worth considering, gull colony (8 plots), sandy plots outside the gull colony (12 plots) and the low northern spit (3 plots) (Table 1). The remaining seven plots stand out and are not easily grouped with the others. The catches from all traps within each habitat were combined, giving the results presented in Table 1 where the higher taxa are summarised. These are raw counts, the differences in trap numbers and sampling duration have not been accounted for. As expected, the superiority of the well vegetated gull colony is obvious considering number of specimens and species, with ca. 35.700 specimens of at least 140 species. In the sandy areas outside the gull colony, vegetation cover is limited, with little or no vegetational succession, and there the surface is unstable and regularly on the move with blowing winds. The fauna on the northern spit does not establish so easily as most winters the low-lying surface is overflooded in harsh storms. The results on species basis are shown for each habitat in Supplements S2–4.

Table 1. Terrestrial Invertebrate, orders and higher taxa, collected on Surtsey during the 2002–2021 survey with no. of specimens and species.

	Gull colony plots		**Sandy plots outside gull colony**		**Spit plots**	
	8 traps/20 years		**12 traps/20 years**		**3 traps/17, 16, 7 years**	
Higer taxa	**No of specimens**	**No. of species**	**No of specimens**	**No. of species**	**No of specimens**	**No. of species**
Collembola	11.726	Uncertain	1.146	Uncertain	679	Uncertain
Hemiptera	941	6	224	3	281	1
Thysanoptera	232	4	3.015	2	175	1
Lepidoptera	6	2	13	4	2	2
Coleoptera	2.490	27	1.524	9	47	3
Hymenoptera	312	26	11	7	3	2
Diptera	1.063	60	2.885	43	373	22
Araneae	2.394	13	1.282	8	229	4
Opiliones	2	1	1	1		
Acari	16.486	Uncertain	10.345	Uncertain	2.169	Uncertain
Enchytridae	16	Uncertain	6	Uncertain	4	Uncertain
Gastropoda	8	1				
Nematoda	71	Uncertain	4		7	Uncertain
Total:	**35.747**	**140**	**20.456**	**77**	**3.969**	**35**

Malaise trap results

Flying insects account for the bulk of collected specimens in the Malaise trap (Table 2). Bugs crawling up the tent sheet to the top and into the collecting jar (*cf.* Hemiptera, Acari, Araneae, Coleoptera) are of minor importance. As the activity of flying insects is dependent on weather conditions which can be either excellent, unfavourable or sometimes impossible, running the Malaise trap for only four days gives results that are rarely comparable between years (Fig. 9).

The combined fourteen-year catch provides a clear indication of the composition and character of the flying insects fauna within the gull colony (Table 2), including both species composition and a rough indication of species populations and their importance. The total number of species equivalent taxa is 196 (Acari omitted), representing the absolute minimum number of species. In total 32.756 specimens were collected, with annual totals ranging from 601 to 5,083, and an annual average of specimens of 2,340 (Supplement S5). Species of the order Diptera dominated the fauna in both specimen count and species richness, followed by the Hymenoptera. Hemipterans ranked third in specimen number, largely due to unidentified aphids (Table 2).

Table 2. Total catch during 2008–2021 by a Malaise trap on Surtsey. Orders and other high taxa, no. of specimens and species caught.

Higer taxa	No. of specimens	No. of species
Diptera	28.809	107
Hymenoptera	1.754	62
Hemiptera	1.725	3
Acari	275	Uncertain
Lepidoptera	119	9
Araneae	40	5
Coleoptera	26	8
Trichoptera	4	1
Thysanoptera	4	1
Total:	**32.756**	**196**

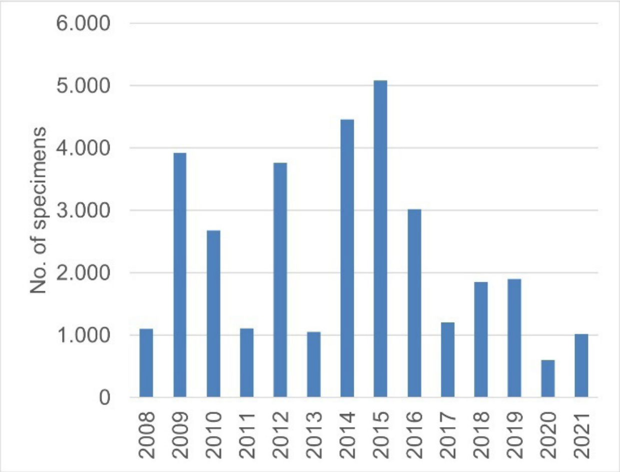

Figure 9. Yearly catches during 2008–2021 (no. of specimens) by a Malaise trap on Surtsey.

DISCUSSION

Since its formation, Surtsey has provided scientists with exceptional opportunities to study how an isolated, barren and inorganic landmass becomes colonised by life. Similar events have been documented in Indonesia, where explosive eruptions on the volcanic island Anak Krakatau destroyed large parts of the island and eliminated its ecosystem. Subsequent recolonisation followed (New 2015). As Anak Krakatau lies in the Asian tropics, the circumstances differ markedly from those of subarctic Surtsey in the North-Atlantic, which is both more isolated and strictly protected.

The terrestrial invertebrate project on Surtsey was initiated in 1965, about a year and a half after the eruption that formed the island began far off the south coast of Iceland, while volcanic activity was still ongoing (Þórarinsson 1968). Colonisation and successional development of the terrestrial fauna was slow during the initial decades but gradually stabilised. A major milestone was reached in 1986 when several pairs of lesser black-backed gulls (*Larus fuscus*) joined the already breeding European herring gulls (*L. argentatus*) to establish a breeding colony on the lava field along the southern side of the island (Petersen 2009). Gull colonisation was a successful, and the number of breeding pairs increased gradually in the years that followed. As the island lacked sufficient nesting material for the expanding colony, the gulls initially transported some from the mainland or neighbouring islands. They also brought food from the ocean to feed their chicks, enriching the soil with food remains and droppings (Magnússon & Magnússon 2000, Sigurdsson & Leblans 2020). This nutrient input had a substantial fertilising effect that benefitted the vegetation and improved the conditions for invertebrate colonisation.

Dispersal of terrestrial invertebrates has been accounted for in a previous publication, wind-borne, sea-drifted and bird-assisted transport (Ólafsson & Ingimarsdóttir 2009). The influx of wind-borne invertebrates, arriving from other islands of the archipelago, from mainland Iceland, and even from distant Europe, was regularly witnessed in the earliest years, when the possibilities for colonisation were extremely limited (Lindroth *et al.* 1973, Ólafsson & Ingimarsdóttir 2009). Such influxes happen regularly with favourable winds, sometimes clearly indicated by the species compositions of samples. In 2005 and 2009, several species originating from Iceland's mainland wetlands were caught, species with no possibility of establishing populations on the island due to the absence of wetlands.

The terrestrial invertebrate faunas of different habitats

The invertebrate fauna within the gull colony has received particular attention in this study. As described earlier, data were collected not only through pitfall trapping and sweep netting, as in other habitats, but also by the use of a Malaise trap. The vegetation in the colony is continuously developing, with the succession still ongoing and the vegetated area gradually expanding (Magnússon *et al.* 2023). The invertebrate fauna shows similar pattern, new settlers continue to be recorded, and their establishment is monitored through the annual surveys.

The character of the invertebrate fauna within the colony is best appreciated by examining the species list in Supplement S2. Among ground-living coleopterans, the staphylinids are dominating, not surprisingly as many are excellent flyers and readily dispersed to islands by favourable winds (Hansen *et al.* 2018). Twenty species of staphylinids have been recorded in the colony, *Atheta fungi* and *A. graminicola* being the far most numerous ones. *Oxypoda haemorrhoa* should also be noted. Seven of these species were also caught by the Malaise trap but in low numbers. One of the most common staphylinid species in Iceland, *Atheta atramentaria*, only a single specimen was extracted from the pitfall material. In the early 1970s, influxes of this species carried by northerly winds were regularly observed, as the beetles are active fliers under calm weather conditions (Ólafsson 1978). In contrast to the pitfall samples, *A. atramentaria* was the species most frequently captured by the Malaise trap. It depends on the presence of livestock feces in order to establish a population (Larsson & Gígja 1959). These beetles are generally active fliers that locate their preferred food while flying, rather than on the ground. This may explain the difference in capture efficiency between the Malaise trap and the pitfall traps for this species, which is not regarded as a potential coloniser of Surtsey.

Figure 10. The carabid beetle *Amara quenseli*, an early settler on Surtsey prefering sandy habitats with low vegetation cover. Photo Erling Ólafsson.

Five species of carabid beetles were recorded in the colony, all caught in low numbers except for *Amara quenseli*. This species, however, is restricted to the marginal areas of the colony as its preferred habitat is the surrounding sandy ground (Fig. 10).

A surprisingly high numbers of hymenopteran species (and species equivalents) were trapped in the colony, a total of 73. The Malaise trap was much more efficient than the pitfall traps with 62 species caught compared with 27 by the latter. Fifteen species were caught by both methods, while 12 recorded only from pitfall traps. The pitfall samples were dominated by small hymenopteran species, primarily parasitoids of aphids or secondary parasitoids.

Aphids are important hosts for parasitic hymenopterans in the gull colony, with a total of 2,354 specimens captured across all traps, and they were also collected in considerable numbers by sweep netting. Unfortunately, the aphids have not been identified to species level.

An interesting agromyzid dipteran *Taumatomyia glabra* was recorded on Surtsey, the first records of this species for Iceland (Fig. 11). It´s larvae feed on aphids that suck plant roots (Nartshuk & Andersson 2012). A braconid species, *Monoctonus caricis*, was the most abundant parasitic wasp, with 317

Figure 11. An agromyzid dipteran, *Thaumatomyia glabra*, which larvae feed on root sucking aphids. First Icelandic records on Surtsey. Photo Erling Ólafsson.

individuals caught in the Malaise trap and 67 in the pitfall traps, another example of a parasite on aphids (Lindroth *et al.* 1973). The second most numerous species was the eulopid *Chrysocharis pallipes* (326 specimens), with all but three specimens collected by Malaise trap. This parasitoid is known to utilize leaf-mining larvae as hosts (Lindroth *et al*. 1973*)*, such as species within the dipteran family Agromyzidae. Ichneumonidae is by far the most diverse family of hymenopterans in the colony with 34 morphospecies listed plus additional ones collected by sweep netting. Unfortunately, many of the hymenopteran morphospecies remain unnamed.

Dipterans are the most species-rich group in the Icelandic terrestrial invertebrate fauna (Ólafsson 1991), a pattern that is reflected in the Surtsey fauna. Although pitfall traps are designed to capture ground-active, often flightless invertebrates, many flying insects are also active on the ground and therefore frequently caught. Anthomyiidae flies were the most numerous of dipterans in the colony, with many species supposed to lay their eggs among plant roots (Baba *et al*. 2019). This was reflected by the pitfall catches, where females dominated over males, whereas the opposite pattern was found in the Malaise trap samples. Another factor that influenced the pitfall catches was the use of lids placed over the traps to protect them from rainfall, flies tended to seek shelter under the lids, which increased their likelihood of being captured.

As expected, Dipteran species dominate in the colony both in species richness and number of specimens. The total number of species trapped was 110. The Malaise trap captured 106 species, whereas 60 were collected by pitfall traps, with only four species obtained exclusively by pitfall trapping (sweep net results are here not considered). As noted above, anthomyiid species were particularly numerous, 17 species were caught by the Malaise trap, 14 of which were also obtained by pitfall traps, indicating that females entered the vegetation cover to oviposit in the soil.

The saltwater chironomid *Halocladius variabilis*, whose larvae develop in marine coastal water (Hrafnsdottir 2005), was collected in the greatest numbers (5,847 individuals), nearly all by the Malaise trap, and it was also collected in additional numbers by sweep netting. Five other species exceeded one thousand specimens: *Rhamphomyia simplex* (2,806), *Leia fascipennis* (2,577), *Dilophus femoratus* (2,025), *Botanophila fugax* (1,596), and *Dolichopus plumipes* (1,318). Many other species were caught in hundreds of specimens.

Spiders, typical ground-dwelling invertebrates, proved to be both diverse and numerous in the colony. A total of 14 linyphiid species were recorded. There were few samples from the Malaise trap and of little significance. The most numerous species were *Erigone arctica* (1,077), *Allomengea scopigera* (421) and *Savignya frontata* (230). Unidentified juveniles were also common (602). Two species of the family Lycosidae were present in the colony, *Pardosa sphagnicola* and *P. palustris* (Fig. 12), the former being encountered more frequently.

Although collembolans and mites obtained during the new research period were not identified to species or potential species level, they were extracted from the trap samples and counted. In total, 11,726 collembolans and 16,486 mites were counted. These

Figure 12. A lycosid spider, *Pardosa palustris* on Surtsey, a female with an egg sack releasing the newly hatched young. Photo Erling Ólafsson.

numbers indicate that soil invertebrates are far more abundant in the gull colony than in other habitats on the island, which is consistent with the substantially greater development of organic soil in that area compared with the sandy plots. Similar results have been reported for soil nematodes inside and outside the gull colony on Surtsey (Ilieva-Makulec *et al.* 2015). Comparative data from the sandy plots are presented later. Further information on other, less prominent species groups is provided in Supplement S2.

A considerable part of the island´s surface outside the gull colony consists of sand-filled lava, where several species of vascular plants grow, although the overall vegetation cover remains very low (Magnússon *et al.* 2023). Consequently, invertebrates have little shelter to seek, as the surface is unstable, sand grains are constantly shifted by wind and become hot and dry under sunny conditions. Consequently, this habitat is unstable and largely inhospitable, suitable only for the lesser part of the invertebrate fauna. The succession of this habitat has been slow over the years, and the fauna appears to have remained unchanged in recent years. The research has been based primarily on pitfall trapping in 12 sandy plots, and to a lesser degree on sweep netting and direct manual collection. Examination of the species list and abundance data in Supplement S3 illustrates the overall composition of the invertebrate fauna under these conditions. The dipteran family Anthomyiidae was particularly notable, with several species presumed to have root-feeding larvae (Baba *et al*. 2019), and no other species group was as diverse. The most abundant species *Botanophila fugax* and *Delia setigera* dominate, followed by *D. fabricii* and *D. platura* and lastly *D. angustifrons*, *D. echinata* and *Lasiomma picipes*. Of other dipteran groups, only the chironomid *Halocladius variabilis* was collected in notable numbers, as in the gull colony. However, this species is blown in from the Surtsey coastline where its larvae develop in marine salt water and is therefore not representative of habitats other than coastal ones. The thripid species *Thrips vulgatissimus* was the invertebrate caught in the greatest numbers. It is a sap-sucking insect on Surtsey associated with sea sandwort (Lindroth *et al*. 1973), the dominant plant in this habitat. This is also the proper habitat for the carabid beetle *Amara quenseli* which prefers open sandy surfaces with limited plant cover (Larsson & Gígja, 1959). Three linyphiid spiders were also characteristic of this environment. *Erigone arctica* was a generalist species abundant both here and in the gull colony, whereas *Meioneta nigripes* and *Islandiana princeps,* were largely confined to this habitat.

Compared with the gull colony, the numbers of caught invertebrates were much less in the sand-filled lava than in the densely vegetated colony where organic soil is forming. A total of 1,146 collembolans and 10,345 mites were counted, the latter number consisting mostly of tiny juveniles. Further information on other less important species groups is provided in Supplement S3.

The conditions on the northern spit adjacent to the northern slopes of the tephra craters, make it difficult for terrestrial invertebrates to settle. The elevation is only few meters above sea level, and the plain is inevitably flooded during winter storms at high tide, with the surface repeatedly eroded and sediment and driftwood washed back and forth. The soil is saline and unsuitable for most terrestrial invertebrates, only species adapted to such oceanic influences were able to persist. As a result, the invertebrate fauna was poor and unstable. The beach vegetation is adapted to these conditions (Magnússon *et al.* 2023), although still subject to considerable erosion. Windborne flying insects tended to gather in the vegetation and were best surveyed by sweep netting.

Three pitfall traps on the spit (R29, R30, R37) were operated for fewer seasons than those in gull colony and the sand-filled lava, and the raw counts are therefore not fully comparable. They nevertheless provided a useful indication of the character of the fauna. Sea sandwort is the dominating plant on the spit (Magnússon *et al.* 2023) and it was heavily parasitised by the thripid *Thrips vulgatissimus* and by aphids, presumably *Acyrthosiphon auctum* (Ólafsson 1982). Coleopterans were less important there, with few species recorded, although *Amara quenseli* was almost always present. The staphylinid *Micralymma marinum*, typically found on Icelandic mainland beaches (Larsson & Gígja 1959), was caught once in a trap located close to the shoreline, most likely after being washed ashore.

As expected, the marine-associated chironomid *Halocladius variabilis* was trapped in numbers on the spit, along with a single specimen of *Telmatogeton japonicus*, another species whose marine larvae develop among algal vegetation on wet rocks (Hrafnsdottir 2005). As in the sand-filled lava anthomyiid dipterans were regular in the vegetation of the spit, particularly within the lyme grass stands where they may breed; *Botanophila fugax* was the most abundant species, *Delia angustifrons*, *D. setigera* and *D. platura* also occurred in notable numbers. Linyphiid spiders were common, with *Erigone arctica* dominating, as it did throughout the island. Finally, the conspicuous predatory bdellid mite *Neomolgus littoralis*, characteristic of coastal beach habitats (Atyeo & Tuxen 1962), was also recorded. The fauna of the northern spit resembled that of the higher sand-filled lava, though it was less diverse due to the unstable conditions, and included several species typically associated with beach habitats. Further information on other less important species groups is provided in Appendix 4.

The terrestrial invertebrate orders and equivalent categories

Actively flying species were the most numerous in the insect fauna, as they can easily be windborne from mainland Iceland and neighbouring islands in the archipelago. The insect orders Diptera and Hymenoptera are the most diverse on mainland Iceland (Ólafsson 1991), which was also reflected in the island fauna. Each species has specific requirements to establish on the island, including access to suitable habitats and resources. This helps explain the high number of species not to have settled, even though some of them were regularly blown to the island.

Approximately half of the dipteran species recorded were regarded as permanent settlers. Many species within the order require aquatic or semi-aquatic habitats for larval development, such as lakes, streams, bogs or wet soil, and were therefore automatically excluded. For example, 20 chironomid species were listed, but only three of them were considered settled, two of which have larval stages in salt water (Hrafnsdottir 2005). Similarly, the three recorded simuliid species all require running water for developing (Nielsen *et al*. 1954) and were therefore not regarded as colonised. These groups illustrate dipterans that were unable to establish viable populations on the island.

All hymenopteran species recorded, except one, were parasitic wasps specialised on specific hosts such as lepidopteran or dipteran larvae, aphids and spiders. This explains the high number of species classified as not settled or of uncertain status compared with those regarded as settled. The bumblebee *Bombus lucorum*, was represented by a single queen, demonstrating the ability of this large and heavy hymenopteran to disperse relatively long distances across open ocean. It was however, not considered to have settled.

Many coleopteran species are not easily dispersed across open ocean but have nevertheless reached Surtsey and are regarded as permanent settlers. Many staphylinid species are excellent fliers and can be carried long distances by wind (Hansen *et al.* 2018). This was regularly observed during the earliest research years, when staphylinids were seen swarming over lava rocks along the north facing shore (pers. obs.). A total of 26 species of staphylinid beetles, about 35% of the Icelandic fauna, have been recorded on Surtsey, of which 18 were regarded settlers.

Many lepidopterans are readily carried by wind across the open sea, not only from mainland Iceland but also from more distant parts of Europe. Almost all species are specialised plant feeders, dependent on a single or a few closely related host plants. The existing flora on Surtsey therefore limits the colonisation possibilities for many lepidopterans. Approximately half of the recorded species (13 of 27) were considered to have settled. Of the remaining 14 species, eight were assumed to have been windborne from Europe, one of which, *Plutella xylostella*, is a classic opportunist whose larvae have been found on Surtsey feeding on northern rock-cress (*Arabidopsis petraea*), a Brassicaceae species.

The number of hemipteran species presented here, 13 in total, represents a minimum estimate, as several aphid species were not identified. Two aphid species were named, one commonly found on sea sandwort on the spit, and a second dependent on downy birch (*Betula pubescens*) which has not colonised Surtsey (Magnússon *et al.* 2023), which therefore cannot be regarded as a potential settler. The coccoids collected might all belong to a single species, except for *Arctorthezia cataphracta*, which was found in a tuft of grass washed ashore in an early year (Ólafsson 1978). The remaining specimens might belong to a newly described species (Gerő *et al.* 2025). Of the remaining seven hemipteran species, five are without doubt colonised, while two were of uncertain status.

Five species of windborne caddisflies were found, all with aquatic larval stages (Gíslason 1978), making colonisation impossible. All four Thysanoptera species recorded had colonised the island with little doubt. Two neuropteran species were recorded, one windborne from mainland Iceland and the other a regular immigrant to Iceland from Europe. A single siphonapteran species was found in 1967 (Lindroth *et al.* 1973), most likely carried to the island by an unknown bird. No signs of colonisation have been observed since.

All birds on the island are no doubt infested with feather lice, making the birds themselves their true “islands” rather than Surtsey itself. Consequently, these parasites are not of direct relevance to this project. Nevertheless, a single record has been published, a feather louse collected from an unnamed bird in 1967. The species (*Eidmanniella pustulosa)* had not been previously recorded from Iceland at the time but is a known parasite of the northern gannet (*Morus bassanus*) (Lindroth *et al*. 1973).

Spiders have been surprisingly successful both in reaching the island and in establishing populations there. The survey documented 26 species, of which 18 are thought to have settled successfully, three were possibly settled and five were considered unlikely to have done so. Juvenile spiders are known to spin silk thread that are caught by the wind, allowing them to become airborne and be carried long distances (Bell *et al*. 2005). The species found only rarely were not regarded as settled.

A single opilionid species, *Mitopus morio*, was first discovered on the island in 2019 and has since been found annually in increasing numbers. It is a very common species throughout Iceland (Agnarsson 1998) and was most likely transported to the island by birds.

Two species of land snails were found, both of which were regarded as settled. They require humid conditions, which they obtain beneath lava stones and within the uppermost soil layer, and they become more evident during rainfall. They were probably carried to Surtsey by birds transporting nesting material.

Enchytraeid annelids were found in soil, beneath driftwood and in gull nests. Although not identified to species, the material appears to include several distinct forms and are thus likely represent more than one species. A single lumbricid specimen was found in a soil sample taken from a dry sand dune formed by lyme grass (Sigurdardóttir 2000). This was highly unexpected and most likely a casual occurrence. The species had been recorded earlier on Heimaey (Lindroth *et al.*1973).

Future work

It is well understood that the terrestrial invertebrates are not easily monitored through short-term annual fieldwork. Effective monitoring of the tiny invertebrates on Surtsey requires extensive knowledge on the island´s fauna, as well as the Icelandic fauna in general, in addition to long-term experience in fieldwork and specimen processing. The single four-day annual visits in mid-July provide only limited insight. Many invertebrate species have restricted periods of adult activity, the stage in which they are typically identifiable. Some species are active throughout the summer, whereas others occur only in early, mid or late summer. Ideally, three visits, in June, July and August, would be recommended. Such frequency is, however, unrealistic due to limited funding, the logistical challenges of accessing the island, and lack of specialised expertise both in the field and in the laboratory.

This research has been maintained for over half a century during the early phases of the island’s primary succession. The ecological succession on the island remains an active and ongoing process. For this reason, it is of great importance that this project continues into the future. Surtsey has offered a unique opportunity for investigations of this kind on northern latitudes.

As noted above, certain important taxonomic groups have been largely overlooked to date. Additional specialist expertise is needed to address them adequately. Soil invertebrates such as collembolans and mites are extremely important components of the ecosystem, and it is hoped that qualified specialists on these groups will engage in the future. The same need applies to aphids, coccoids and several unresolved hymenopteran taxa.

A comprehensive description of the island´s ecosystems, integrating terrestrial invertebrates, vegetation and birdlife, would also be highly desirable, and would best be achieved through a collaborative effort among all specialists involved in Surtsey research.

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The status of breeding birds and other visitors in Surtsey since 2008

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ABSTRACT

This paper aims to provide an overview on the status of breeding birds and visitors on Surtsey since 2008 and is a continuation from Petersen's overview from 2009 of the status after the formation of the island. Specific ornithological expeditions to Surtsey have not taken place since 2003, besides a visit in Surtsey in May 2025. Annual research expeditions have been undertaken in mid-July in 2009–2025. Although the timing is not optimal for bird observations, various information regarding birds has been collected during those visits, including general observations on the presence - absence of known breeding species and regular visitors as well as anecdotes of new species for the island. Gull and fulmar nests have been counted annually on monitoring plots since 2003. Evening counts of gulls present in the colony were performed annually during July visits between 2011 and 2016, in 2023 and in May 2025. One aerial survey was conducted in June 2023 and the gull colony photographed. In May 2025 a breeding bird survey on ground nesting land birds was carried out. By 2025, a total of 95 bird species has been recorded for Surtsey, on the island itself and close by offshore. Out of those, 59 are regular breeders in Iceland, 24 are vagrants and the rest are migrants and winter visitors. Only four species have been recorded for the first time on Surtsey since 2008, of which three are vagrants and one an Icelandic breeder. During the same time, three new breeding species have been recorded, and all of them have been irregular breeders since.

INTRODUCTION

The island Surtsey, formed by a volcanic eruption in 1963–1967, has been studied comprehensively since the very beginning (Baldursson & Ingadóttir 2007). Birds hold a key role in the development of the island's new ecosystem as well as the island playing an important role for both breeding birds and migrants. The present paper is a follow-up of the overview published by Petersen (2009), summarizing bird observations since the formation of Surtsey in 1963 up until 2008. This earlier paper included continuous observations in the early years of the island: in spring and autumn 1967–1971 and summers 1970–1973, as well as whole island censuses in 1990 and 2003. There, Petersen puts forward several recommendations for future monitoring, regarding: a) Breeding bird surveys, by recording distribution and numbers of all breeding birds on the island every third year, using different census techniques, including aerial photography. b) Registration of visitors and other incidental observations during the annual mid-July expeditions and data collection in an appropriate database. c) Recording sea birds on sea during a) and b). Finally, d) Bird ringing. No additional ornithological expeditions to the island were carried out after 2003.

Annual expeditions of a team of researchers (biologists, geologists and others) have been undertaken in mid-July each year from 2009 to 2025, and they have collected various data regarding the birds on the island. They have partly met the monitoring suggestions of Petersen (2009). That is a), b) and c) which includes registration of some breeding birds, visitors and other incidental observations and recording of sea birds on sea. Twice during this period Surtsey was also visited by biologists in May, in 2009 to mount a weather station and in 2025 for

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Pálsbær research hut maintenance. May is a more suitable time for evaluating breeding status of many breeding birds than July. Although the peak breeding season is in May-June for most species, it can be assumed that many individuals of most bird species are still around the breeding area in July, but it is too late in the season for accurate breeding bird surveys of ground nesting land birds (passerines and waders) (Davíðsdóttir 2010). From 2023, the objective has been that every two to four years a scientist with an ornithological background would join the annual July expedition to ensure comprehensive coverage of bird observations.

This paper aims to provide an overview on the status of breeding birds and visitors on Surtsey since 2008, what data has been collected, and which methods have been used. It is a continuation from Petersen's (2009) overview of the status since the formation of the island.

MATERIALS AND METHODS

Study area

Surtsey is the southernmost island of the Vestmannaeyjar archipelago south of the coast of Iceland. It is 1,2 km2 in size with dominant surface types being lava fields on the southern part, in some places filled by tephra sand, two palagonite craters in the centre, each nestling the lava craters Surtur and Surtungur, and a sandy spit on the northern side, fringed by boulders that wave action has transported from the eroding lava fields. The island is sparsely vegetated for the most part, except for the gull colony on the south part where vegetation cover is dense (Fig. 1).

Figure 1. Surtsey and the main landmarks used in the text. Map by Bjarney Guðbjörnsdóttir, satellite image 5.5.2018, Maxar 2018.

Breeding birds

During the annual July visits since 2009, various information regarding the island's bird fauna has been collected by the participating biologists. General observations on presence - absence of known breeding species and regular visitors as well as anecdotes of new species for the island were recorded. The July visits cover partly monitoring suggestions a.), b.) and c.) (registration of some breeding birds, visitors and other incidental observations and recording of sea birds on sea) mentioned in the introduction. However, July is too late in the season for accurate breeding bird surveys of ground nesting land birds (passerines and waders) (Davíðsdóttir 2010). Species were only considered as breeding if nests with eggs or chicks were found, or behavioural indications were observed such as adult puffins carrying food into nest sites. During each expedition, rough estimates of individual gull species numbers and their distribution throughout the colony were also made. This information was collected from different sources such as field books and Pálsbær guest book.

In May 2025 (29.-31.), a breeding bird survey on ground nesting land birds (passerines and waders) was carried out by mapping territorial (singing or alarming) individuals all over the island as well a general assessment on breeding status of various other species.

Gull colony

Since 2003, nests of gulls and fulmars have been counted annually in mid-July within a 1,000 m² circular area around permanent monitoring plots in the gull colony. The counts were carried out at the same time as the vegetation surveys. Only nests showing signs of use earlier in the summer were recorded. The gull species seen within the gull colony included great black-backed gull (*Larus marinus*), lesser black-backed gull (*Larus fuscus*), herring gull (*Larus argentatus*) and glaucous gull (*Larus hyperboreus*). The chicks of these species have generally left the nests by the time the counts were made, and nests were therefore not differentiated between individual gull species, but nest bowls were still visible. Northern fulmar (*Fulmarus glacialis)* nests were counted separately from gull species as fulmars were either incubating, or chicks recently hatched and remained in the nests in mid-July. Over time, as the gull colony has expanded, more permanent monitoring plots on the southern part of the island and on the NNE spit have been added to the survey. Those results have been published in several papers, most recently in Magnússon *et. al.* (2023).

Evening counts of gulls present in the colony on the southern part of the island were performed from a fixed location south of the crater Surtur (Fig. 1), situated above the colony, during July visits in 2011 to 2016, 2023 and in May 2025. There are no counts available for the period 2017 to 2020 due to unfavourable weather conditions. Those are total counts of adult gulls (identified per species) present and visible in the colony late in the evening when human disturbance is minimal during research expeditions and the likelihood of birds being absent foraging is assumed to be less than during daytime (Conover & Miller 1980, Enners *et. al.* 2018). This is comparable to the method described in Petersen (2009) with the observer having a minimum impact on reactivity in the colony. The visibility of different gull species varies depending on the habitat and as the colony has expanded further east into rougher lava terrain it has become more difficult to observe both birds and nests.

To test for correlation between the number of gull nests found in the colony on the monitoring plots and the evening counts, a pearson correlation analysis was performed

One aerial survey was conducted on 10 June 2023 when the gull colony was photographed in order to generate more accurate numbers of breeding gull pairs. Seven transects were flown on a Partenavia P-68 Observer (TF-BMW), and vertical photographs were taken through a floor hatch at an altitude of 600 to 700 feet (189 m). Two Canon 5D SR (50.6 MP) cameras were used — one equipped with a fixed 50 mm Zeiss lens (Planar f/1.4), and the other with a Canon zoom lens (24–105 mm, f/4L) set at a 24 mm focal length. Both cameras were manually focused to infinity, with the setting secured using tape. A fixed shutter speed of 1/4000 was used, and the ISO was set to 800. The cameras were synchronized with an interval timer, capturing one image per second while flying over the colony. Photographs were later merged into seven transects, numbered 0–6. From the combined transect images, gull species were identified (great black-backed gull, lesser black-backed gull and herring gull and possibly glaucous gull), breeding status assessed (individuals or pairs evidently lying on nests / standing next to obvious nest bowls or chicks), and number of breeding units / pairs counted.

Other information

A special effort was made in July 2009 to find both of the Icelandic petrel species, storm petrel (*Hydrobates pelagicus*) and Leach's petrel (*Oceanodroma leucorhoa*). Staff from the South Iceland Nature Research Centre took part in the July-expedition and specifically investigated whether European storm-petrels and Leach's storm-petrels had colonized Surtsey, as these species are found on several of the Vestmannaeyjar islands. These birds are elusive and are mainly active at night. The team visited likely nesting sites and played recordings of their calls

In context with this article, available data from GPS-tagged birds from Iceland were also analysed to detect rare or undocumented species for Surtsey.

Table 1. Bird species seen on or around Surtsey 1963 – 2025. Species that have bred are marked with *, new breeding species since 2008 marked with **, new species overall to the island marked with ***. Note consistency of recordings differs between years and expeditions depending on individual scientists involved in each annual July visit.

English name	Latin name
Red-throated diver	*Gavia stellata*
Great Northern diver	*Gavia immer*
Northern fulmar*	*Fulmarus glacialis glacialis*
Manx shearwater	*Puffinus puffinus*
Storm petrel	*Hydrobates pelagicus*
Leach's petrel	*Oceanodroma leucorhoa leucorhoa*
Northern gannet	*Sula bassana*
Great cormorant	*Phalacrocorax carbo carbo*
European shag	*Phalacrocorax aristotelis aristotelis*
Squacco heron	*Ardeola ralloides*
Grey heron	*Ardea cinerea*
Whooper swan	*Cygnus cygnus*

Pink-footed goose	*Anser brachyrhynchus*
Greylag goose*	*Anser anser anser*
Barnacle goose	*Branta leucopsis*
Brent goose	*Branta bernicla hrota*
Canada goose***	*Branta canadensis*
European widgeon	*Anas penelope*
European teal	*Anas crecca crecca*
Mallard	*Anas platyrhynchos platyrhynchos*
Tufted duck	*Aythya fuligula*
Common eider**	*Somateria mollissima borealis*
King eider	*Somateria spectabilis*
Harlequin duck	*Histrionicus histrionicus*
Long-tailed duck	*Clangula hyemalis*
Common scoter	*Melanitta nigra*
Red-breasted merganser	*Mergus serrator*
Merlin	*Falco columbarius subaesalon*
Gyrfalcon	*Falco rusticolus*
White-tailed eagle***	*Haliaeetus albicilla*
Corncrake	*Crex crex*
Eurasian oystercatcher	*Haematopus ostralegus ostralegus*
Ringed plover**	*Charadrius hiaticula hiaticula*
Golden plover **	*Pluvialis apricaria altifrons*
Knot	*Calidris canutus islandica*
Sanderling	*Calidris alba*
Purple sandpiper	*Calidris maritima littoralis*
Dunlin	*Calidris alpina schinzii*
Common snipe	*Gallinago gallinago faeroeensis*
Eurasian Whimbrel	*Numenius phaeopus islandicus*
Redshank	*Tringa totanus robusta*
Turnstone	*Arenaria interpres interpres*
Red-necked phalarope	*Phalaropus lobatus*
Grey phalarope	*Phalaropus fulicarius*
Arctic skua	*Stercorarius parasiticus*
Great skua	*Stercorarius skua*
Little gull	*Larus minutus*
Black-headed gull	*Larus ridibundus*
Common gull	*Larus canus canus*
Lesser black-backed gull*	*Larus fuscus graellsii*
Herring gull*	*Larus argentatus argentatus*
Iceland gull	*Larus glaucoides*
Glaucous gull*	*Larus hyperboreus leuceretes*
Great black-backed gull*	*Larus marinus*
Kittiwake*	*Rissa tridactyla tridactyla*
Arctic tern*	*Sterna paradisaea*
Common tern	*Sterna hirundo*
Common guillemot	*Uria aalge aalge*
Brünnich´s guillemot	*Uria lomvia lomvia*
Razorbill	*Alca torda islandica*
Black guillemot*	*Cepphus grylle islandicus*
Little auk	*Alle alle*
Atlantic puffin*	*Fratercula arctica*
Turtle dove	*Streptopelia turtur*
Domestic (razing?) pigeon	*Columba livia domestica*
Long-eared owl	*Asio otus*
Short-eared owl	*Asio flammeus flammeus*
Sky lark	*Alauda arvensis*
Swallow	*Hirundo rustica*
Meadow pipit*	*Anthus pratensis pratensis*
Rock pipit	*Anthus spinoletta*
White wagtail*	*Motacilla alba alba*
European robin	*Erithacus rubecula*
Redstart	*Phoenicurus phoenicurus*
Wheatear	*Oenanthe oenanthe leucorhoa*
Ring ouzel	*Turdus torquatus*
European blackbird	*Turdus merula merula*
Fieldfare	*Turdus pilaris*
Song thrush	*Turdus philomelos*
European redwing	*Turdus iliacus coburni*
Garden warbler	*Sylvia borin*
Chiffchaff	*Phylloscopus collybita*
Willow warbler	*Phylloscopus trochilus*
Jackdaw	*Corvus monedula*
Raven*	*Corvus corax varius*
Starling	*Sturnus vulgaris vulgaris*
Chaffinch	*Fringilla coelebs*
Brambling	*Fringilla montifringilla*
Redpoll	*Acanthis flammea islandica*
Crossbill	*Loxia curvirostra*
Lapland bunting	*Calcarius lapponicus*
Snow bunting*	*Plectrophenax nivalis insulae*
Northern oriole	*Icterus galbula*
Common swift***	*Apus apus*
White-winged crossbill***	*Loxia leucoptera*

RESULTS AND DISCUSSION

The total species list

By 2025, a total of 95 bird species has been recorded for Surtsey, on the island itself and close by offshore (Table 1). Out of those, 59 are regular breeders in Iceland, 24 vagrants and the rest are migrants and winter visitors. Only four new species have been found on Surtsey since 2008, three vagrants, common swift (*Apus apus*) in 2013, white-winged crossbill (*Loxia leucoptera*) in 2021 and Canada goose (*Branta canadensis*) in 2025, and one Icelandic breeder, white-tailed eagle (*Haliaeetus albicilla*) in 2023.

Table 2. Breeding species in Surtsey and Icelandic breeding birds that are regular visitors or prospect breeders on and close to Surtsey. Species recorded are marked as white 1, species with breeding confirmed are marked as grey 1, species with only evidence of presence are marked white x, breeding not confirmed is marked grey ?, presence not confirmed marked white ?.

	Northern fulmar	Northern Gannet	Great cormorant	Greylag goose	Common eider	Eurasian oystercatcher	Ringed plover	Golden plover	Purple sandpiper	Redshank	Turnstone	Red-necked phalarope	Great skua	Lesser black-backed gull	Herring gull	Glaucous gull	Great black-backed gull	Kittiwake	Arctic tern	Black guillemot	Atlantic puffin	Meadow pipit	White wagtail	Wheatear	European redwing	Raven	Snow bunting	Recorded	Breeding
1969	1		1																		1					1	1	5	0
1970	1																			1	1							3	2
1971	1																			1								2	2
1972	1																			1	1							3	2
1973	1																			1								2	2
1974	1																1			1								3	3
1975	1																1	1	1	1								5	5
1976	1	1									1	1	1				1	1	1	1			1	1		1		12	4
1977	1											1					1	1	1	1			1			1		8	4
1978	1	1															1	1	1	1	1							7	4
1979	1																1	1		1								4	4
1980	1											1					1	1	1	1		1						7	4
1981	1														1		1	1		1								5	5
1982	1														1		1	1		1								5	5
1983	1														1		1	1		1								5	5
1984	1														1		1	1		1								5	5
1985	1													1	1		1	1		1								6	6
1986	1													1	1		1	1		1						1		7	6
1987	1													1	1		1	1		1								6	6
1988	1													1	1		1	1		1								6	6
1989	1													1	1		1	1		1								6	6
1990	1					1								1	1		1	1		1		1		1		1		10	6
1991	1													1	1		1	1		1						1		7	6
1992	1				1									1	1		1	1		1						1	1	9	6
1993	1													1	1	1	1	1		1						1		8	7
1994	1													1	1	1	1	1		1							1	8	7
1995	1					1	1							1	1	1	1	1		1			1		1			11	7
1996	1				1	1								1	1	1	1	1	1	1		1	1				1	13	8
1997	1													1	1	1	1	1		1							1	8	8
1998	1						1							1	1	1	1	1		1			1	1		1	1	12	8
1999	1													1	1	1	1	1		1		1		1		1	1	11	8
2000	1			1					1					1	1	1	1	1		1			1				1	11	8
2001	1			1					1					1	1	1	1	1		1	1		1				1	12	8
2002	1			1										1	1	1	1	1		1		1	1				1	11	11
2003	1			1										1	1	1	1	1		1	1	1	1	1		1	1	14	11
2004	1	1		1					1				1	1	1	1	1	1		1	1	1	1				1	15	12
2005	1	1		1	1		1		1					1	1	1	1	1		1	1	1					1	15	11
2006	1	1		1					1	1			1	1	1	1	1	1		1	1	1	1			1	1	17	12
2007	1						1							1	1	1	1	1		1	1	1	1	1		1	1	14	11
2008	1					1	1	1					1	1	1	1	1	1		1	1	1		1		1	1	16	11
2009	1			1	1	1		1		1			1	1	1	1	1	1		1	1	1	1			1	1	18	14
2010	1													1	1		1	1		1	?	1	1			1	1	10	11
2011	1													1	1		1	1		1	1	1	1			1	1	11	11
2012	1													1	1		1	1		1	1	1	1			1	1	11	11
2013	1				1	1			1					1	1	1	1	1		1	?	1	1			1	1	15	11

2014	1													1	1		1	1		1	1	1	1			1	1	11	11
2015	1				1									1	1		1	1		1	1	1	1			1	1	12	12
2016	1				1									1	1		1	?		1	?	1	1	1		1	1	13	10
2017	1	1			1			1	1				1	1	1		1	1	1	1	?	1	1	1		1	1	18	8
2018	1				1									1	1		1	?		1	?	1	1			1	1	12	9
2019	1				1			1	1		1			1	1		1	?		1	1	1	1			1	1	15	10
2020	1			x	1		1		1					1	1		1	?		1	1	1	1	1		1	1	15	10
2021	1		1	1			1							1	1		1	?		1	?	1	1			1	1	13	12
2022	1	1	1	1			1				1			1	1		1	?		1	?	1	1			1	1	16	10
2023	1	1	1	1	1			1	1			1		1	1	1	1	1		1	?	1	1	1	1	?	1	21	12
2024	1			x	1									1	1		1	1		1	1	1	1			1	1	12	10
2025	1	1		1	1		1	1	1					1	1		1	1		1	1	1	1			1	1	17	12
Total	**57**	**9**	**4**	**12**	**14**	**6**	**9**	**6**	**11**	**2**	**3**	**4**	**6**	**41**	**45**	**19**	**52**	**51**	**7**	**56**	**26**	**28**	**29**	**11**	**2**	**31**	**33**		
Years breeding	**56**	**0**	**0**	**10**	**4**	**0**	**1**	**2**	**0**	**0**	**0**	**0**	**0**	**41**	**45**	**17**	**52**	**42**	**1**	**56**	**16**	**23**	**22**	**0**	**0**	**18**	**30**		

Irregular or rare breeders

Three new breeding species have been recorded since 2008 for Surtsey and all of them have been irregular breeders since: Common eider (*Somateria mollissima*), golden plover (*Pluvialis apricaria)* and ringed plover (*Charadrius hiaticula*).

Common eider was first confirmed breeding in 2015 when a female with three chicks was found on the NNE spit (Fig. 2). For several years before that, common eiders were observed on and around the island, as well as after the first confirmed breeding (Table 2). In 2023, two nests with eider down were found on the NNE spit (Fig. 1) and one nest in 2024. In May 2025 a male eider held close to the spit during the whole expedition, and in July 2025, two eider nests with down were found on the NNE spit of the island. All three incidents are interpreted as breeding attempts here. An eider nest found with proper down means that the female had laid eggs inn it and can be interpreted as confirmed breeding (Þorvaldur Björnsson, pers. comm.), though breeding success remains unconfirmed, and eider males remain close to their mate while the female is incubating (Honza & Sládeček 2009).

Figure 2. Female common eider (*Somateria mollissima*) with its three chicks the first time breeding was confirmed for the species in Surtsey 2015. Photo: Erling Ólafsson

Golden plover was first confirmed breeding (nest found) in May 2009 and again in July 2025. Three observations were recorded in between, one of them in July 2019 when territorial behaviour (display flight) was observed but not interpreted further as this was judged as too late into the breeding season. Nonetheless golden plovers can be quite late breeders so this could possibly have been the second breeding attempt of three since 2009. There is only one breeding record for ringed plover (nest with eggs in July 2021) but there are several other records of the species being present in Surtsey (Table 2). Arctic tern (*Sterna paradisaea*) has not been found breeding since breeding attempts 1975 and 1978.

Other breeders

Greylag geese (*Anser anser)* were first found breeding in 2002 and have been confirmed breeding in small numbers (< 5 breeding pairs) in the gull colony 10 times since. In some years, only signs of geese activity on the island were found (Table 2). The geese have shown a high level of sensitivity to human disturbance during research expeditions. They have been expected to leave the island as soon as they are aware of human presence. However, during evening count above the gull colony in 2023, geese were found and are suspected to be

Figure 3. White wagtail (*Motacilla alba)* collecting insects as food for its offspring, an example of behavioural indication for breeding. Picture Erling Ólafsson.

hiding during daytime on inaccessible ledges on the edge of the colony. Since 2008, one raven pair (*Corvus corax*) has been breeding regularly in crater Surtungur (Fig. 1), or in a pit crater above a lava tube close by, in the western part of the island. Still, breeding could not be confirmed every year, when no recently used nests could be found, even with an adult pair along with juveniles being present during the expedition.

Three passerines breed on the island: Snow bunting (*Plectrophenax nivalis* in 1996), meadow pipit (*Anthus pratensis* in 2002*)* and white wagtail (*Motacilla alba* in 2002; Fig. 3), all consistent breeders since first breeding. In May 2025, 10 territorial meadow pipits, 3 territorial snow buntings and 7 territorial white wagtails were found. Their breeding distribution is largely unchanged from what was described in Petersen (2009), with meadow pipits breeding in the grassy gull colony and white wagtails and snow buntings breeding in the central and eastern part of the island from Pálsbær (Fig. 1) north towards the rocky shore.

Breeding seabirds

The first breeders on the island (1970) were northern fulmar and black guillemot (*Cepphus grylle*), which have been nesting there consistently ever since with no or little changes in distribution since the census in 2003 (Table 2). Fulmar nest counts on the monitoring plots within the gull colony showed a gradual increase with time, especially in recent years, although numbers fluctuate between years (Fig. 4). The fulmar colony in Surtsey is in some ways unusual since most of the birds do nest on level ground, not in the sheer cliffs of the island as is usually the case for other seabird colonies in Iceland. This can both be due to the fact that the sea-cliffs in Surtsey are constantly changing as the lava that makes up most of the cliffs is easily eroded by wave action. The lava fields on the island do however provide suitable nesting sites for the fulmar as it makes use of the diverse surface morphology to shield under. In addition, no land predators are present in Surtsey which may also affect the fulmar breeding distribution on the island. In May 2025 a dark morph, which predominantly resides in the Svalbard area (Flood & van Grouw 2015) was found at a nest site close to crater Surtur (Fig 1), but breeding could not be confirmed. The fulmar was sitting as on a nest but could also have been a prospector.

The Atlantic puffin (*Fratercula arctica*) was first confirmed as a breeding bird in 2004 and has been recorded present for most recent years (Table 2), but breeding has only been confirmed unregularly and as for northern fulmar and black guillemot no new census data are available since 2003. Kittiwakes (*Rissa tridactyla)* were last recorded breeding in 2015, and again in 2023, when birds on nests in the cliffs south of the gull colony were detected in aerial photographs taken in June 2023 (Table 2).

A special effort was made in July 2009 to find both of the Icelandic petrel species, storm petrel (*Hydrobates pelagicus*) and Leach's petrel

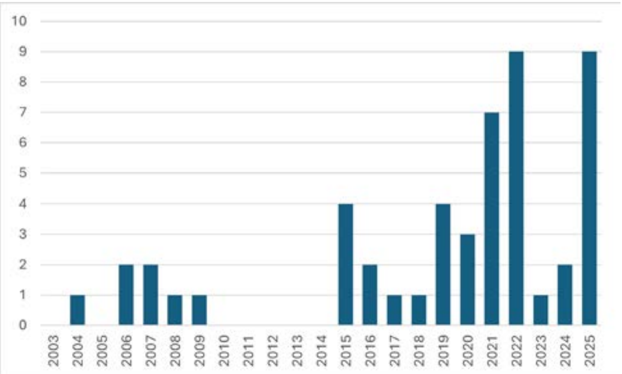

Figure 4. Numbers of northern fulmar (*Fulmarus glacialis*) nests in the vicinity of permanent monitoring plots within the gull colony on the south part of Surtsey during 2003-2025.

(*Oceanodroma leucorhoa*). No responses or other signs were detected, indicating that these species have not settled on Surtsey.

Gull colony

Species distribution in the gull colony has shifted since it was last censored in 2003. Today, great black-backed gulls nest in the centre and western part of the colony where vegetation cover is the densest. Lesser black-backed gulls nest predominantly in the eastern part of the colony and have been extending further east into the rough lava field with no or only sparse vegetation. Herring gulls nest primarily in the southern part of the colony closest to the cliffs. Just south of the automatic weather station (Fig 1) is the contact point of the three colony parts described.

When gull numbers in the colony were assessed in both in 1990 and 2003, breeding lesser blacked gulls were the most numerous. Since then, only rough estimates and evening counts from 2011 – 2016, 2023 and 2025 are available to evaluate any changes in numbers and species composition. Observational notes from the annual expeditions, as well as numbers from evening counts, indicate that great black-backed gull numbers have increased since 2003 (Table 3). Anecdotes from the excursion in 2010 first mentioned that great black-blacked gulls held higher numbers in the breeding colony than lesser black-backed gulls whose numbers had declined. However, the observed changes in numbers of lesser black-backed gull could also have been affected by the species gradually extending into lava habitat of rougher terrain and becoming less visible. Different visibility of the two species in their nesting habitats could therefore have masked possible changes in lesser black-backed gulls numbers. Great black-backed gulls (Fig. 6) are easily counted from the observation point while lesser black-backed gull numbers in cracks in the lava field are most certainly underestimated. Herring gull numbers from the 2003 census, observational notes recorded since then, and evening counts, all appear comparable and rather stable.

Glaucous gulls were recorded breeding up to 11 pairs in 2003, but only very low numbers have been recorded lately (Table 3). Mixed pairs of herring gulls and glaucous gulls have been documented on Surtsey, and hybridization of those species is common (Ingólfsson 1970, Vigfúsdóttir *et al.* 2008). With ongoing hybrid breeding, differentiation between herring gulls, glaucous gulls and hybrid individuals becomes increasingly more difficult. Several glaucous gulls were observed in the colony in 2023 identified from body size but could also possibly have been large hybrids. In 2025, only hybrids were observed.

Number of gull nests around monitoring plots in the gull colony was rather stable over the two last decades with annual numbers fluctuating between 20-50 nests. No correlation was found between total gull numbers from evening counts (Table 3) and numbers of gull nests in the colony around permanent plots (Fig. 5) (Pearson correlation: r=0.36, p=0.38).

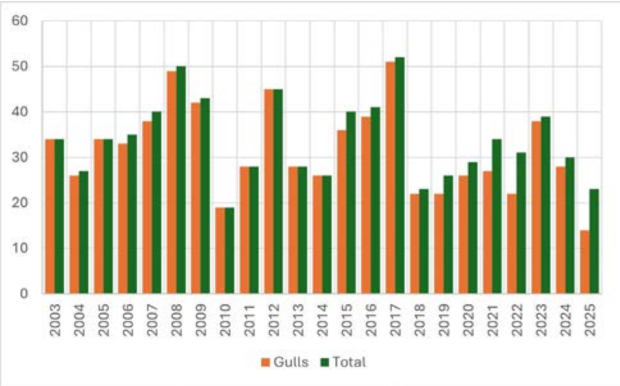

Figure 5. Number of gull nests around permanent monitoring plots in the gull colony on the south part of Surtsey.

Table 3. Gull numbers in Surtsey during evening counts in mid-July (2011–2023) and May 2025 (numbers in parentheses are breeding pairs detected in aerial photographs in May 2023).

	2011	2012	2013	2014	2015	2016	2023		2025
Great black-backed gull	162	112	180	180	262	268	200	(115)	167
Lesser black-backed gull	66	167	123	100	60	87	57	(127)	98
Herring gull	61	61	36	82	38	60	45	(52)	45
Glaucous gull	-	-	1	-	-	-	-	(2)	-
Total	**289**	**340**	**340**	**362**	**360**	**415**	**302**	**(296)**	**310**

Figure 6. Pair of great black-backed gulls (*Larus marinus)* easily detectable both in evening counts and on aerial pictures. Picture Erling Ólafsson

Individual gull species appeared to respond differently to aerial disturbance during the aerial survey. From pictures derived from the aerial survey great black-backed gull pairs or individuals by or on nests were easily detectable, no non-breeders were found on the photographs and were presumably flushed by the plane. In total, 115 nesting pairs/individuals were counted (Table 3). Nesting herring gulls were not as obvious as great black-backed gulls, but rather easily detectable, with few extra birds on photographs whose status was difficult to determine. From the photographs, hybrids could not be clearly differentiated from glaucous gulls but there was an obvious size variation in gulls identified as herring gulls. Overall, 52 nesting pairs/individuals of herring gulls were counted and 2 pairs of either glaucous gulls or very large hybrids (Table 3). Lesser black-backed gull pairs or individuals on nests were more challenging to identify from the aerial photographs as their nests are more difficult to distinguish in the breeding habitat and non-breeders appear not to be flushed as easily as the other species. The resulting estimate was 127 nesting pairs/individuals (Table 3). These numbers compared to the 2023 evening count (Table 3) indicate that great black-backed gulls are fairly well represented in the evening counts, but lesser black-backed gull numbers are highly underestimated. Herring gull numbers are both possibly underestimated in the evening counts and/or overestimated from the aerial photographs.

Visitors

Various Icelandic (breeding) birds are visitors to Surtsey. Some use the island as a stop-over site, such as purple sandpipers (*Calidris maritima*), which are recorded regularly along with other waders. Other species could be prospective breeders, such as wheatear (*Oenanthe oenanthe*) that has regularly been observed in July past breeding time, and great cormorant (*Phalacrocorax carbo*) that uses the island as a resting site (Table 2).

All Icelandic geese species except white-fronted goose have been recorded on Surtsey (greylag goose, pink-footed goose (*Anser brachyrhynchus*), barnacle goose (*Branta leucopsis*) and brent goose (*Branta bernicla*). In 2025, one pink-footed goose was recorded flying just past the gull colony and a pair of Canada geese was observed several times during the expedition, the first record of the species in Surtsey. It could not be determined which of the various subspecies those Canada geese were, but their size was approximately between barnacle and greylag goose size which rules out the largest subspecies and the cackling goose (*Branta hutchinsii;* the smallest of all subspecies, defined as a separate species today). Data from GPS tagged barnacle geese has shown that at least one individual stayed on the island for one day from 3.–4. of April 2023, during spring migration from Scotland to Iceland, before continuing to the South coast of Iceland and from there along the coastline to the breeding grounds in the Southeast (Natural Science Institute of Iceland, unpublished data).

A young GPS-tagged white-tailed eagle, hatched in 2023 in the Northern highlands of Iceland, stayed in Surtsey for some time according to data recorded from 2.–6. December 2023 (Natural Science Institute of Iceland, unpublished data). That was the bird's first journey leaving its parents' territory. Young eagles, from first calendar year leaving their parents territory until settling at a breeding site with sexual maturity at about 5-6 years, show this behaviour of travelling widely over the species breeding distribution area (Whitfield *et al* 2009). The bird's transmitter stopped sending data after 6. December when the bird was still located on Surtsey but neither the bird's remains, nor the transmitter, could be found in the following expedition in July 2024, and its fate entirely unknown.

Future prospects for bird life in Surtsey

Surtsey is the southernmost point of Iceland and therefore provides a key position for travelling and migrating birds. Multiple vagrants were recorded in the early years when ornithological expeditions were more frequent, as well as in annual biological expeditions since. Many Icelandic migrants have also been recorded, which has revealed a large range of species using the island as a stopover site.

The composition of breeding birds in Surtsey has changed little since 2008. All seabird species that bred in the island before 2008 remain as such and only a few new breeding species have been recorded since then. The development of both breeding seabird numbers and species composition is probably mainly controlled by food availability at sea and the erosion of their breeding habitat on the island. Limiting factors for other possible future breeding species, with Surtsey being a suitable habitat otherwise, are food and freshwater availability as discussed by Petersen (2009).

The number of breeding greylag geese pairs has the potential to increase but the human disturbance in annual July expeditions at a sensitive point during their breeding season could possibly be a limiting factor. Common eider, ringed plover and golden plover are now probably only irregular breeders, but their numbers could potentially increase.

Arctic terns might begin nesting again in Surtsey and Eurasian oystercatcher (*Haematopus ostralegus*) could also be mentioned as a prospective breeder. Wheatears have been recorded regularly without breeding confirmed and European redwings (*Turdus iliacus*) have been observed in July and could possibly colonize the island if the shrub species already present (Magnússon *et al.* 2023) disperse progressively.

Passerine species composition has changed since 2003 when snow buntings were dominant among passerine species, with 11 breeding pairs, 2 meadow pipit breeding pairs and one white wagtail breeding pair (Petersen 2009). This can be compared to the findings in May 2025, when 10 territorial meadow pipits, 3 territorial snow buntings and 7 territorial white wagtails were found. Although based on scant data, this can be interpreted to reflect both habitat changes on the island with more grassy habitat available in the gull colony for meadow pipits as well as a recent decrease in the Icelandic snow bunting population (Natural Science Institute of Iceland 2025).

Recommendations for future monitoring

Regular bird observations are essential to ensure a comprehensive coverage of the development of avian communities in Surtsey. From 2023 the aim has been to regularly (every 2-4 years) involve a scientist with an ornithological background in the annual July expeditions. On those occasions, if feasible, sailing around Surtsey upon arrival or departure to assess breeding seabirds in cliffs around the island is recommended. Breeding bird survey on ground nesting land birds (passerines and waders) at peak breeding season in May-June should be routinely conducted (every 5-10 years).

Since seagulls are an important driver of ecological change in Surtsey it is of high importance to monitor their numbers and distribution. For assessing numbers in the gull colony, regular evening counts in July (every 2-4 years) combined with aerial surveys (every 5 years) during early breeding season while the birds are lying on eggs or young chicks should be conducted. The option of performing evening counts in the colony from two different advantage points should be explored as well as including a count on the NNE spit.

Northern fulmars are long-living species, and it is of interest to monitor the nesting site where the dark morph was found to verify if the bird returns and if it turns out being a breeder rather than a prospector.

No bird ringing has been carried out since 2003. During the annual expeditions, many different aspects of research are conducted simultaneously in the gull colony, which means a near constant disturbance. Bird ringing, although it would provide useful information on e.g. foraging of seagulls, would increase disturbance substantially, as also mentioned by Petersen (2009), and is therefore not recommended during the annual July expeditions.

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Guðmundur A. Guðmundsson and pilot Úlfar Henningson carried out the aerial survey along with the author.

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SOIL SCIENCE

Early soil development on Surtsey Island: insights from 20 profile descriptions

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ABSTRACT

Surtsey, a young volcanic island under strict protection from human activities, provides a unique natural laboratory to study soil formation on newly formed land. In July 2024, we examined 20 soil profiles across the island under varying influence of seabird activity and vegetation cover. Although all profiles reflected early-stage pedogenesis, seabird activity and vegetation clearly enhanced horizon development and organic matter accumulation, as reflected by frequent O and Bw horizons at vegetated sites within bird colonies. In contrast, sparsely vegetated or barren sites outside seabird colonies showed minimal organic matter accumulation, with no O-horizons and only occasional weakly developed Bw horizons. Our visual descriptions of soil profiles corroborate previous studies showing the strong role of ornithogenic inputs in organic matter and nutrient accumulation on the island. Future research should aim to better understand the influence of ornithogenic inputs and vegetation on weathering processes and the formation of secondary pedogenic minerals in soils of the island.

INTRODUCTION

Formed during a sub-oceanic volcanic eruption over the years 1963 to 1967, and protected since 1965, Surtsey island has for several decades served as a pristine natural laboratory for studying early succession of life on newly formed land without human interference (Einarsson 2009). Systematic monitoring of vegetation, birds, and other organisms is conducted on the island on a regular basis. Various other studies have been carried out more sporadically, including several on soil development and soil properties.

Surtsey offers a unique opportunity to follow the early stages of soil development on young land in real time – knowledge which becomes increasingly relevant as new land emerges, e.g. in front of receding glaciers (e.g. Vilmundardóttir *et al.* 2015). The majority of pedogenic studies on Surtsey so far have focused on the accumulation of soil organic carbon (SOC) and nitrogen (e.g. Leblans *et al.* 2014, Stefansdottir *et al.* 2014) and on the nutrient status of the island´s soils (e.g. Aerts *et al.* 2020, Sigurdsson & Leblans 2020). A few studies have also been conducted on soil organisms, first and foremost bacteria (Marteinsson *et al.* 2015) and nematodes (Ilieva-Makulec *et al.* 2015). The overriding and common narrative of these studies is the great importance of the seagull colony on the island for soil development and soil characteristics. For example, a study on soil nutritional parameters by Aerts *et al.* (2020) found higher N and P concentrations in soils from within the colony than outside, with higher N concentrations in shallow soils than in deep soils. By comparing the nitrogen isotopic fingerprints of bird faeces and pellets, soils and vegetation, the authors demonstrated that most of the N accumulation in soils in the bird colony was derived from the influx of ornithogenic organic material. At the northern spit of the island, seal colonies also contribute to the input of nutrients from the sea to the land (Magnusson *et al.* 2020).

The importance of birds for soil formation is also known elsewhere, for example in coastal areas of Antarctica, where the redistribution of nutrients from the ocean to land through birds positively influences soil organic carbon and nutrient levels (Bockheim 2015). Importantly, the influence of seabirds there is known to reach beyond the boundaries of their colonies, as wind erosion and water solutions can distribute nutrients to areas distant from the bird colonies. Seabirds can also play a role in shaping soil characteristics in warmer and drier climatic zones. For instance, in the gulf of California, Wait *et al.* (2005) demonstrated significantly higher soil moisture contents, soil respiration rates, higher N, P and K contents, and δ^{15}N enrichment in arid soils affected by ornithogenic organic influxes than in soils with similar climatic conditions not affected by seabirds.

In July 2024, descriptions of soil profiles were conducted across Surtsey to gain a general overview of the state of soil formation, the variety of soils found, and to form a foundation for further research on soil development on this young land. Below, we provide an overview of the field work approach, as well as the described soil profiles. Suggestions for future research are also discussed.

METHODS

Site selection and soil profile descriptions

Fieldwork for soil profile descriptions took place between 16. and 18. July 2024. All soil profiles were located near permanent vegetation survey plots of the island (≤ 5 m from each plot). A subsample of 20 plots was chosen (Fig. 1) based on the seabird influence, density and type of vegetation cover, topography and type or grain size of parent material.

Eight vegetated sites within a seagull colony (dominated by *Larus fuscus;* sites 1, 3, 4, 6, 7, 8, 9, 10), five sparsely vegetated sites under some influence of seabirds (sites 12, 22, 23, 30, 37) and seven sparsely vegetated or unvegetated sites under little influence of birds (sites 13, 14, 15, 16, 18, 19, 21) were described (Fig. 1). Sites 30 and 37 additionally receive nutrients from seal colonies. By the time of fieldwork, the seagull colony had been established for nearly 40 years (since 1986) and had increased in area and number of birds since that time (Magnusson *et al.* 2020, Magnusson & Magnússon 2000). Amongst dominant vascular plants at permanent vegetation monitoring plots in the colony are *Leymus arenarius*, *Poa pratensis*, *Tripleurospermum maritimum*, *Stellaria media*, *Festuca richardsonii*, *Puccinelia coarctata* and *Honckenya peploides* subsp. *diffusa.* (Table 1).

At each site, a soil pit of ≤ 1 m was dug, which at many sites allowed for excavation of complete soil profiles. At some sites (particularly at slopes), the total soil depth exceeded 1 m. For each soil profile, horizon occurrence and depth were recorded. For each soil horizon, clearness and shape of horizon boundary, Munsell soil colour, structure, consistence, roots and texture were recorded following Schoeneberger *et al.* (2012). Soils ≥ 30 cm deep were defined as deep, soils < 30 cm were defined as shallow.

Soils at sites 1, 3, 4 are relatively deep, forming from tephra-sands deposited on sheet lava, and from organic remains from local vegetation. Soils at sites 6-10 are rather shallow, likewise forming from tephra-sands overlying sheet lava, and from vegetation remains. Soils at sites 22 and 23 are

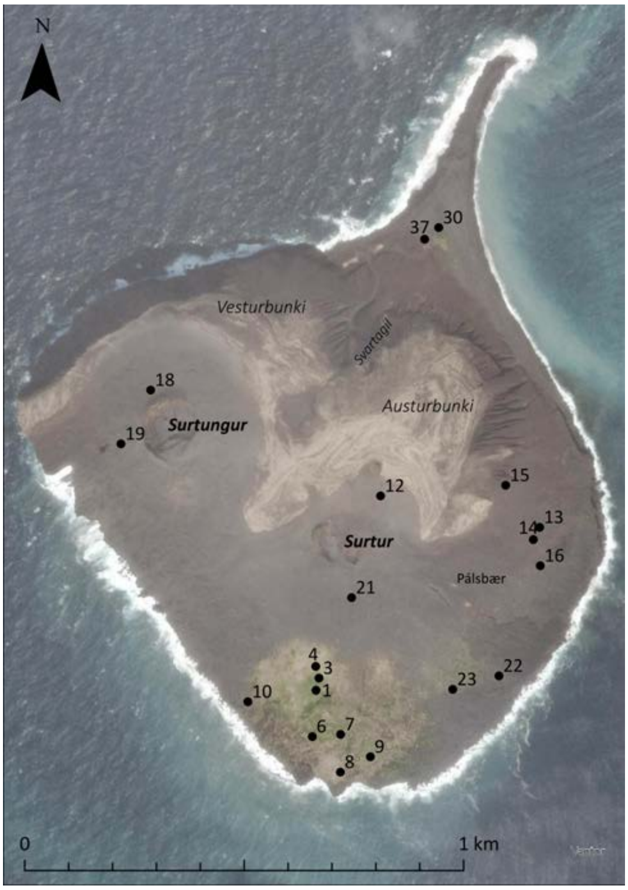

Figure 1. Aerial view of Surtsey showing the main place names on the island and the locations of the soil profiles described in this study (numbered dots). The numbers correspond to permanent vegetation survey plots. Basemap from Esri *et al.* (2023).

shallow, forming in rather fine-grained tephra on sheet lava. Soils at sites 30 and 37 are deep (> 1 m), forming in sand deposits; notably, the environment of these sites is very dynamic, with constant erosion and deposition of material by wave action. Soils at sites 12, 13, 14, 15 and 21 form in tephra sand of various grain size overlying sheet lava; soils of sites 12, 15 and 21 are deep soils, while soils at sites 13 and 14 are rather shallow. Finally, soils at sites 18 and 19 are shallow, forming in coarse-grained tephra on sheet lava, in close vicinity to the crater Surtungur (Fig. 1).

RESULTS AND DISCUSSION

Ornithogenic influence on soil development

Our profile descriptions reflect the strong ornithogenic influence on the island´s soils, as shown by earlier studies on SOC and nitrogen (Aerts *et al.* 2020, Leblans *et al.* 2014, Sigurdsson & Leblans 2020), but no such profile descriptions have been published before for the island.

All profiles showed soils at very early stages of soil formation, with soil colour ranging from dark brown to black (Tables 1 and 2). Colour mainly reflects the volcanic mineral parent material, though significant

Table 1. Selected soil morphological properties for vegetated sites within a seagull colony with deep and shallow soils. Profile descriptions followed Schoeneberger *et al.* (2012). Colour codes: 7.5YR 2.5/2 = very dark brown, N 2.5/0 = black, 7.5YR 4/2 = brown, 7.5YR 3/2 = dark brown, 10YR 2/2 = very dark brown, 7.5YR 3/1 = very dark gray, 10YR 3/2 = very dark grayish brown. Structure (grade, size, type): 1 = weak, f = fine, m = medium, co = coarse, gr = granular. Roots: 1 = few, 2 = common, 3 = many, vf = very fine, f = fine, m = medium.

Pedon no.	Horizon	Depth (cm)	Boundary	Colour	Structure	Consistence	Roots	Texture	Dominant vegetation
Vegetated sites, deep soils									
1	O	0 – 5	abrupt smooth	7.5YR 2.5/2	NA	NA	3 vf, 2 f	NA	*Leymus arenarius, Poa pratensis, Tripleurospermum maritimum, Stellaria media*
	OBw	5 – 12	abrupt smooth	O: 7.5YR 2.5/2; Bw: N 2.5/0	1, f, gr	NA	3 vf, 2 f	loamy sand	
	C	12 – 35		N 2.5/0	1, m-co, gr	loose	3 vf	sand	
3	O	0 – 4	abrupt smooth	7.5YR 2.5/2	NA	NA	3 vf, 3 f, 2 m	NA	*Leymus arenarius, Poa pratensis*
	OBw	4 – 12	abrupt smooth	O: 7.5YR 2.5/2; Bw: N 2.5/0	1, f, gr	NA	3 vf, 3 f, 2 m	loamy sand	
	C	12 – 32		N 2.5/0	1, m-co, gr	loose	3 vf, 1 f, 1 m	sand	
4	O	0 – 7	abrupt smooth	7.5YR 2.5/2	NA	NA	3 vf, 3 f, 2 m	NA	*Leymus arenarius, Poa pratensis*
	C	7 – 77		N 2.5/0	1, m-co, gr	loose	3 vf, 1 f, 1 m	sand	
Vegetated sites, shallow soils									
6	O	0 – 14	clear smooth	7.5YR 4/2	NA	NA	3 f	NA	*Festuca richardsonii, Stellaria media, Poa pratensis*
	OBw	14 – 20		7.5YR 3/2	1, f, gr	very friable	3 f	loamy sand	
7	O	0 – 10	clear smooth	7.5YR 4/2	NA	NA	3 f	NA	*Festuca richardsonii, Poa pratensis*
	OBw	10 – 19		7.5YR 3/2	1, f, gr	very friable	3 f	loamy sand	
8	O	0 – 4	abrupt smooth	7.5YR 2.5/2	NA	NA	3 f	NA	*Festuca richardsonii, Puccinellia coarctatas, Poa pratensis*
	Bw	4 – 22		10YR 2/2	1, f, gr	very friable	3 f	loamy sand	
9	O	0 – 10	abrupt smooth	7.5YR 2.5/2	NA	NA	3 f	NA	*Festuca richardsonii, Poa pratensis*
	Bw	10 – 28		10YR 2/2	1, f, gr	very friable	3 f	loamy sand	
10	OC	0 – 4	abrupt smooth	7.5YR 3/1	1, f, gr	NA	3 vf, 2 f	sand	*Festuca richardsonii, Honckenya peploides* subsp. *diffusa, Leymus arenarius*
	C	4 – 16		10YR 3/2	1, f, gr	loose	3 vf, 2 f, 1 m	sand	

vegetation cover adds organic influence at some sites. Soil structure is generally weakly developed, dominated by single-grain horizons; some vegetated sites show weak granular structure, typically with loamy sand texture, while other horizons are mostly sandy (Tables 1 and 2).

Despite the characteristics of early-stage soil formation in all profiles, clear differences emerge between the vegetated soils within the seagull colony and sparsely or unvegetated soils under lower seabird influence (Fig. 2 and 3, Tables 1 and 2). Profiles in the colony (1, 3, 4, 6–10) exhibit O or OC horizons at the surface, with high organic content sometimes mixed with mineral material. Many also have young Bw (or OBw) horizons, indicating early pedogenic mineral formation. Likely, ornithogenic inputs not only enhance vegetation establishment and contribute organic matter to the soils but also shape weathering processes and secondary mineral formation. While the glassy nature and high porosity of volcanic ejecta facilitates high weathering rates and rapid soil formation, not least in volcanic areas dominated by basaltic materials (Bonatotzky *et al.* 2021, Ugolini & Dahlgren 2002), abiotic and biotic factors play a regulating role. For example, the influence of seabirds on soil pH could be of importance for weathering rates (Oelkers and Gislason 2001) and the formation of some secondary minerals. Sigurdsson and Magnusson (2010) demonstrated an average pH of 6.7 in soils from vegetated sites within the seagull colony in contrast to a higher average soil pH of 7.6 in non- or sparsely vegetated soils outside the colony. This significantly lower pH of the bird influenced soils might promote the formation of allophane, which is favoured at pH 5-7 (Parfitt 2009). Haus *et al.* (2016) demonstrated that oxalic acid in guano enhanced weathering of tephra and precipitation of poorly crystalline minerals in young soils of Antarctica. The reduction of pH with increased vegetation colonisation and organic matter decomposition of parent material of basaltic origin may, however, not be solely a direct response to the seabird allochthonous inputs. Similar reductions in pH have also been found in young soils on nunataks

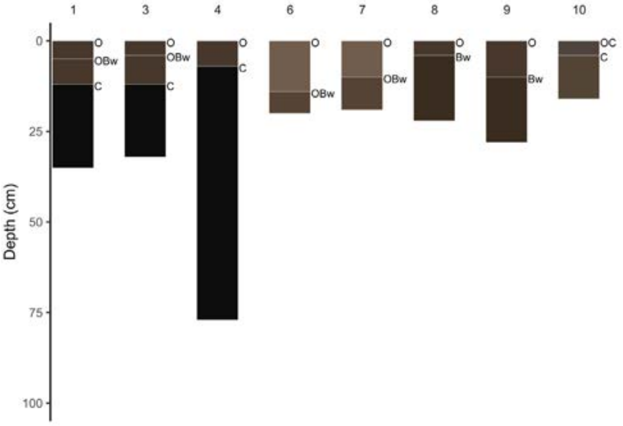

Figure 2. Schematic illustration of soil horizonation at vegetated sites on Surtsey island. Sites 1, 3 and 4 have relatively deep soils (≥ 30 cm), while sites 6 - 10 have shallow soils (< 30 cm).

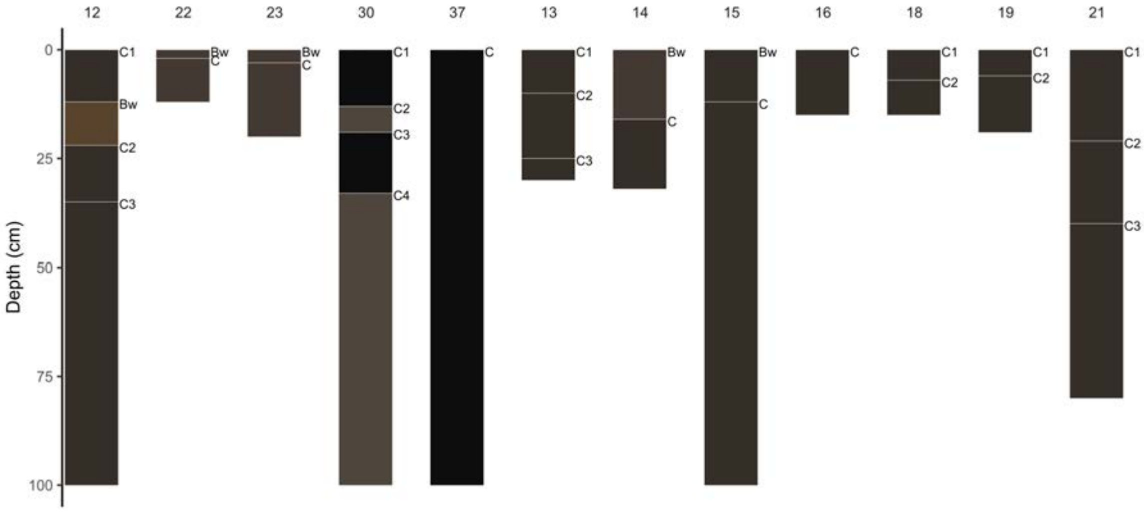

Figure 3. Schematic illustration of soil horizonation at sparsely vegetated or barren sites on Surtsey island. Sites 12, 15, 21, 30 and 37 have deep soils (≥ 30 cm), while sites 13, 14, 16-19, 22 and 23 have shallow soils (< 30 cm). The total soil depth of profiles reaching 100 cm exceeded 1 m. Some influence of seabirds is at sites 12, 22, 23, 30 and 37, while seabird influence is little at sites 13, 14, 15, 16, 18, 19 and 21.

Table 2. Selected soil morphological properties for sparsely vegetated or barren sites under some (12, 22, 23, 30, 37) or little influence of seabirds (13, 14, 15, 16, 18, 19, 21). Profile descriptions followed Schoeneberger *et al.* (2012). Colour codes: 10YR 2/1 = black, 10YR 3/3 = dark brown, N 2.5/0 = black, 10YR 3/1 = very dark gray; 7.5YR 2.5/1 = black. Structure (grade, size, type): 1 = weak, f = fine, m = medium, gr = granular, sg = single grain. Roots: 1 = few, 2 = common, 3 = many, vf = very fine, f = fine, m = medium.

Pedon no.	Horizon	Depth (cm)	Boundary	Colour	Structure	Consistence	Roots	Texture	Dominant vegetation
Sparsely vegetated or barren sites, deep soils									
12	C1	0 – 12	abrupt smooth	10YR 2/1	sg	loose	3 vf	sand	*Tripleurospermum maritimum, Silene uniflora, Leymus arenarius, Honckenya peploides* subsp. *diffusa, Rumex acetosella*
	Bw	12 – 22	clear smooth	10YR 3/3	sg	loose	3 vf	sand	
	C2	22 – 35	clear smooth	10YR 2/1	sg	loose	2 vf	sand	
	C3	35 – > 100		10YR 2/1	sg	loose	2 vf	sand	
15	Bw	0 – 12	clear smooth	10YR 2/1	sg	loose	2 vf	sand	*Honckenya peploides* subsp. *diffusa, Leymus arenarius*
	C	12 – > 100		10YR 2/1	sg	loose	2 vf, 1 f	sand	
21	C1	0 – 21	clear smooth	10YR 2/1	sg	loose	1 vf	sand	*Honckenya peploides* subsp. *diffusa, Silene uniflora*
	C2	21 – 40	clear smooth	10YR 2/1	sg	loose	very few vf	sand	
	C3	40 – 80		10YR 2/1	sg	loose	none	sand	
30	C1	0 – 13	abrupt smooth	N 2.5/0	sg	loose	2 vf, 1 f	sand	*Leymus arenarius, Honckenya peploides subsp. diffusa, Cakile maritima* subsp. *islandica*
	C2	13 – 19	abrupt smooth	10YR 3/1	sg	loose	2 vf	sand	
	C3	19 – 33	abrupt smooth	N 2.5/0	sg	loose	1 vf	sand	
	C4	33 – > 100		10YR 3/1	sg	loose	3 vf, 2 f	sand	
37	C	0 – > 100	NA	N 2.5/0	sg	loose	none	sand	*Leymus arenarius, Honckenya peploides* subsp. *diffusa, Cakile maritima* subsp. *islandica*
Sparsely vegetated or barren sites, shallow soils									
13	C1	0 – 10	clear smooth	10YR 2/1	sg	loose	1 vf	sand	*Leymus arenarius, Honckenya peploides* subsp. *diffusa, Silene uniflora*
	C2	10 – 25	abrupt smooth	10YR 2/1	sg	loose	1 vf	sand	
	C3	25 – 30		10YR 2/1	sg	loose	1 vf	sand	
14	Bw	0 – 16	abrupt smooth	7.5YR 2.5/1	sg	loose	2 vf	sand	*Honckenya peploides* subsp. *diffusa, Leymus arenarius, Silene uniflora*
	C	16 – 32		10YR 2/1	sg	loose	very few f	sand	
16	C	0 – 15		10YR 2/1	sg	loose	3 vf., 3 f, 1 m	sand	*Silene uniflora, Leymus arenarius, Honckenya peploides* subsp. *Diffusa*
18	C1	0 – 7	clear smooth	10YR 2/1	1, f, gr	loose	1 vf	sand	*Honckenya peploides* subsp. *diffusa, Silene uniflora, Armeria maritima* subsp. *maritima*
	C2	7 – 15		10YR 2/1	1, f, gr	loose	very few vf	sand	
19	C1	0 – 6	clear smooth	10YR 2/1	1, f, gr	loose	1 vf, 1 m	sand	*Honckenya peploides* subsp. *diffusa, Silene uniflora, Armeria maritima* subsp. *maritima*
	C2	6 – 19		10YR 2/1	1, f, gr	loose	very few vf	sand	
22	Bw	0 – 2	abrupt smooth	7.5YR 2.5/1	1, f, gr	very friable	3 vf	loamy sand	*Silene uniflora, Festuca richardsonii, Poa pratensis*
	C	2 – 12		7.5YR 2.5/1	1, f-m, gr	loose	2 vf, 2 f	sand	
23	Bw	0 – 3	abrupt smooth	7.5YR 2.5/1	1, f, gr	very friable	3 vf	loamy sand	*Silene uniflora, Festuca richardsonii, Poa pratensis*
	C	3 – 20		7.5YR 2.5/1	1, f-m, gr	very friable	3 vf	loamy sand	

(glacier islands) during primary vascular plant succession over longer time periods without bird allochthonous influences (Sigurdsson & Leblans 2020, Vilmundardóttir *et al*. 2014).

In sparsely and non-vegetated soils, organic accumulation is limited, yet profiles 12, 14, 15, 22, and 23 show early Bw horizons. At sites 12, 22 and 23 there is an increasing influence of seabirds in recent years, possibly enhancing weathering processes through addition of organic acids (Haus *et al.* 2016) and lowering of pH (Parfitt 2009, Sigurdsson & Magnusson 2010). Formation of Bw horizons at the less bird-influenced sites 14 and 15 may be influenced by the presence of deep-rooting plants *Leymus arenarius* and *Honckenya peploides* (Table 2). Work by Stefansdottir *et al.* (2014) identifies *Leymus arenarius* as a likely key factor for soil development on the island outside the seagull colony. They showed significantly increased N accumulation, and higher SOM levels in *Leymus arenarius* dunes, positively correlating with dune age.

Suggestions for future soil research on Surtsey island

We propose a timely investigation of weathering processes and the formation of clay-sized secondary minerals in the soils of Surtsey. Research on the amount and characteristics of pedogenic minerals has, to our knowledge, not yet been conducted on the island, despite the fundamental role these constituents play in soils. Clay-sized minerals are crucial for many soil properties and processes, including specific surface area, water holding capacity, nutrient retention, cation exchange capacity, pH buffering, organic matter accumulation, soil aeration, and more soil characteristics (Ito & Wagai 2017). Importantly, clay-sized minerals vary considerably in structure, composition, and chemical reactivity, which strongly influences the properties of individual soils.

A key characteristic of Andosols - soils formed from volcanic ejecta, such as in Iceland - is the formation of nanocrystalline clay-sized minerals allophane and imogolite, as well as ferrihydrite (Arnalds 2015). In warmer regions with xeric moisture regimes and sufficient Si in the soil solution, halloysite formation is favoured (Harsh 2012, Parfitt 2009). Allophane, the most common clay mineral in Icelandic Andosols, is closely linked to many characteristic properties of volcanic soils, including their high potential for organic matter stabilization, low bulk densities, great water holding capacities, poor cohesion and phosphorus fixation (Arnalds 2015). As this mineral, together with other nanocrystalline phases, profoundly shapes soil properties, its formation is a crucial indicator of pedogenesis in volcanic ejecta, and a fundamental component of the functioning of Andosols.

Thus, a timely question is whether seabirds not only influence organic matter accumulation in the soils of Surtsey but also influence weathering processes and the formation of pedogenic minerals. As discussed above, it is plausible that the island´s sea gull colony affects the formation of nanocrystalline mineral phases such as allophane, for instance through enhanced weathering and pH modification by ornithogenic material and vegetation (Haus *et al.* 2016, Parfitt 2009).

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GEOLOGY

Sinkholes observed at Vesturbunki, Surtsey

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ABSTRACT

We report observations and monitoring of sinkholes and tensional fissures occurring along the outer margin of the lava shield within Vesturbunki, one of Surtsey's two tuff cones. The features were first noted in summer 2015 and traced nearly continuously along roughly 500 m of the lava–tuff contact. In 2015, 49 sinkholes and fissures were observed; subsequent field work in 2017, 2019 and 2025 recorded approximately 20 features per visit, including some previously unrecorded openings. Field data includes GPS locations and photographs. To contextualize these observations, we compare them with geodetic and seismic data from the area and report maximum surface temperatures for the two tuff cones, Vesturbunki and Austurbunki, from surveys we conducted between 2008 and 2025. Earlier geodetic data on Surtsey indicates ongoing subsidence of the island, with a decaying rate since the eruption and Austurbunki is more stable than Vesturbunki. Seismicity near Surtsey during the years 2009–2024 was examined and was found to be low to moderate with five events ≥M 2.5. The seismic hypocentre locations are uncertain because of sparse station coverage. Surface temperature monitoring shows Vesturbunki is consistently hotter, up to 100°C, and fluctuates by up to 4.5°C between measurements, while Austurbunki is stabler and slightly cooler, up to 96°C, with only 2°C fluctuations. The sinkholes were likely produced and maintained by a combination of island-wide subsidence, local compaction of volcanogenic material, and possibly by seismicity that may trigger opening of fissures in the palagonite tuff cone that enhance upward heat flow locally and temporarily. Continued monitoring and mapping, as well as installation of a local seismic station on Surtsey, is recommended to better resolve the processes that produce these features.

INTRODUCTION

Jakobsson and Moore (1982) described how Vesturbunki was formed as a tephra cone during a phreatomagmatic eruption that began on February 1st, 1964. On April 4th, the character of the eruption changed to Hawaiian-style lava effusion when the sea no longer reached the vent, and lava erupted from the crater Surtungur. The eruption at Surtungur ended on May 17th, 1965, by which time a relatively flat lava shield had formed within the tephra cone. Geodetic surveys on August 24th, 1964, showed that Vesturbunki reached its highest elevation in the western part of the cone, 169 m above sea level (Þórarinsson 1966), but is today 140 m above sea level (Óskarsson *et al.* 2021).

The tephra on Surtsey was rapidly altered to palagonite tuff, and by 1998 it was estimated that about 80–85% of the tephra had been converted to palagonite (Jakobsson *et al.* 2000). While the tephra remained unconsolidated, the westernmost part of Vesturbunki was subject to intense marine erosion. When the erosion reached the hardened palagonite core, it decreased substantially. Today the sea-facing part of Vesturbunki is characterized by steep palagonite cliffs.

https://doi.org/10.33112/surtsey.16.9

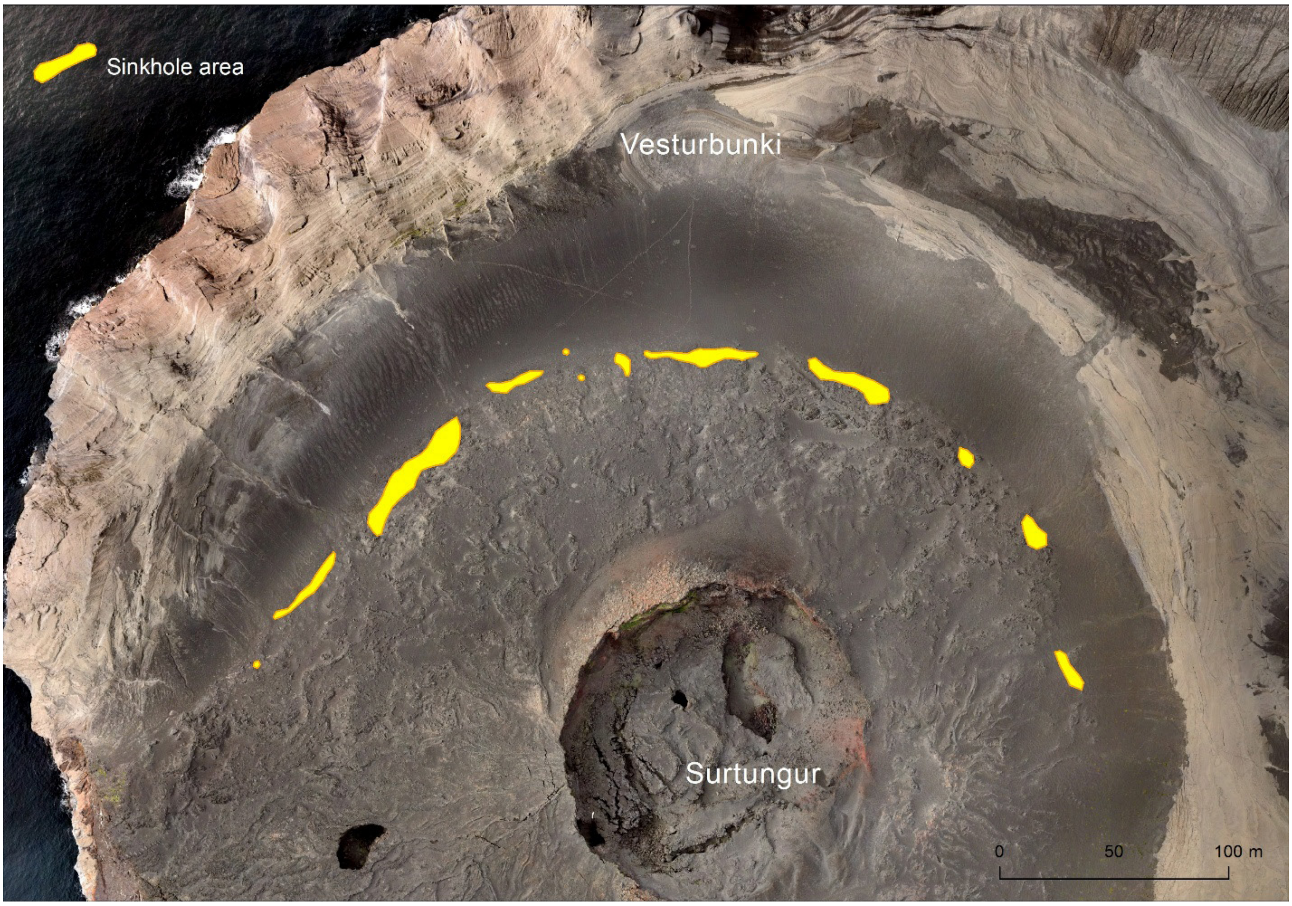

Figure 1. Distribution of sinkholes and tensional fissures along the lava margin within Vesturbunki. Orthoimage from 2023 (Natural Science Institute of Iceland, 2023. Unpublished data).

METHODS

In summer 2015 the authors noticed sinkholes and tensional fissures along the lava margin within Vesturbunki that could be traced almost continuously for about 500 m within the palagonite tuff cone (Fig. 1). Time did not allow detailed inspection on that expedition, but visible features were photographed and recorded with Garmin and Trimble Yuma GPS units. During geological field expeditions in summers 2017, 2019, and 2025, the features were examined further, and sinkholes and fissures were measured and photographed (Fig. 2).

The authors have also conducted regular surveys of surface temperatures in fissures on the palagonite tuff cones Austurbunki and Vesturbunki. The measurements are conducted with electronic thermometer that can be used either with an infrared sensor with a laser pointer or with an attached temperature-sensor thermocouple. For further discussion of the employment of these methods in Surtsey, see Perez et al. (2022).

Two further datasets were examined in search of potential explanations for localized sinkhole formation on the lava shield margin in Vesturbunki:

1. Results of regular geodetic surveys in Surtsey since 1967 to monitor island subsidence (Sturkell et al. 2009, 2025)
2. Seismic activity near Surtsey back to 2009, from the Icelandic Meteorological Office earthquake web viewer, Skjálfta-Lísa (Icelandic Meteorological Office 2025)

The seismic activity is considered in conjunction with temperature measurements from fissures on Surtsey's surface (see also Perez et al. 2022) to explore potential seismic influence on Surtsey's surface features.

Figure 2. The diversity of sinkholes and tensional fissures along the lava margin within Vesturbunki on Surtsey. Photos: Lovísa Ásbjörnsdóttir, Kristján Jónasson.

RESULTS AND DISCUSSION

Sinkholes

A total of 49 sinkholes and fissures were recorded in Vesturbunki in 2015; subsequent expeditions recorded fewer features (around 20 per campaign), and several new sinkholes were noted. Most of the prominent features are on the western and northern margin of the lava and generally remain visible between expeditions; a map of the sinkhole areas is shown in Fig. 1. In 2017 the opening width of fissures in the lava margin was measured, most being in the range of 10–12 cm wide. In addition to clear fissures in the lava, disrupted lava is visible within several sinkholes.

The inside slopes of Vesturbunki are steep and largely covered by aeolian deposits. Substantial aeolian sediment has also accumulated on the lava below the slopes. It is therefore likely that many sinkholes are obscured by sediment. During the 2025 expedition, the authors observed sinkholes that were hidden beneath aeolian deposits but had voids underneath, making walking across the area potentially hazardous. No sinkholes have been observed along the lava margin within the eastern cone, Austurbunki.

Temperature Measurements

Table 1 presents a summary of maximum surface temperature measurements made in Vesturbunki and Austurbunki on research expeditions by the Natural Science Institute of Iceland (before 2024, the Icelandic Institute of Natural History) and the Surtsey Research Society. The number of points and fissures measured near this maximum temperature in each of the two areas varies from survey to survey, but the maxima give a good indication of the overall state of the geothermal system. Maximum temperatures at Austurbunki have been more stable than those of Vesturbunki, fluctuating between 93,1°C and 94,4°C from 2013 to 2021 and declining slightly since then, to 91,3°C in 2025. Vesturbunki, on the other hand, shows larger temperature oscillations, ranging between 93°C and 100°C over the entire period from 2008 to 2021 and fluctuating from measurement to measurement by up to 4.5°C.

Table 1. Maximum temperature measurements from Vesturbunki and Austurbunki, 2008–2025. Dates refer to the start date of each expedition. Initials of participants in the monitoring: SPJ: Sveinn P. Jakobsson, LÁ: Lovísa Ásbjörnsdóttir, KJ: Kristján Jónasson, MHG: María Helga Guðmundsdóttir.

Date	Vesturbunki T_{max} (°C)	Austurbunki T_{max} (°C)	Measured by
11.4.2008	100	94	SPJ, LÁ
18.7.2011	98	96	LÁ, KJ
19.7.2013	93	94	LÁ, KJ
14.7.2015	99.6	93.9	LÁ, KJ
17.7.2017	95.7	94.4	LÁ, KJ
18.7.2019	99.3	93.1	LÁ, KJ
15.07.2021	94.8	94.3	LÁ, KJ
14.07.2023	98.5	92.1	KJ, MHG
15.07.2025	97.7	91.3	LÁ, MHG

Deformation

Sturkell et al. (2009, 2025) describe how geodetic measurements show continuing subsidence across the island whose rate has decreased with time. Surtsey subsided rapidly during the first 10–15 years after formation, since which time the subsidence rate has decayed. In the period 1992–2000 the average subsidence rate was approximately 10 mm/yr, and for 2000–2023 approximately 3.8 mm/yr. One GPS station, SURG, is located on Vesturbunki; it shows linear vertical displacement and total subsidence of 78 mm since the year 2002. The measured horizontal displacements indicate constant horizontal velocities, unlike the vertical time series.

It has been suggested that the deformation processes currently active on Surtsey include compaction of volcanogenic material, slumping of the island flanks, lithospheric sagging due to the load of erupted material, and possible compaction of seabed sediments (Sturkell *et al.* 2009). Differential movement between the lava shield and the surrounding tuff cone rim, resulting in the observed sinkholes, might be a consequence of this subsidence.

The fastest-subsiding areas in Surtsey are at the edge of the island due to marine erosion, but the slowest-subsiding GPS station (512) is within the eastern cone, Austurbunki (Sturkell *et al.* 2025). Sinkholes have not been observed within Austurbunki, a fact that corresponds well with the observation that Austurbunki is subsiding less than any other part of the island.

Seismicity and Geothermal Activity

The authors examined whether seismic activity near Surtsey could have influenced movements at the lava margin, as the sinkholes were first observed

Table 2. Earthquakes ≥ M 2.5 recorded near Surtsey, 2009–2024 (Icelandic Meteorological Office 2025).

Date	Latitude	Longitude	Depth (km)	Magnitude (M)
17.08.2009	63.33	-20.633	15	2.5
25.04.2015	63.309	-20.631	16	2.8
24.04.2018	63.342	-20.617	14	2.5
31.01.2019	63.319	-20.64	14	3.4
06.09.2020	63.343	-20.604	18	2.6
06.06.2023	63.321	-20.637	15	3.1

in July 2015, shortly after the M 2.8 earthquake of April 25th, 2015. The Icelandic Meteorological Office earthquake web viewer, Skjálfta-Lísa (Icelandic Meteorological Office), provides earthquake data back to 2009. Typically, about 5–10 earthquakes are recorded annually near Surtsey, most of them at depths of roughly 10–15 km. Magnitudes are generally in the range M 1–2, although several larger earthquakes (≥ M 2.5) have occurred (Table 2). The hypocentres appear about 1.2–2.3 km northwest of Surtsey. However, it has been pointed out that earthquake locations in the Vestmannaeyjar area should be treated with caution because there are few seismic stations in the region and the earthquakes are deep, which reduces location accuracy (Kristín Vogfjörð, pers. comm., 1 October 2025).

When maximum surface temperatures are plotted against the timing of these earthquakes (Fig. 3), it becomes apparent that the upward jumps in temperature in Vesturbunki (in 2015, 2019, and 2023) were all preceded by an earthquake in the six months preceding the measurement. No such correlation can be observed for the temperatures in Austurbunki, which, as previously mentioned, shows far less fluctuation in its maximum temperature. It is suggestive that both geodesy and thermal monitoring reveal Austurbunki to be more stable than Vesturbunki.

One possible interpretation of this correlation for Vesturbunki is that it relates to movement on fissures in the palagonite tuff, which could provide a more direct pathway for heat to reach the surface. These temperature changes are suggestive that larger earthquakes could have some effect on the geological features of Surtsey, and a seismic contribution to the formation of sinkholes cannot be ruled out. The temporal sparsity of temperature measurements does, however, demand a degree of caution when interpreting the data.

Conclusions

It is not well understood what caused these sinkholes along the lava margin within Vesturbunki, or what maintained them between field expeditions. A plausible explanation is that multiple interacting factors are involved, related to island subsidence and possibly seismicity. It is important to continue to monitor the sinkholes and fissures at the lava margin of Vesturbunki and it would be desirable to map these features in more detail and measure their extent and depth. The authors recommend that the Icelandic Meteorological Office, in cooperation with the Surtsey Research Society and research

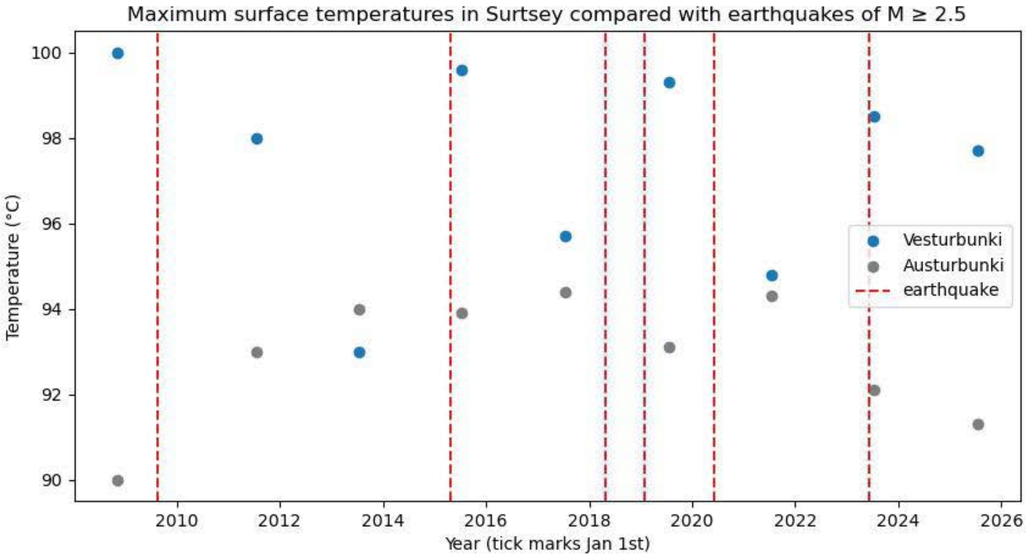

Figure 3. Time series of maximum temperatures measured in fissures in Austurbunki and Vesturbunki and earthquakes with ≥ M 2.5.

institutions associated with Surtsey, install a seismic station on Surtsey to obtain more accurate earthquake measurements, particularly hypocentre locations. A seismic station on Surtsey would also be crucial for monitoring the Vestmannaeyjar volcanic system.

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Continuing subsidence and deformation of the Surtsey volcano, Iceland

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ABSTRACT

The Surtsey Island was built from 130 m water depth during the period 1963–1967. Two tephra cones formed above sea level reaching a height of 170 m a.s.l. The final surface area of Surtsey reached 2.65 km^2 with a volume of 0.8 km^3 (dense rock equivalent). Repeated levelling and Global Position System (GPS) campaigns have been carried out every 5–10 years to monitor the internal deformation and subsidence of the island. The first levelling measurements were made in the summer of 1967. Surtsey follows an exponentially decaying subsidence curve, with total subsidence reaching 1 m since 1967. The 2000–2023 GPS surveys confirmed that Surtsey moves horizontally with the Eurasian plate. The average subsidence rate for the three GPS monitoring sites during 2000-2023 was 3.8 mm/yr, a total of 9 cm. About 2/3 of the total subsidence is contributed by compaction of sedimentary and volcaniclastic material, thermal contraction, and palagonization. Up to 1/3 of the total subsidence can be explained by loading of the island on the asthenosphere.

INTRODUCTION

The Surtsey fires of 1963–1967 off the south coast of Iceland are one of the most significant volcanic episodes in Iceland in the twentieth century. A total of about 0.8 km^3 DRE (dense rock equivalent) of basaltic material erupted during the 3 ½ years of the activity. The course of Surtsey eruptive events has been described extensively (e.g., Thorarinsson *et al*. 1964, Thórarinsson 1965, 1967, Þórarinsson 1964, 1965, 1966, 1969, Einarsson 1966, Jakobsson *et al*. 2000). The submarine eruption was first detected on November 14, 1963, and the last sign of activity was observed in early June 1967 (Þórarinsson 1969). In a series of eruptions three islands were formed, only Surtsey survived the oceanic erosion. The activity attracted considerable attention in the scientific community, in connection with the newly proposed hypothesis of seafloor spreading with Iceland located on the mid-Atlantic spreading zone. The activity was conventionally defined as one, slightly discontinuous eruption (e.g., Thorarinsson *et al*. 1964, Þórarinsson 1964, 1965, 1966, 1967, 1969, Einarsson 1966). Later revision of available seismic data, and experience from subsequent episodes of volcanic activity in Iceland, e.g. the Krafla volcano-tectonic episode of 1975-1984 (Björnsson *et al.* 1977, Einarsson 1991, Einarsson & Brandsdóttir 2021) and the ongoing series of events on the Reykjanes Peninsula (e.g., Parks *et al.* 2025, Geirsson *et al.* 2024) has led to the general view that

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the formation of Surtsey is better described as a series of at least six distinct eruptions fed from a single source (e.g., Sayyadi *et al.* 2021, 2022).

Prior to these events, the eruption site was a flat insular shelf at a depth of about 130 m (Jakobsson *et al*. 2000). The eruption site is the southernmost one within the Vestmannaeyjar volcanic system (VVS), the southernmost system within the Eastern Volcanic Zone of Iceland (EVZ) (Fig. 1). The volcanic zone extends south-westwards from the rift-transform junction of the EVZ with the South Iceland Seismic Zone (SISZ, Fig. 1). This part of the volcanic zone, sometimes called the South Iceland Volcanic Zone (SIVZ in Figure 1), has been interpreted as a propagating rift (e.g., Oskarsson *et al*. 1985, Meyer *et al*. 1985, Einarsson 1991), extending into the Eurasia Plate. Surtsey is located at the tip of this intraplate rift, where the rift propagation is driven by volcanic processes. Inter-plate tectonic motion is only observed across the EVZ and SISZ but currently not across the South Iceland Volcanic Zone, SIVZ. This is confirmed by recent GPS and InSAR measurements, showing that the nearby Heimaey, as well as the Eyjafjallajökull and Katla volcanoes also belong to the Eurasian plate (Geirsson *et al*. 2006, 2012, Árnadóttir *et al*. 2009, Cao *et al*. 2023).

The Vestmannaeyjar Volcanic System consists of several islands, the largest of which are Heimaey and Surtsey, and several seamounts (Sayyadi *et al.* 2024). Most of these are remnants of eruptions that began on the sea floor, and some of them reached the surface and formed lava flows. The competing processes of erosion by the sea and palagonitization of the tephra have subsequently shaped these structures. There are

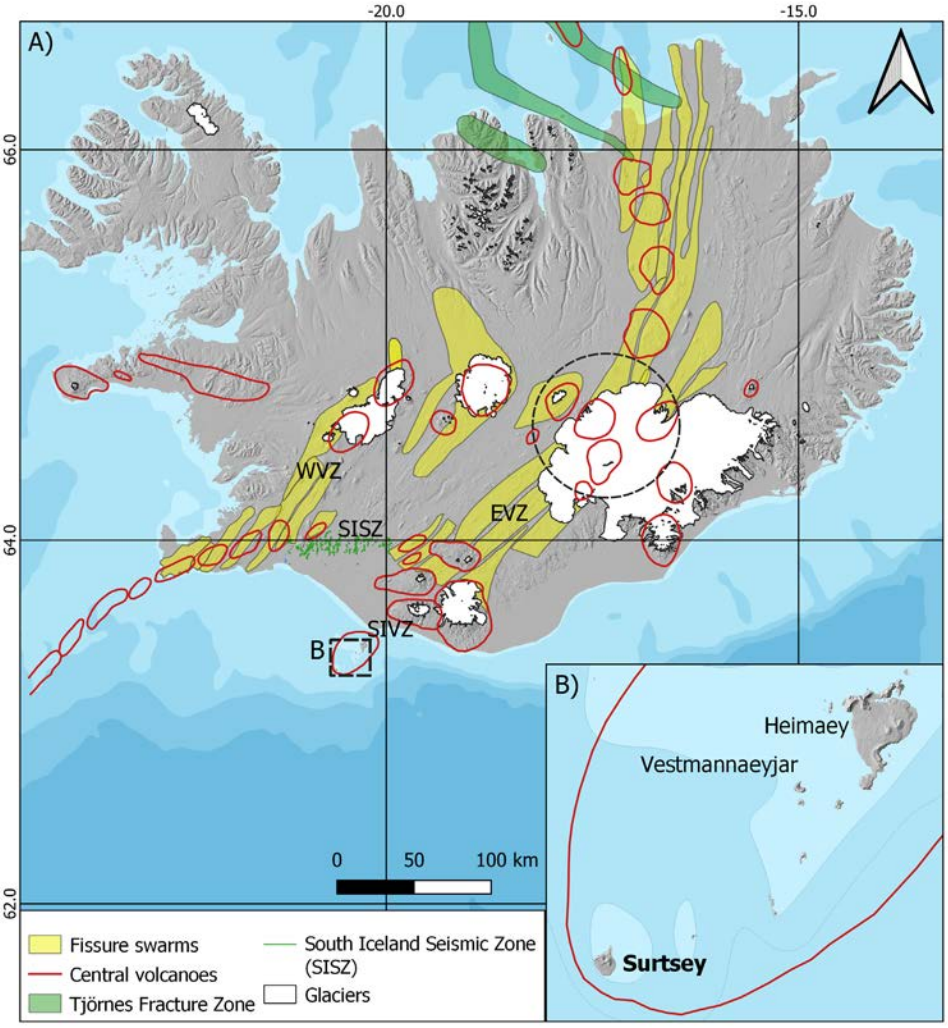

Figure 1. Map of Iceland showing the plate boundary and volcanic flank zones with Surtsey at the southernmost end. On the map, the Western Volcanic Zone (WVZ), the Eastern Volcanic Zone of Iceland (EVZ), the South Iceland Seismic Zone (SISZ) and the South Iceland Volcanic Zone (SIVZ) are marked. The centre of the Icelandic mantle plume is marked with a dashed circle with the Bardarbunga volcano in the centre.

no signs of normal faulting or graben structures in the Vestmannaeyjar archipelago, consistent with its intraplate location. Long term GPS measurements show that Vestmannaeyjar (GPS site VMEY) moves completely with the Eurasian plate (Geirsson *et al.* 2006). Eruptive fissures are mostly short and oriented NE-SW.

The 1963–1967 eruptions and the formation of Surtsey Island have been the subject of a multitude of scientific experiments, both in biology and geology. A significant mass of volcanic material was transferred from depth to the surface during the Surtsey eruptions. This mass is subject to internal evolution and furthermore has a mechanical effect on the underlying crust. Processes to be considered include elastic response of the lithosphere, isostatic adjustment, gradual compaction of loose materials, gravitational spreading of the edifice, lithification because of palagonitization, and erosion.

Ground deformation observations in Surtsey were initiated in 1967 when Tryggvason (1968) installed a levelling profile across the island. The profile has been re-measured several times and in 1992 it was connected to the GPS network in south Iceland (Einarsson *et al.* 1994). Sturkell *et al.* (2009) assembled all the levelling and GPS data on Surtsey obtained until 2002. In this paper, we summarize the results of previous measurements, as well as new measurements from 2013 and 2023, and evaluate the results with respect to deformation processes and recently acquired structural data from boreholes drilled in 2017 (Moore & Jackson 2020).

METHODS

Levelling

In 1967 a levelling line was installed across the new island consisting of 42 benchmarks cemented in bedrock (Tryggvason 1968) spaced approximately 50 m apart (Fig. 2). The erosive forces of the sea have shortened the original levelling line by 16 benchmarks. Several benchmarks have also been lost in the sand drift over the years. However, some have been re-exposed, and their coordinates determined by GPS measurements (prior to GPS, a theodolite and a geodimeter were used). All coordinates of the benchmarks prior to 2013 are tabulated in Sturkell *et al.* (2009) together with the raw data from the eleven levelling campaigns. The levelling from 2002 onwards is performed with a Zeiss Dini-12 levelling

Table 1. Data for the levelling performed across Surtsey in 1991, 2002, 2013, and 2023. Heights are given in meters relative to benchmark 606. For levelling data 1967–2002 see Sturkell *et al.* (2009).

Site	1991	2002	2013	2023
WP	-20.017			
605			-2.290	
606	0.000	0.000	0.000	0.0000
607	2.561	2.562	2.561	25.591
608			2.095	20.935
609	3.216	3.246	3.261	32.676
610				
611		7.890	7.924	79.430
612	10.096	10.156	10.191	102.091
613				
614				
615				
616		21.654	21.692	217.129
617		23.129	23.166	231.886
618			26.253	
619				
620				
621	30.374	30.414	30.435	304.454
622	31.399	31.450	31.477	314.916
623	31.583	31.638	31.668	316.783
624	32.629	32.689	32.720	327.306
625	35.064	35.122	35.143	351.264
626	34.035	34.089	34.094	340.224
627	25.876	25.920	25.883	
628	17.953	17.807		
629	11.282			
630	9.926			
510	-5.399	-5.386	-5.383	-53.924
511	-4.364	-4.364	-4.365	-43.641
512	41.860	41.929	41.966	419.846
513	46.471	46.539	46.578	465.966
514	50.184	50.248	50.283	502.935
515	50.831	50.892	50.925	509.402
516	50.653	50.714		
517	45.407	45.461	45.486	454.950
518	47.891	47.946	47.975	480.043
519	41.668	41.721	47.975	417.699
520	33.660	33.706	33.729	337.414
P-1	-15.130			
S-1	6.938			
S-2	14.613	14.678	14.717	147.380
S-3	20.974	21.049	21.090	211.124
S-4	37.117	37.184	37.221	372.386
S-6				
S-7	-15.989			
SDH-1	38.530			
SDH-2				
NE07*		14.251		
NE09		29.721	29.754	297.730
NE10		30.274	30.303	303.191
TW	29.229			

* Benchmark NE07 is in the centre of the helicopter platform (GPS SURP).

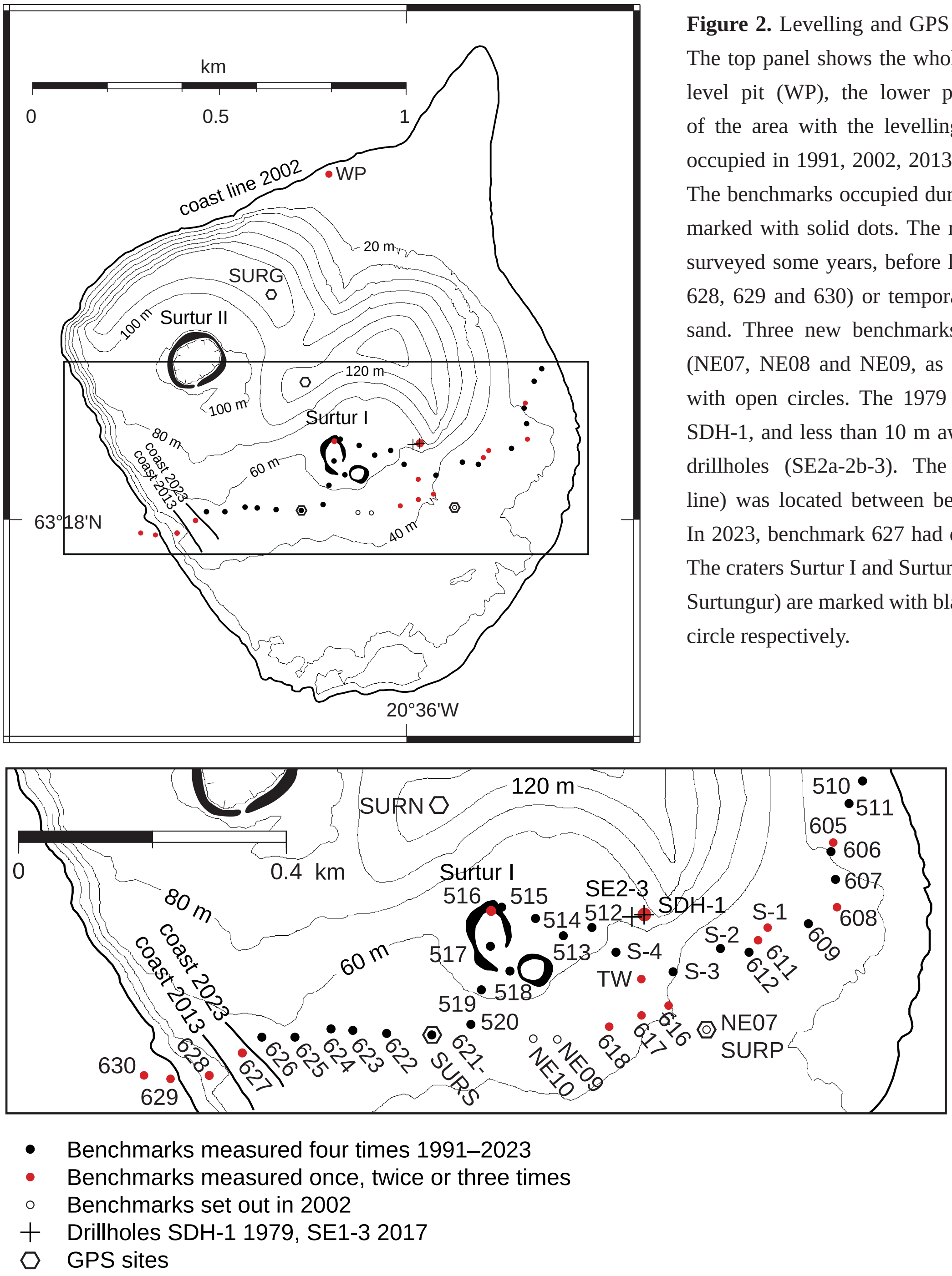

Figure 2. Levelling and GPS benchmarks on Surtsey. The top panel shows the whole island with the water-level pit (WP), the lower panel is an enlargement of the area with the levelling line. The benchmarks occupied in 1991, 2002, 2013 and 2023 (see Table 1). The benchmarks occupied during all these surveys are marked with solid dots. The red dots are benchmarks surveyed some years, before lost to the sea (WP, 627, 628, 629 and 630) or temporarily lost due to drifting sand. Three new benchmarks were set out in 2002 (NE07, NE08 and NE09, as shown on map) marked with open circles. The 1979 drill hole is located by SDH-1, and less than 10 m away from the three 2017 drillholes (SE2a-2b-3). The 2013 coastline (black line) was located between benchmarks 627 and 628. In 2023, benchmark 627 had disappeared into the sea. The craters Surtur I and Surtur II (usually referred to as Surtungur) are marked with black half circles and a full circle respectively.

instrument and two Zeiss levelling rods with digital barcodes which are read by the instrument (Fig. 3). The height difference between consecutive benchmarks is measured, and for redundancy the readings are repeated by swapping rods and re-setting the levelling instrument, until a difference of less than 0.20 mm is obtained between each reading, from which an average is calculated. Height of the benchmarks relative to any benchmark in the line can then be computed. The levelling results from 1991, 2002, 2013 and 2023 are given in Table 1 relative to benchmark 606, located on the east part of Surtsey (Fig. 2b).

To determine the absolute subsidence or uplift of Surtsey is a challenge because of the relative nature of levelling measurements and distance to the next island. Before the era of GPS, the height reference of the Surtsey levelling line was tied to the surface of a pond located by the northern shore of Surtsey (point WP in Fig. 2) that was initially assumed to represent mean sea level (Tryggvason 1968). However, as the water level in the pond was out of phase with the

Figure 3. Levelling on Surtsey in 2023, the levelling instrument is located between the rods. The rod to the left is on a temporary benchmark to bridge between permanent benchmarks. The benchmark to the right is number 622. Photograph: Kristján Jónasson.

predicted ocean tide at Heimaey, it was considered to be somewhat higher than the sea level (Tryggvason 1968). The pond had disappeared in 1969, but as the groundwater table was close to the surface, a pit was dug to observe the water table (Tryggvason 1972). The water level in a dug pit corrected for the ocean tide was used as the datum for the levelling campaigns made in 1967 to 1991 (Moore *et al*. 1992, and references there in). Moore (1982) reported that in 1979 the best available estimate places the average water level in the dug pit at 32 ± 15 cm above the mean sea level. One of the benchmarks (SURS/621) has been occupied since 1992 as a GPS point (Fig. 4). The elevation of this benchmark relative to the water level in the dug pit or the water pit (WP), which was located 100 m east of the old northern cabin (see Section 4.2 for details), shows the exponentially decaying rate of the long-term absolute vertical movements.

The levelling in 1979 tied the drill hole top (SDH-1) and its water level (Moore *et al*. 1992) with the water-level pit (WP, Fig. 2). Benchmarks S-1 to S-7 were installed in 1979 and benchmarks 510 to 520 in 1982. Benchmarks 510 and 511 were installed to fill gaps in the original levelling line, and benchmarks 512 to 520 were laid out in a loop through the centre of the Surtur I crater. During the levelling in 2002 two new benchmarks (NE09 and NE10, Fig. 2) were installed along the line because benchmarks 618, 619 and 620 were not found that year.

GPS measurements

GPS campaigns were performed on Surtsey in 1992, 2000, 2002, 2013, 2017 and 2023. In 1992 SURS (same as BM 621, Fig. 2) was measured. In 2000 SURS and a new GPS-point (SURN) were measured. The description of the processing of the 1992, 2000 and 2002 data is given by Sturkell *et al*. (2009). In 2002 SURS and SURN were re-occupied and two new points added: One point in palagonite on the crest of the western mountain (SURG, inscription NE08); and the second point in the centre of the helicopter platform (SURP, inscription NE07, Fig. 2). The

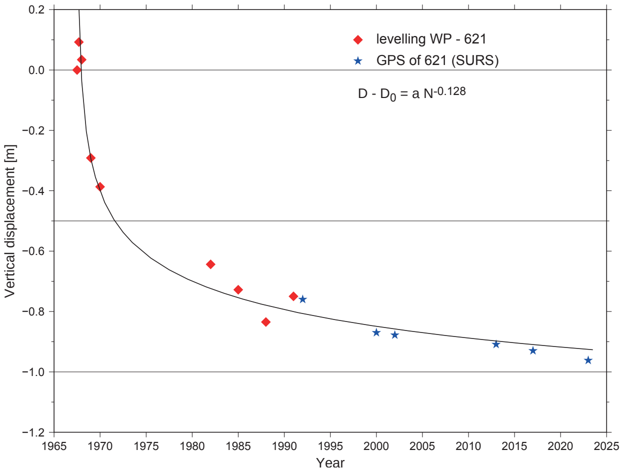

Figure 4. The vertical displacement between the water table in the dug pit (WP) and benchmark 621 from June 1967 to 1991, extended with GPS data for the site SURS (BM 621). The levelling and GPS data are presented in Tables 2 and 3.

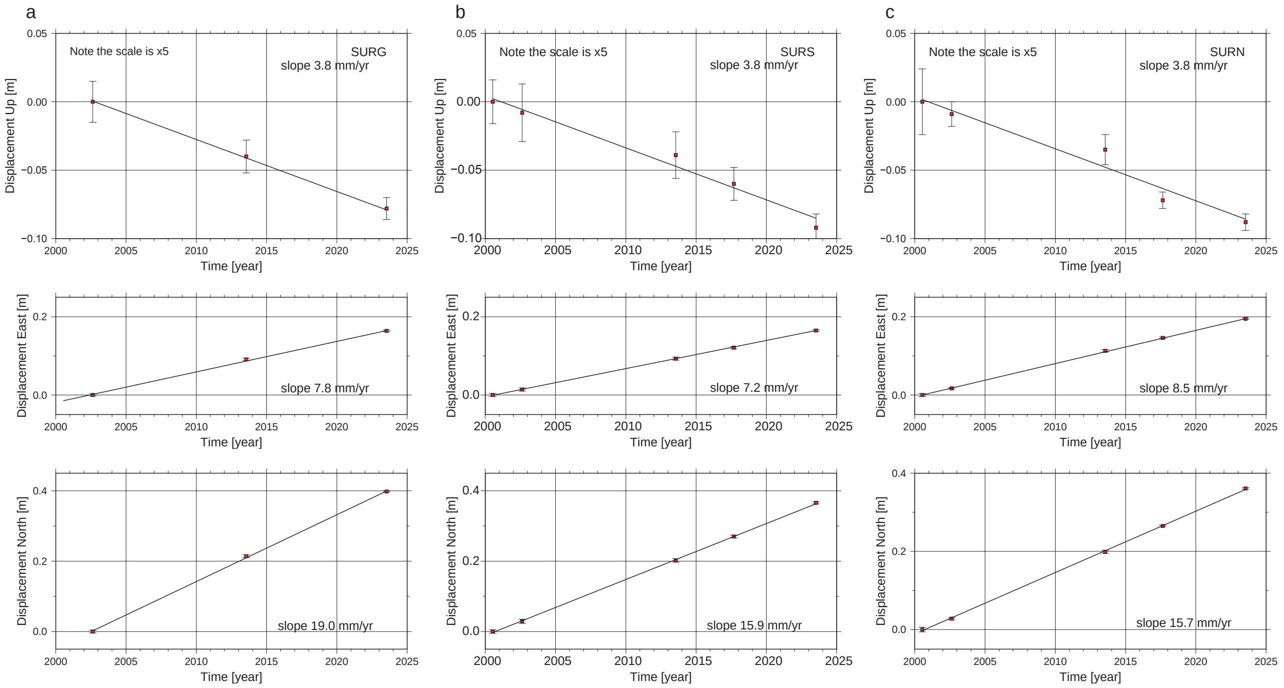

Figure 5. a: Time series for GPS station SURG in the IGS14 reference frame. The vertical displacement appears linear, but with only three points, with a total subsidence of 78 mm since year 2002. b: Time series for GPS station SURS in the IGS14 reference frame (BM 621). The vertical displacement gives a total subsidence of 92 mm since year 2000. c: Time series for GPS station SURN in the IGS14 reference frame. The vertical displacement gives a total subsidence of 88 mm since year 2000.

purpose of a GPS-point in the helicopter platform is mainly for aerial photography as the concrete plate makes an excellent aerial marker. In 2013 and 2023 SURS, SURN and SURG were measured. SURS was also measured in 2017 during drilling operations on Surtsey.

Each GPS point was measured using an antenna on a tripod, collecting data sampled every 15 seconds for approximately 36 to 72 hours. The collected data (2000–2023) were processed using the GAMIT/GLOBK software package (version 10.7, Herring *et al*. 2010). Site positions were determined for each UTC Day in the IGS14 reference frame by referencing over 100 global stations (see Hreinsdóttir *et al*. 2009 for details). The data were corrected for ocean tidal loading effects using the FES2004 model (Lyard *et al*. 2006). For each campaign the average station coordinates and displacements relative to the earliest point in the time series were computed (Table 2). The plate motion model of Altamimi *et al*. (2016) was used to transform the time series from a no-net-rotation reference to stable Eurasia (Table 2). We then calculated the displacement rate from the best fitting line through the data (Figs. 5a–c). The horizontal displacement vectors relative to stable Eurasia (Fig. 6), show similar rates of movement with slight deviation from Eurasia.

Time series for GPS sites SURG (Fig. 5a), SURS (Fig. 5b) and SURN (Fig. 5c), are presented within the IGS14 reference frame. The horizontal displacements are a straight line, indicating constant horizontal velocities. The vertical time series, however, do not fit a straight line as well. Whether the deviations are due to measurement noise or real changes in the subsidence rate is uncertain. The average vertical rates for the three stations are quite similar, with a subsidence of approximately 3.8 mm/yr.

RESULTS

Vertical deformation observations

Overall, Surtsey has been subsiding at a declining rate (Fig. 3). We model the decay as a power law, where D is the vertical displacement, D_0 is chosen such that D-D_0 approaches zero with time, N is the number of years since start of measurements, and p the power law exponent. We find that $p = -0.128$ and $a = 2\ m$ fits the data reasonably well (R^2=0.978). To apply a

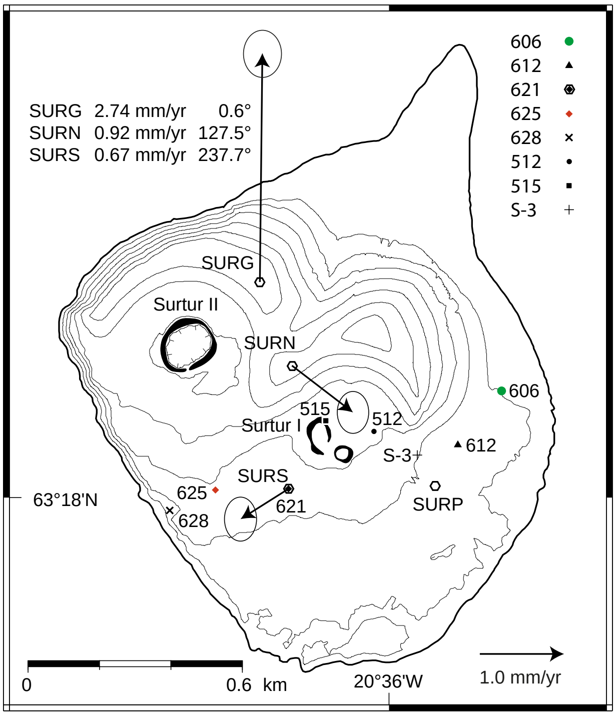

Figure 6. Map of GPS and selected levelling points. The horizontal velocities from GPS measurements 2000–2023 and 2002–2023, relative to Eurasia, are shown as black arrows. Levelling benchmarks are coded by colour and symbol for ease of recognition in subsequent time series figures.

power law equation on negative values is difficult, therefore the data differences are arbitrarily shifted by a constant of 2 m to make all values positive. Subsequently, obtained values are shifted down into the negative range for plotting purposes.

Significant spatial variations are observed in vertical deformation along the levelling line. In all surveys except 1967 and 1991 all benchmarks subsided relative to the water level in WP. The subsidence from August 1967 to August 1991 relative to sea level (WP) was 80–130 cm (Moore *et al*. 1992). During 1967–1968 the subsidence rate was at its maximum at 15–20 cm/year (Tryggvason 1972) and had slowed down to 1–2 cm/year between 1988 and 1991 (Moore *et al*. 1992).

Having been measured in every survey, benchmark (BM) 606 was used as a reference point until 1991 (Moore *et al*. 1992, Sturkell *et al*. 2009).

In recent measurements (1991 onwards) BM 621 was used as the reference for the levelling line and has been surveyed with GPS since 1992. BM 621 has been measured in all surveys but one, as it was not measured 1979 (Table 1a in Sturkell *et al*. 2009). Vertical changes from 1967 to 2023 of selected

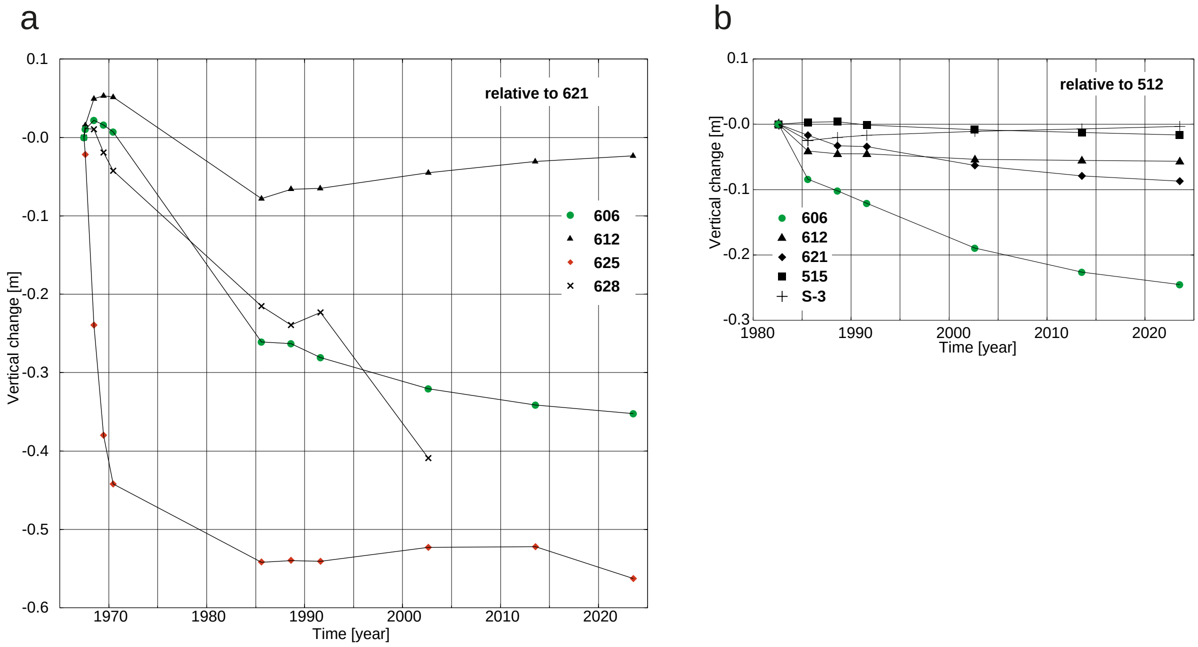

Figure 7. Vertical displacements of selected benchmarks (Fig. 6). The estimated uncertainty of levelling between benchmarks is ±0.1 mm. However, on Surtsey the weather conditions are not always perfect so an estimated uncertainty might be ±0.2 mm. **a:** Displacements relative to BM 621 (the GPS point SURS). Maximum vertical displacements were observed at BM 625 during the first years, slowing down until 1985 and thereafter following BM 621 closely. Currently BM 606 shows the most rapid subsidence if BM 628 is excluded. **b:** Vertical displacements of selected benchmarks (Fig. 6) since 1982 relative to BM 512. BM 515 and BM S-3 have the smallest vertical displacements. They are located on a thin lava flow that overlies the Surtur 1 tuff cone. Benchmark 606 near the eastern coast, used as a reference by Moore *et al*. (1992), has the highest subsidence rate relative to BM 512 in this group of benchmarks. Note, currently BM 606 has the highest rate relative to BM 621.

Table 2. GPS displacements for sites SURS, SURN and SURG. The displacements are in the IGS14 reference frame and relative to the earliest data point.

SURS

Year	N [m] IGS14	N [m] Eurasia	Uncertainty	E [m] IGS14	E [m] Eurasia	Uncertainty	Up [m]	Uncertainty
2000.531	0	0	0.0047	0	0	0.0032	0	0.0153
2000.534	0.0015	0.0015	0.0039	0.0002	0.0002	0.003	-0.0036	0.0125
2000.537	0	-0.0001	0.0067	-0.0034	-0.0034	0.0047	-0.0050	0.0206
2002.623	0.0305	-0.0035	0.0087	0.0127	-0.0036	0.0055	-0.0026	0.0347
2002.626	0.0305	-0.0036	0.0027	0.0138	-0.0025	0.0020	-0.0122	0.0087
2002.629	0.0283	-0.0058	0.0057	0.0122	-0.0041	0.0043	-0.0165	0.0192
2013.547	0.1960	-0.0156	0.0072	0.0935	-0.0076	0.0046	-0.0440	0.0199
2013.549	0.2090	-0.0027	0.0049	0.0896	-0.0115	0.0038	-0.0352	0.0149
2013.552	0.2021	-0.0096	0.0043	0.0924	-0.0088	0.0032	-0.0419	0.0128
2013.555	0.2033	-0.0085	0.0056	0.0913	-0.0099	0.0046	-0.0448	0.0194
2017.689	0.2710	-0.0080	0.0035	0.1207	-0.0126	0.0023	-0.0680	0.0114
2017.692	0.2697	-0.0093	0.0043	0.1194	-0.0139	0.0034	-0.0580	0.0130
2023.533	0.3652	-0.0088	0.0038	0.1628	-0.0159	0.0028	-0.0921	0.0123
2023.536	0.3669	-0.0072	0.0028	0.1649	-0.0138	0.0023	-0.0933	0.0084
2023.538	0.3676	-0.0065	0.0028	0.165	-0.0138	0.0023	-0.0980	0.0087

SURN

Year	N [m] IGS14	N [m] Eurasia	Uncertainty	E [m] IGS14	E [m] Eurasia	Uncertainty	Up [m]	Uncertainty
2000.537	0	0	0.0093	0	0	0.0058	0	0.0371
2000.54	0.0009	0.0009	0.0032	0.0034	0.0034	0.0023	-0.0075	0.01
2002.623	0.0295	-0.0044	0.0024	0.0186	0.0024	0.0017	-0.0102	0.0076
2002.626	0.0292	-0.0048	0.0020	0.0191	0.0029	0.0016	-0.0117	0.0065
2002.629	0.0279	-0.0061	0.0033	0.0193	0.0030	0.0026	-0.0158	0.0115
2013.547	0.1952	-0.0163	0.0039	0.1169	0.0158	0.0026	-0.0537	0.0109
2013.549	0.2064	-0.0052	0.0041	0.1124	0.0113	0.0033	-0.0393	0.0123
2013.552	0.2004	-0.0112	0.0032	0.1153	0.0142	0.0025	-0.0524	0.0094
2013.555	0.1977	-0.0140	0.0037	0.1128	0.0117	0.0039	-0.0454	0.0128
2017.640	0.2656	-0.0125	0.0022	0.1472	0.0143	0.0015	-0.0783	0.0070
2017.642	0.2658	-0.0123	0.0021	0.1467	0.0138	0.0016	-0.0747	0.0063
2017.645	0.2663	-0.0119	0.0018	0.1483	0.0154	0.0015	-0.0731	0.0055
2023.536	0.3609	-0.0131	0.0022	0.1965	0.0178	0.0017	-0.0896	0.0068
2023.538	0.3615	-0.0125	0.0017	0.196	0.0173	0.0015	-0.0949	0.0053

SURG

Year	N [m] IGS14	N [m] Eurasia	Uncertainty	E [m] IGS14	E [m] Eurasia	Uncertainty	Up [m]	Uncertainty
2002.629	0	0	0.0038	0	0	0.0027	0	0.0130
2002.632	-0.0012	-0.0012	0.0046	0.0007	0.0007	0.0035	-0.0138	0.0172
2013.547	0.2076	0.0301	0.0044	0.0938	0.0090	0.0029	-0.0504	0.0124
2013.549	0.2191	0.0415	0.0044	0.0889	0.0041	0.0035	-0.0372	0.0134
2013.552	0.2133	0.0357	0.0034	0.0914	0.0065	0.0026	-0.0504	0.0102
2013.555	0.2127	0.0350	0.0038	0.0894	0.0045	0.0039	-0.0492	0.0132
2023.536	0.3967	0.0568	0.0027	0.1642	0.0018	0.0020	-0.0814	0.0088
2023.538	0.3971	0.0571	0.0021	0.1638	0.0013	0.0018	-0.0893	0.0064

benchmarks (Fig. 6) relative to BM 621 are presented in Figure 7. BM 606 appeared to have a constant rate during the first few years but then plunges into subsidence. BM 612 rose in the first years relative to BM 621, subsided until 1985 and has been rising since. BM 628 subsided 0.4 m until it was lost to the sea, sometime between 2002 and 2013. The cliff hosting BM 627 was lost to sea sometime between 2013 and 2023. The 2003 survey shows accelerated subsidence at BM628, most readily interpreted as the benchmark cliff edge had already started giving in to the sea.

Based on the levelling data we can infer which parts of the island are most stable. From the 1985 survey onwards the relative displacement between BM 606, near the eastern shore, and BM 625 (Fig. 7a), near the southwestern shore, is relative stable. In the period 1985 to 2013 the BM621 had very limited vertical displacement. In the most recent survey BM625 has started to subside. This is likely because of its growing proximity to the southwestern coastline. The steep cliff to the southwest of the island is currently affected the most by intense erosion (Óskarsson *et al.* 2020). These authors also report a system of cracks running parallel to the cliff, about 1–5 meters into the lava field with cracks that can be up to 170 meters long.

Benchmarks 512 to 520 showed about 8 cm of uplift relative to BM 606 in the period 1982–1985 decreasing to 2 cm in the period 1985–1988 (Moore *et al*. 1992). This indicates that the most “stable” area (i.e., with the least subsidence) is around BM 512, in vicinity of the Surtur 1 crater near the centre of the island (Fig. 6). After 1985, benchmarks 612, 621, S-3, and 515 kept rather stable relative to BM 512, while BM 606, near the NE coast started a steady subsidence **(**Fig 7b). Overall, the benchmarks closer to the sea subside faster compared to the benchmarks in the inner parts, especially around Surtur I.

With GPS measurements from 1991, an absolute elevation-reference could be established for the levelling line instead of relying on water level measurements in the dug pit. The GPS measurements also add information of horizontal deformation. The GPS site SURS (BM 621) subsided 8 ±1 cm between 1992 and 2000 relative to sites REYK and ARNA in Reykjavík (Sturkell *et al*. 2009), giving an average rate of 10 mm/yr. The absolute subsidence of SURS between 2000 and 2023 is 9.2 cm (Table 2), corresponding to a subsidence rate of 3.8 mm/yr (Table 3).

Table 3. Velocities of GPS stations in the IGS14 and Eurasian reference frames. Units are in mm/yr unless otherwise noted.

Station Reference	N	E	U	Horizontal rate	Azimuth [°]
SURS IGS14	19.0	7.8	-3.8	20.5	24.9
SURG IGS14	15.9	7.2	-3.8	17.4	27.9
SURN IGS14	15.7	8.5	-3.8	17.8	34.5
SURS Eurasia	2.7	0.0	-3.8	2.7	0.6
SURG Eurasia	-0.4	-0.6	-3.8	0.7	237.7
SURN Eurasia	-0.6	0.7	-3.8	0.9	127.5

The 1993 and 2004 nationwide ISNET GPS campaigns (Árnadóttir *et al*. 2009) are useful to estimate the regional deformation field that may affect our estimate of the subsidence of Surtsey. Using the ITRF2005 (Altamimi *et al*. 2007) reference frame, Árnadóttir *et al*. (2009) obtained a subsidence of 0.4 ± 0.8 mm/yr and uplift of 3.2 ± 1.5 mm/yr for sites 0082 (Valhúsahæð, Reykjavík) and 0353 (Heimaey), respectively, resulting in a net uplift rate of 3.6 mm/yr of Heimaey relative to Reykjavík. This result is similar to the rate of 3.5 ± 1.5 mm/yr of site VMEY relative to REYK estimated by Geirsson *et al*. (2006), using continuous GPS data from 2000 to 2004. It has been established that a large part of Iceland is rising because of glacial isostatic adjustment (GIA, Árnadóttir *et al*. 2009, Cao *et al*. 2023). The glacial rebound model of Árnadóttir *et al*. (2009) predicts a differential uplift of VMEY (and site 0353) relative to REYK (and 0082) of 1.5 mm/yr. This difference will be slightly smaller for Surtsey since it is at a greater distance from the ice caps than Heimaey, perhaps 1 mm/yr. Considering the average subsidence rate of BM 621 during 1992 to 2002 (~1 cm/yr), we thus regard the glacio-isostatic effects as of little importance for this time period. However, GIA in Iceland has accelerated due to warming climate (Geirsson *et al*. 2012, Cao *et al*. 2023), so the recent (~20 years) deceleration in subsidence at Surtsey may be partly explained by faster regional uplift due to GIA. In fact, assuming ~2–3 mm/yr increase in GIA since after 2004 (as suggested by Geirsson *et al*., 2012), nearly half of the subsidence decrease from ~1 mm/yr in 1992–2002 to 3.8 mm/yr in 2002–2023 may be explained by faster GIA. More detailed GIA models are being developed that will be of importance to quantify this effect better (Bellagamba *et al*. 2024).

Table 4. Combination of GPS data at SURS (BM 621) with the levelling results between the WP and BM 621.
A: The height changes relative to the water pipe (WP) site and the BM 621 between June 1967 to 1991.
B: The cumulative subsidence from the GPS measurements 2000–2023 (Table 2) relative to year 2000.
C: The combined vertical displacements for BM 621 (see also Figure 2).

A.

Year	WP to 621 [m]	displacement [m]
1967 June	511409	0
1967 Aug	512333	0.0924
1968	51175	0.0341
1969	508494	-0.2915
1970	507541	-0.3868
1982	50497	-0.6439
1985	50413	-0.7279
1988	50306	-0.8349
1991	50391	-0.7499

B.

Year	displacement [m]
2000	0.0000
2002	-0.0076
2013	-0.0386
2017	-0.0601
2023	-0.0916

C.

Year	displacement [m]
1967.5	0
1967.7	0.0924
1968	0.0341
1969	-0.2915
1970	-0.3868
1982	-0.6439
1985	-0.7279
1988	-0.8349
1991	-0.7499
1992	-0.7599
2000	-0.8699
2002	-0.8779
2013	-0.9089
2017	-0.9299
2023	-0.9619

Using the levelling data from 1967 to 1991 and the GPS data of 1992–2023 to constrain elevation changes of BM 621 relative to WP (Fig. 6, Table 4), we obtained the absolute vertical displacement of BM 621. The GPS subsidence rates observed 1992–2002 were applied to the one-year gap 1991–1992. The absolute vertical data is dominated by subsidence. The only interval that shows uplift is between the first two measurements in 1967. The data (Fig. 4) shows higher subsidence rates during the first ten years and lower subsidence rates from 1982 onwards.

Models of Vertical Deformation

At least seven geological processes possibly contribute to the vertical displacement of Surtsey (e.g., Moore *et al*. 1992):

a) lithostatic load from the weight of the erupted material, b) compaction of the pre-existing seabed sediments (vertical strain), c) palagonitization of the tephra, d) compaction of the volcanogenic material, e) thermal contraction of the lava field; and f) magma withdrawal or other movements in the magmatic plumbing system. We do not consider thermal contraction of the tuff under the lava flows as they were cooled by seawater directly as they formed. We discuss each of the processes mentioned above in the following sections.

Lithosphere flexure

To calculate the load effect caused by the added weight of Surtsey on the lithosphere we assume a surface load that will cause time-dependent flexure of the lithosphere. We implement a model detailed in Islam (2016). The shape of Surtsey is nearly circular and simplified to a cone (Fig. 8a). The width of Surtsey is estimated to be 3200 m along a profile which crosses the centre of Surtsey aligned N125°E. The two small temporal islands Jólnir and Syrtlingur were not included in the model. The total elevation of the Surtsey edifice is 260 m with half under water (Fig. 8a). The load is calculated using radial symmetry in three segments; AB = 400 m, BC = 400 m and CD = 800 m (Fig. 8b) and $P = \rho gh$ where ρ represents the density of Surtsey, assumed to be 1800 kg/m^3, g is gravitational acceleration and h is height. For the submarine part of Surtsey, the buoyancy effect is managed by considering density difference (Δρ) between seawater and Surtsey. The load on segment AB is calculated as

$P_{AB} = \Delta\rho g\times 130\text{m} + \rho g\times 65\text{m} + \rho g(0.5\times 65\text{m}) =$

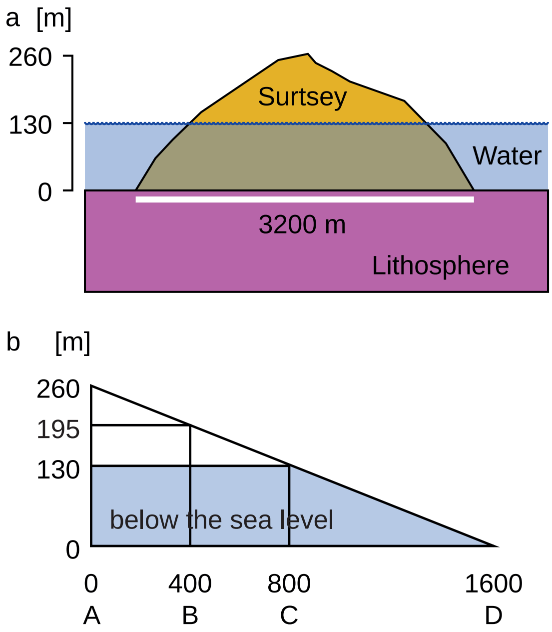

Figure 8. Modelling Surtsey. (a) Surtsey is simplified as a cone with its lower half below sea level. (b) Axisymmetric shape of one-half of Surtsey for calculation of its circular load. Here A designates the centre of Surtsey. The load is distributed along the radius profile in three segments. e.g., AB, BC, and CD.

$800 kg/m^3 \times 9.82 m/s^2 \times 130 m + 1800 kg/m^3 \times 9.82 m/s^2 \times 65 m + 1800 kg/m^3 \times 9.82 m/s^2 \times (0.5 \times 65 m) = 2.7$ MPa. The load for segments BC and CD is similarly calculated as 1.6 and 0.5 MPa, respectively.

The loading calculations of Surtsey on the lithosphere as well as on the asthenosphere is conducted by two-dimensional circle-load axisymmetric mechanical models using commercial Finite Element Modelling package Abaqus/CAE 6.11. The width and depth of the model space is 100 × 410 km, respectively (Fig. 9). The depth of the model is constrained by the depth of lithosphere and asthenosphere. The width is kept ~60 times larger than the length of applied load to avoid boundary effects.

Our model has two uniform layers: a viscoelastic asthenosphere beneath an elastic lithosphere. Different lithospheric thicknesses (30 to 65 km) were tested using three different Newtonian viscosities of the underlying asthenosphere (Figs. 9 and 10). The models ran for a period set to 50 years by applying the instantaneous load calculated in the previous section. The Winkler Foundation is given by $\Delta\rho g$ where ρ is density and g is the gravitational acceleration as Archimedes' principle of boundary condition to maintain isostasy (see Wu (1992) for

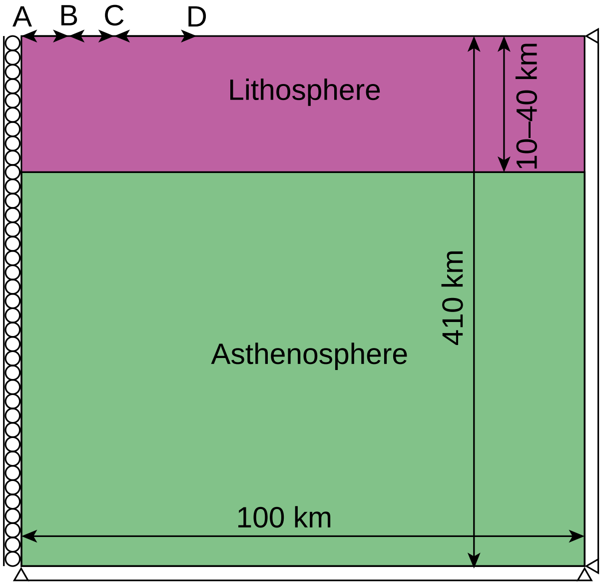

Figure 9. Geometry and boundary conditions of two-dimensional circular-load models. "A" designates the centre of Surtsey. We apply roller conditions on the left axis, allowing this vertical section to move only vertically, and being fixed horizontally. The bottom and vertical right boundaries are fixed. The length of AD is the radius of Surtsey. The length of AB, BC and CD is as in Figure 7b, however, shown here in exaggerated scale compared to the model dimensions. Different lithospheric thicknesses and viscosities were tested.

Table 5. Mechanical material properties of the loading model. The density of Surtsey is based on Moore *et al.* (1992), and properties of the lithosphere and asthenosphere on Turcotte & Schubert (2002:436). The viscosity of the asthenosphere beneath Surtsey is assumed as similar as beneath Iceland from glacioisostatic studies (Auriac *et al.* 2013; Barnhoorn *et al.* 2011; Pagli *et al.* 2007).

Parameters		**Value**
Surtsey	Density, ρ_S (kg m^{-3})	1800
Seawater	Density, ρ_w (kg m^{-3})	1000
Lithosphere	Average density, ρ_L (kg m^{-3})	2950
	Young's modulus, E_L (Pa)	8×10^{10}
	Poisson's ratio, v_L	0.25
Asthenosphere	Average density, ρ_A (kg m^{-3})	3350
	Young's modulus, E_A (Pa)	1.3×10^{11}
	Poisson's ratio, v_A	0.28
	Viscosity, η (Pa S)	3×10^{18}, 5×10^{18}, 1×10^{19}
Gravitational acceleration, g (m S^{-2})		9.82

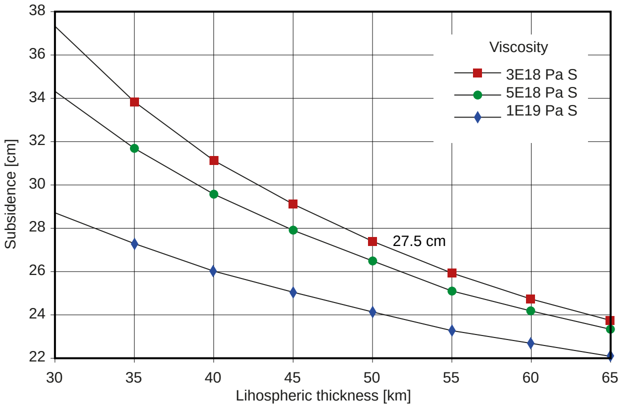

Figure 10. Three circular-load models of Surtsey, spanning 50 years. Total subsidence at the centre of the model, calculated for different asthenosphere viscosities.

more details). Winkler Foundation was applied at the surface (where Δρ is density difference between water and lithosphere) and at the interface between the lithosphere and asthenosphere (where Δρ is density difference between lithosphere and asthenosphere). Other boundary conditions are described in Figure 9. The mechanical properties used in our modelling are presented in Table 5.

The strain models contain three-node linear triangle elements. Deformation is calculated as sum of elastic and creep responses (see Wu (1992) for more details). Abaqus (2011, pages 21.2.1-1 and 22.2.4-4) derives elastic response using Hooke's principle, where the total stress $\sigma = C^{el}\varepsilon^{el}$ where C^{el} is the fourth-order elasticity tensor and ε^{el} is the total elastic strain. Creep response is conducted by a power law for the strain rate: $\delta\varepsilon = [A\sigma^{n}\{(m+1)\varepsilon\}^{m}]^{1/(m+1)}$, where A is a material parameter, n is the power of the stress σ, and m is the power of the strain hardening. The Newtonian viscosity can be related to this power law by inserting m=0 and A=1/(3η), if normal stress and strain rate are considered (Ranalli 1987, p. 75–80).

Loading models (Fig. 10) for different viscosities (3, 5, 10 x 10^{18} Pa s), and lithospheric thicknesses ranging from 30-65 km yield a total subsidence ranging from 22 to 37 cm, or approximately 1/3 of the currently observed subsidence. The subsidence over 50 years for a 50 km thick lithosphere and a viscosity of 3×10^{18} Pa s is 27.5 cm. Thinner lithospheric plates and lower viscosities predict higher subsidence. Surtsey is located on the edge of the Icelandic mantle plume. Considering the inferred lithospheric thickness of ~50 km and the intermediate thermal regime beneath Surtsey, an average asthenospheric viscosity of approximately 3×10^{18} í Pa s provides the best fit for the study area. The lithosphere is getting thinner towards the south into normal ocean crust thickness. The viscosity is probably in the lower end.

Palagonitization and consolidation

The degree of alteration of the original basaltic tephra is related to the temperature of the hydrothermal fluid (Jakobsson 1978, Jakobsson & Moore 1986). At temperatures of 100 °C, the main constituent of the tephra, the sideromelane glass, turns into palagonite, and consequently, the rock is consolidated. Jakobsson (1978) estimated that already in 1975, 64% of the two tephra-cones in Surtsey had consolidated to dense palagonite tuff. The porosity of the basaltic tephra in Surtsey is reduced in the palagonitization process as pores become filled with secondary minerals, thus causing net contraction of the hyaloclastite as pores are filled partly by the rocks' own materials. Assuming this effect could cause 1 % reduction pore space could cause as much as 2 m of subsidence. However, as pore space is also decreased by compaction (Section 5.3) it is difficult to separate these two mechanisms.

Compaction of pre-existing sea-bed sediments

The new island was built up on top of sediments, and the added weight will cause some compaction of the unconsolidated seabed deposits. To evaluate this contribution, the total amount of unconsolidated sediments must be estimated. In 1980 two seismic reflection profiles were measured just south of Surtsey across the submarine part of Jólnir (Thors & Jakobsson, 1982). The profiles show volcanic features resting on a stratified sequence with layering visible some 100 meters below the seafloor. Thors & Jakobsson (1982) interpreted a reflector as the top of Pleistocene. We assume this reflector marks the bottom of the unconsolidated sediments and evaluate the thickness of the Holocene deposit from the reflector up to the seafloor, using the east-west profile located 1–2 km south of Surtsey. The two-way travel time to the reflector is 17 ms. Thus, assuming a compressional velocity for the seafloor sediments of 1650 m/s gives thickness of the Holocene sediments as approximately 14 m. However, the reflector undulates so values of 14–20 m for unconsolidated sediments at the Surtsey eruptive site are reasonable.

We assume the porosity – depth relation is exponential and use sea bottom porosity of f_0 = 49% and a porosity-depth coefficient c = 0.27 km^{-1} for sandstone (Sclater & Christie (1980: page 3732)). The relation $f = f_0e^{-cy}$ gives the porosity at depth y, which decreases from the initial porosity because of the weight of the overload. Using a load corresponding to 130 m (Fig. 8) applying the formula (f_0 – (f_0e^{-cy}) for porosity change gives 0.49 – (0.49e-0.27*0.13) = 0.017, or a porosity reduction of 1.7 %, which for the 20 m thick sediments gives a compaction of 34 cm. At the vent we presume unconsolidated sediments were blown out by the eruption.

Compaction of volcanoclastic materials

The tuff and hyaloclastite (breccia and coarse to fine-grained sandstone) are subject to gravity-driven compaction. Porosity decreases as the compaction and cementation increase with time. The material will compact from its own weight and applying the calculations above for the seabed sediments gives an average porosity loss of 1.7 % "(at the top zero compaction and at the base 1.7 % compaction) gives 1.7/2 = 0.85 % and with 130 m of material the resulting subsidence will be 110 cm.

Thermal contraction

Fresh lava flows will exhibit subsidence due to thermal contraction. This subsidence acts in proportion to the thickness of the lava and it decays with time. At Etna, Sicily, for example, lava flows show a subsidence rate of 0.7 mm/day (256 mm/yr) during the first 70 days of a 50-m thick lava. The subsidence rates then decay rapidly (Stevens *et al*. 2001). It is suggested that lava flows of Etna that are thicker than 30 m can continue to subside for up to 20 years (Stevens *et al*. 2001). The lava flows at Surtsey are of similar thickness and they are intercalated by numerous scoria horizons. Early on. thermal contraction was probably a sizable contributor to the subsidence at Surtsey.

Measurement of tidally driven rise and fall of hot water within the drill hole demonstrates the importance of water circulation within the volcanic pile. This no doubt sped up thermal contraction during the first years. The thermal contraction during the first 20 years was larger than in recent years so that current subsidence is probably little affected, compared to Etna.

Thermal logging repeated in the borehole (Perez *et al*., 2022) shows mainly two areas of cooling: above sea-level (cooling of up to 60°C during 1980–2018) and a narrow area approximately 50 m below sea-level (cooling of up to 20°C during 1980–2018). Weaver *et al*. (2020) experimentally found a value of 5 x 10^{-6} /°C for the thermal expansion coefficient for hyaloclastite sampled at 70 m depth in Krafla, comparable to typical values for basalts and glass (0.5-9 x 10^{-6} /°C). We can use these values to find a range of possible effects of thermal contraction on subsidence, assuming thickness of 200 m. We do not know the thermal evolution prior to 1980; however, it is likely the maximum temperatures were on average below the boiling curve (maximum 160°C) since the tuff is deposited into cool ocean waters. Assuming an average minimum (maximum) temperature change of 10°C (100°C) and a minimum (maximum) thermal expansion coefficient of 0.5 x 10^{-6} /°C (5 x 10^{-6} /°C) we obtain possible total subsidence of 1 mm to 10 cm for contribution of thermal contraction.

Magma withdrawal or other movements in the magmatic plumbing system

A study of U-series disequilibria in the volcanic products of Surtsey indicates that they originated in the mantle and rose to the surface on a timescale shorter than a decade (Sigmarsson 2013). No indications support the existence of a shallow-level storage region. Because surface deformation for deep sources is small, the magmatic system likely has negligible effects. Furthermore, one might rather expect inflation and uplift following the eruptions, as in Krafla (e.g., Tryggvason 1994).

Land erosion of Surtsey

Óskarsson *et al*. (2020) identify three main processes related to the erosion of Surtsey; 1) A rapid initial erosion, 2) the prevailing SW coastal wave erosion, and 3) intense wind and runoff erosion. In the beginning a rapid erosion of the lava apron by wave erosion took place. Additionally, the unconsolidated tephra suffered by erosion. After the initial erosion slowed down (during 1967–1974) and became minor, the prevailing wave action from the southwest was still very efficient. According to figure 6 in Óskarsson *et al*. (2020) the southwest flank of the island lost 9.7 million m^3 from 1967–74 (1.38 million m^3 /year) and 18.4 million m^3 from 1974–2019 (0.41 million m^3 / year). This is a drastic drop in Surtsey's erosion rate but with time it adds up to considerable volumes. Eysteinn Tryggvason installed a levelling line across the island with twelve of the benchmarks up to number 624 along the southwest coast of Surtsey (Tryggvason 1968). In 1985 the end of the line was marked by benchmark 633. In the most recent survey benchmark 626 represented the end of the line. Óskarsson *et al*. (2020) also address the wind redeposition of sand. This drifting sand has hidden several benchmarks but also exposed some. Since the end of the eruption in 1967 to 2019 over 53% of Surtsey's area has been lost, however, with the erosion rate decreasing with time (Óskarsson *et al*. 2020).

DISCUSSION

Deformation observations

Subsidence has been observed at Surtsey from 1967 through 2023 relative to an external reference frame; first the tidal pond and since 1992 by GPS in relative or absolute terms (Fig. 4). A subsidence rate of 10 mm/yr (1992–2002), and 3.8 mm/yr (2000–2023) is observed for BM 621.

The most "stable" benchmarks are BM 512 and S-3 (Fig. 6), as they subside the least (Table 1). The relative uplift rates 1991-2023 for BM 512 and S-3 relative to BM 621 are 1.7 mm/yr and 2.1 mm/yr, respectively. In the period 1991 to 2002 the BM 512 was the most "stable" and in the two most recent measurements (2017-2023) the S-3 is the most "stable". All the benchmarks close to the Surtur-I crater have uplift relative BM 621. We note that no measurements have been done around the crater Surtur-II (Fig. 2). The least stable (i.e., fastest subsiding) benchmarks are at the edge of the island, and indeed many have been lost to sea already due to erosion. The accelerated subsidence observed prior to when the benchmarks are lost is due to slope failure processes, as the rocks have begun detaching and sagging before failing completely (e.g., Leshchinsky *et al*. 2019).

The horizontal motion of GPS sites largely follows the Eurasian plate (Fig. 6). Deviations of a few mm per year need though to be explained. There are variations in the vertical deformation across the island (e.g., Fig. 7), which likely also have horizontal counterparts.

Comparison of subsidence processes

The different processes considered here to affect vertical deformation of Surtsey are: 1. the lithostatic load of the erupted material; 2. compaction of seabed sediments; 3. palagonitization of the tephra; 4. compaction of the volcanogenic material; 5. thermal contraction of the lava field; and 6. the magmatic plumbing system. These have different spatial behaviour and temporal spans. Some decay rapidly, some slower. The different subsidence processes generate different amounts of subsidence, ranging from essentially zero to meter-level displacements. Compaction of the volcanoclastic pile predicts the largest displacements of our models. Each of our models relies on various assumptions, often leading to uncertain values.

The finite element load model (Section 5.1) predicts up to 27.5 cm of subsidence in the first 50 years (Fig. 10). The centre of the Icelandic mantle plume is in the north-western part of Vatnajökull, situated approximately under Bardarbunga (Fig. 1). Surtsey is located at 150–200 km's distance from the central part of the mantle plume. With Surtsey far from the mantle plume centre, and into "normal" ocean crust suggests effectively thinner lithosphere and lower viscosity, such that total subsidence due to loading may be more reasonable at 25-30 cm since the formation of Surtsey. The asthenosphere response to the load is still ongoing, with a rate today less than 3.8 mm/yr. The load model would give an exponential subsidence of the island. The amount of subsidence of the GPS site SURS (BM 621) since year 2000 is 91.6 mm or 3.8 mm/yr. During the same time interval, the relative subsidence between S-3 and BM 621 is 67 mm (Fig. 7b, Table 3). The S-3 and BM 512 (Fig. 6) are close to the feeder conduit and this is expected to be the most "stabile" area as the tephra is almost completely palagonitized. The compaction of sediment and volcaniclastic rocks (Sections 5.2-5.4) contributes very little today.

We therefore suggest that all vertical deformation of the benchmarks (512 – 518 and S-3 & 4) in and around the Surtur I crater, that have moved uniformly, are to the greatest extent caused by the lithospheric load. The subsidence from the lithospheric load is today 1.1 mm/yr.

The erosion and sedimentation described by Óskarsson *et al*. (2020) gives a picture of the dynamics of the surface of the island. In the period 1974–2019 the dDEM reveal massive erosion to the southwest and the south there the lava apron is lost to the sea. Also, the north-western rock face of the Surtur II (Surtungur) experienced significant erosion. The shifting sand on the island accumulates primarily on the northern and eastern flank of the eastern tuff cone (Surtur I). The amount of sedimentation suggested in figure 3 in Óskarsson *et al*. (2020) is up to 6.5 m and erosion of the eastern tuff cone is at one place 22.8 m. However, these are small areas that show these numbers and this has no effect on the lithospheric load. All the benchmarks are in bedrock, and some are buried under sediments or eroded away on the southwest flank of the island.

In the most recent survey 2023, the end of the levelling line is at benchmark 626 which has started to subside faster. In the period 2013–23 it subsided 4.0 cm (with BM 621 fixed). The cliff is moving outward to the sea and after a short time this benchmark will be gone. Benchmark 625 is getting closer to the cliff face and it is moving outward. The open cracks described by Óskarsson *et al*. (2020) are growing and one runs between benchmarks 625 and 626.

The time series of the vertical displacement relative to BM 621 (Fig. 7a) indicate high subsidence rates during the first twenty years since the island formed (until 1985). This pattern is also observed relative to BM 512 (Fig. 7b). Since 1985, two sites close to BM 512 (BM 515 and BM S-3) experienced only small changes, and the two benchmarks 612 and 621 have a low relative subsidence rate (Fig. 7a). This excessive subsidence is probably caused by compaction of loose volcanogenic and seabed material. The closer to the crater and the feeder dykes the more stable the ground gets. Closer to the shoreline (the lava feed delta) and away from the crater the material is less compacted. Also, the seaside offers less support than the land side. The suggested compaction seems to decline with time and is today less than 1 mm/yr.

In 1979 a 181 m deep hole was drilled on Surtsey ending just a few meters above the original seabed (SDH-1 in Fig. 2). The final meters of the drilling penetrated loose tephra (Moore *et al*. 1992), which indicates that the palagonitization reaches almost down to the original seabed at the drill site. Three drill holes were made in 2017 at almost the same location (SE02a-b, SE03 in Fig. 2): two vertical holes (combined length 186 m) and the third 354 m long, dipping 55° in direction 264°W toward the Surtur-I crater (Moore & Jackson 2020). Over 95% of the drill core from 2017 consists of lapilli tuff (McPhie *et al*. 2020). The slanting SE03 drill hole reached a thick (342 to 352 m) coherent basalt just above the end of the drilling, interpreted as the feeder dyke (McPhie *et al*. 2020).

The information from the drilling gives a suggestion of the extent of the palagonitization. Each of the two tuff cones I and II form inverted cones of more or less palagonitized material. As the cones do not overlap completely, an un-palagonitized tuff area is suggested to be present in the core of the island. The GPS site SURN measured in 2000, 2002, 2013 and 2023 is located on the crest that divides the Surtur I and II craters. The GPS measurements of the three sites show a similar subsidence rate (3.8 mm/yr) and they are similar distance from the centre of respective crater (Fig. 8). This indicates a similar amount of palagonitization has occurred under all three GPS sites.

The thermal contraction of the lava flows is comparable to the lava flows at Etna. The contraction was largest in the first 20 years and is now likely negligible. Continued cooling of the hyaloclastite mass, averaged over the length of the borehole, is approximately 0.2°C/yr (Perez *et al*. 2022), resulting in current subsidence rate of 0.2 mm/yr.

The additional subsidence is attributed to compaction of the tuff cone and material in the lava feed delta, with exception of the areas closest to the coast. The deformation of the benchmarks located in the central part of the island is used to estimate the vertical strain caused by the compaction of the tuff and the fragmented (diamictite) material in the lava fed delta. Under the GPS site SURS (benchmark 621) a slightly higher amount of subsidence is observed. Possibly it is located over an area that is less palagonitized.

Need for continued measurements

The vertical strain (subsidence) is currently reasonably small, below 5 mm/yr, but still significant. Both the compaction and asthenosphere response are almost complete for the island. The “major” deformation now and in the future will be that the sides slump out into the sea as the sea erosion digs in. Some of this slumping would be interesting to observe with GPS to capture horizontal motion. The levelling benchmarks were measured kinematically with GPS in 1992 (Einarsson *et al.* 1994), and it may be of interest to add GPS measurements to the levelling observations. There are still subtle changes in deformation across the island that will be interesting to research further with precision levelling every 10 years or so. It may be feasible to apply high-precision modes of InSAR, however, the island is so small, with high topography and abundant sand-drifts, that it would be challenging to detect its slow deformation using that technique.

However, the sagging of sizable blocks by the island edges may well be recorded with repeat precision photogrammetry. Finally, by all chances, another eruption will occur in the Surtsey and Vestmannaeyjar region. It is impossible to say what it's precursors will be, but recent unrest periods in Krafla and Reykjanes Peninsula indicate that detailed seismic and geodetic observations are primary monitoring tools for such precursors. Therefore, geodetic monitoring of Surtsey needs to be continued.

Conclusions

Two processes dominate the subsidence at Surtsey: Flexure of the lithosphere under the load of the new island and compaction of the volcanic edifice. Since the formation of Surtsey with its volume of 0.8 km^3, the load has depressed the surface by 25-30 cm.

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