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

GRÓA VALGERDUR INGIMUNDARDÓTTIR[1], NILS CRONBERG[1]
AND BORGTHÓR MAGNÚSSON[2]

[1]Department of Biology, Lund University, Ecology building, 223 62 Lund, Sweden
[2] Icelandic Institute of Natural History, Urridaholtsstræti 6–8, 210 Gardabær, Iceland
Corresponding author: Nils Cronberg (nils.cronberg@biol.lu.se)

ABSTRACT

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

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

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

INTRODUCTION

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

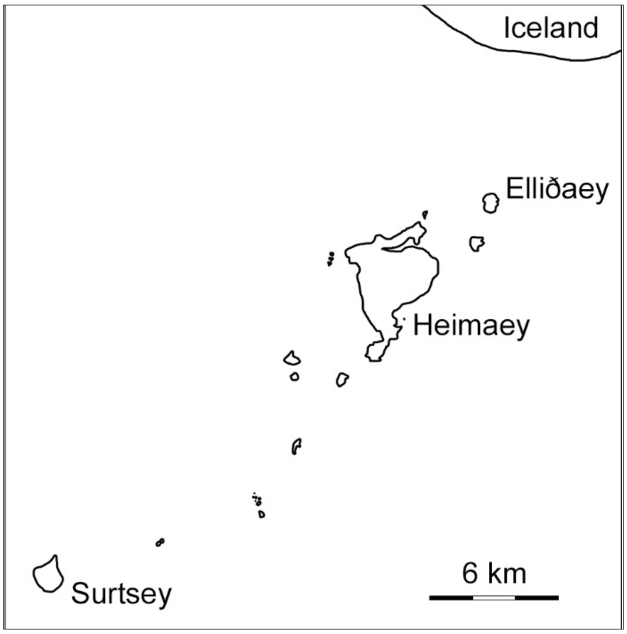

Figure 1. An overview of the Vestmannaeyjar archipelago, off the south coast of Iceland. The archipelago stretches about 38 km, with Surtsey at the south-western end and Elliðaey at the north-eastern end. Map: GVI, based on a satellite image from Google Maps (accessed on April 15, 2022).

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

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

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

BRYOPHYTE COLONIZATION ON SURTSEY

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

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

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

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

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

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

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

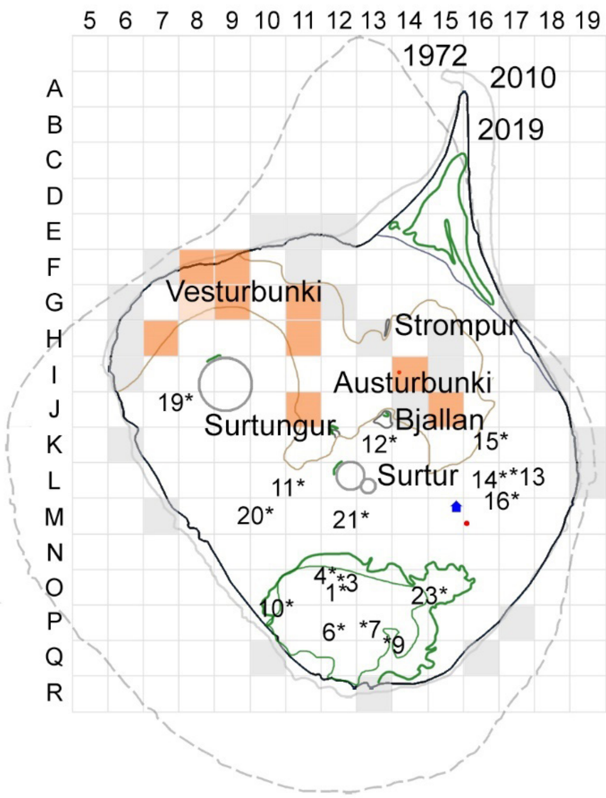

Figure 2. The figure shows the 100 m × 100 m grid system used to monitor the distribution of bryophytes, as well as the main habitat types on Surtsey and examples of past shorelines. The northern spit of the island, roughly denoted by blue contour, is made up of coastal sediments. The area denoted by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

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

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

MATERIALS AND METHODS

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

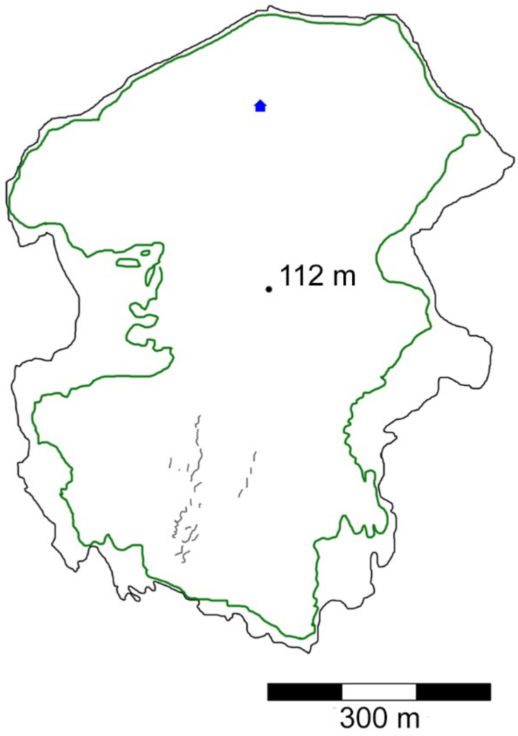

Figure 3. The contours of Elliðaey. The area within the green contour is covered with a lush grassland in a sloping landscape (see Fig. 15), except for an occasional protruding lava formation (grey lines indicate where they are mostly to be found). The shoreline and the core are made up of palagonite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

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

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

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

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

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

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

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

RESULTS AND DISCUSSION

Bryophyte distribution

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

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

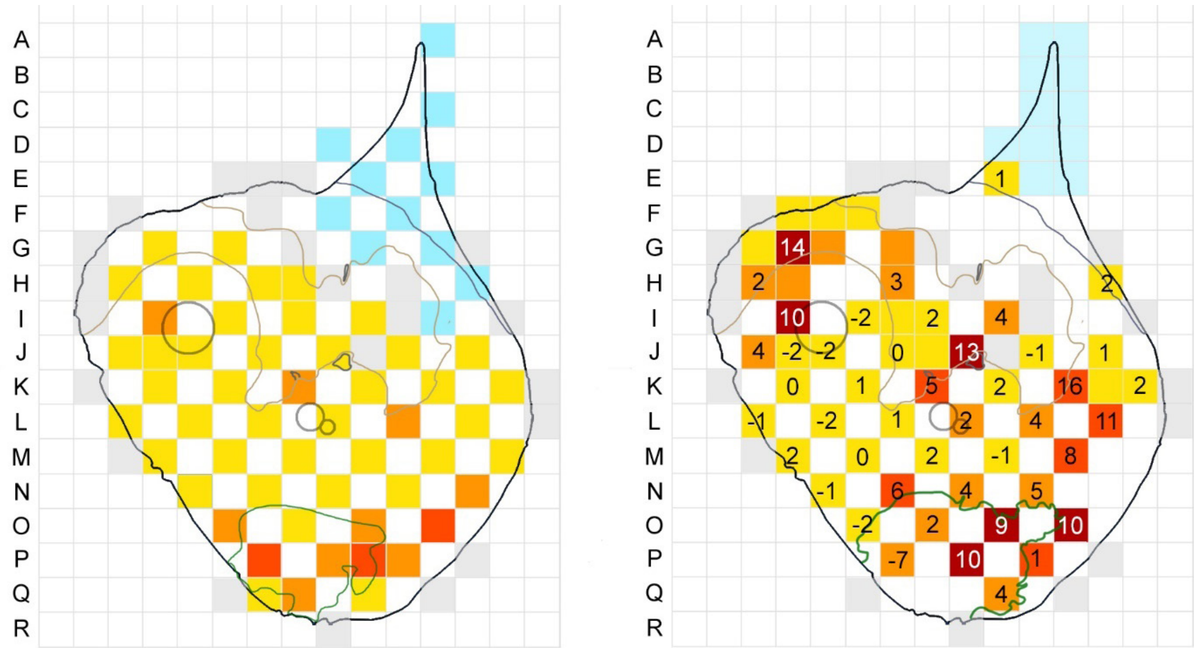

Figure 6. Number of bryophyte taxa found per quadrat in summer 2008 (left image) and 2018 (right image); see in-image colour legend. Trends in species numbers per quadrat between 2008 and 2018 are marked with numbers in the right image, where available. Quadrats filled with grey were deemed unsafe to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

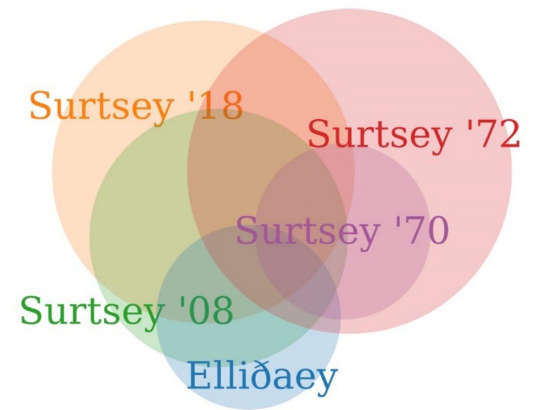

Figure 7. Area proportional Venn diagram for the total number of taxa (Appendix B) found on Surtsey in the surveys in 1970, 1972, 2008 and 2018. Each circle represents a total species number for a given year: 1970 = 17, 1972 = 72, 2008 = 39, 2018 = 59; the intersections indicate the species in common.

Species richness

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

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

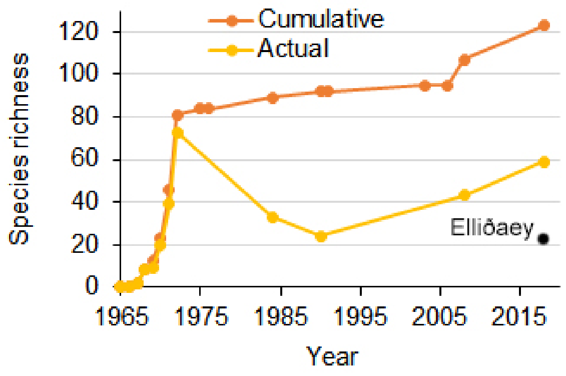

Figure 8. Bryophyte species richness on Surtsey, both actual and cumulative. The species richness on Elliðaey in 2018 is also shown.

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

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

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

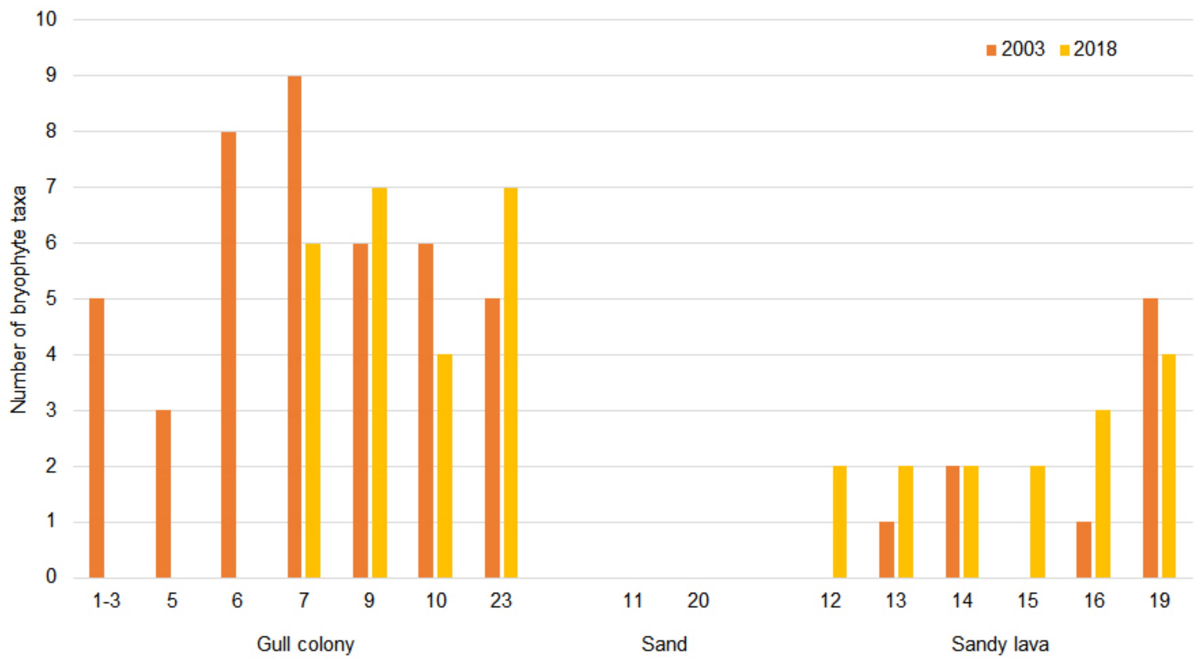

Figure 9. Number of bryophyte taxa found in permanent plots on Surtsey, investigated in both 2003 and 2018 (numbers on X-axis). See figure 1 for the plots' location on Surtsey.

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

Missing species

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

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

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

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

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

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

New species

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

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

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

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

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

Habitats

The spit

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

The palagonite tuff and fumaroles

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

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

The skirt of the palagonite cone

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

Surtungur

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

Sandy lava-fields

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

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

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

'A'ā lava

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

Gull colony

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

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

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

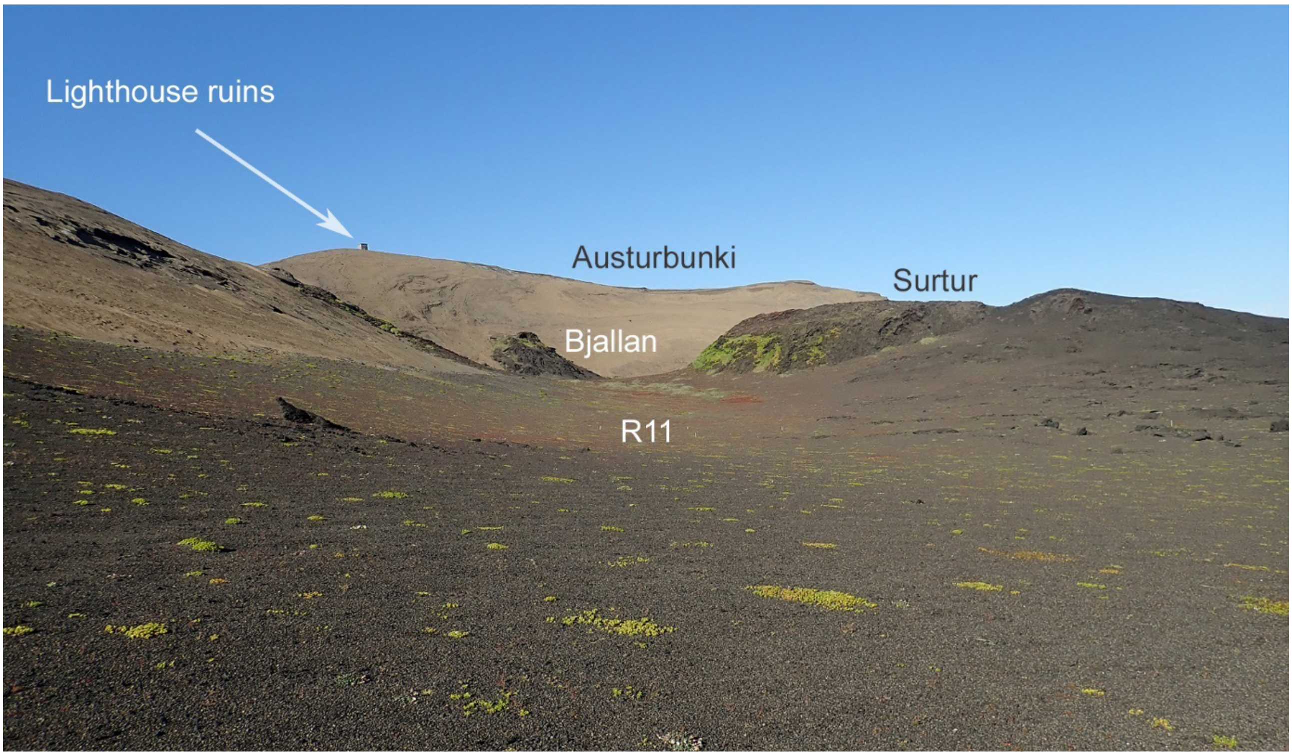

Figure 11. Standing roughly in quadrat M10, looking northeast, with permanent plot R11 in the centre, characterized by the red colour of *Rumex acetosella* L. The small crater Bjallan is seen to the centre of the palagonite tuff cone Austurbunki and the main crater Surtur. See figure 1 for perspective.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

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

Distributional changes of selected species

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

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

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

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

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

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

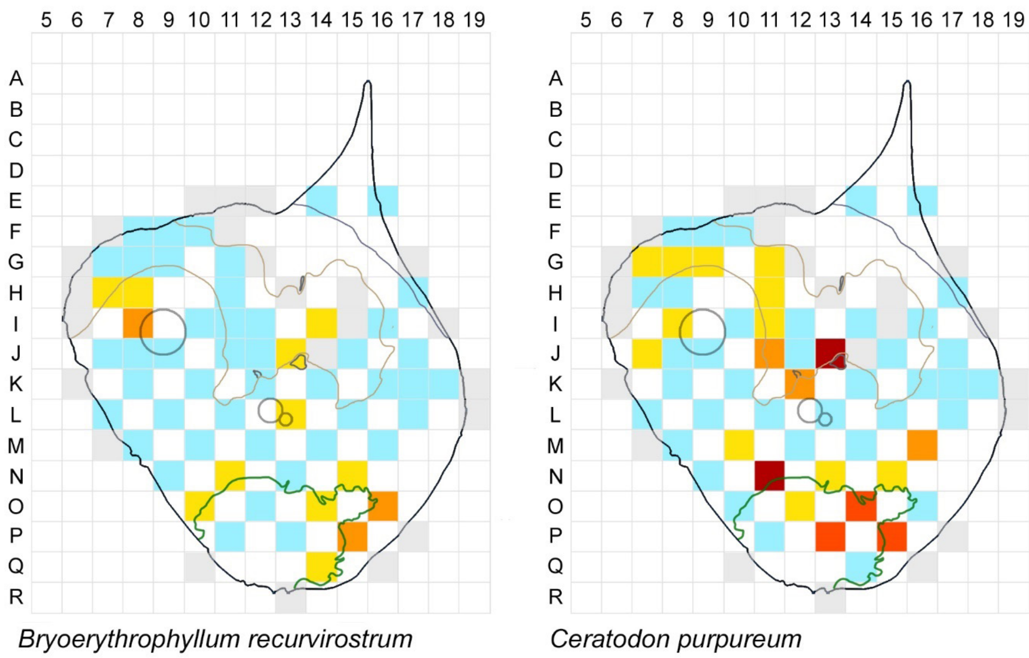

Figure 12. Distribution maps for *Bryoerythrophyllum recurvirostrum* and *Ceratodon purpureum,* two of the bryophyte species that showed greatest changes in distribution between 2008 and 2018. Only data from quadrats investigated in 1971, 1972, 2008 and 2018, are included. Legend: Pale blue = species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

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

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

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

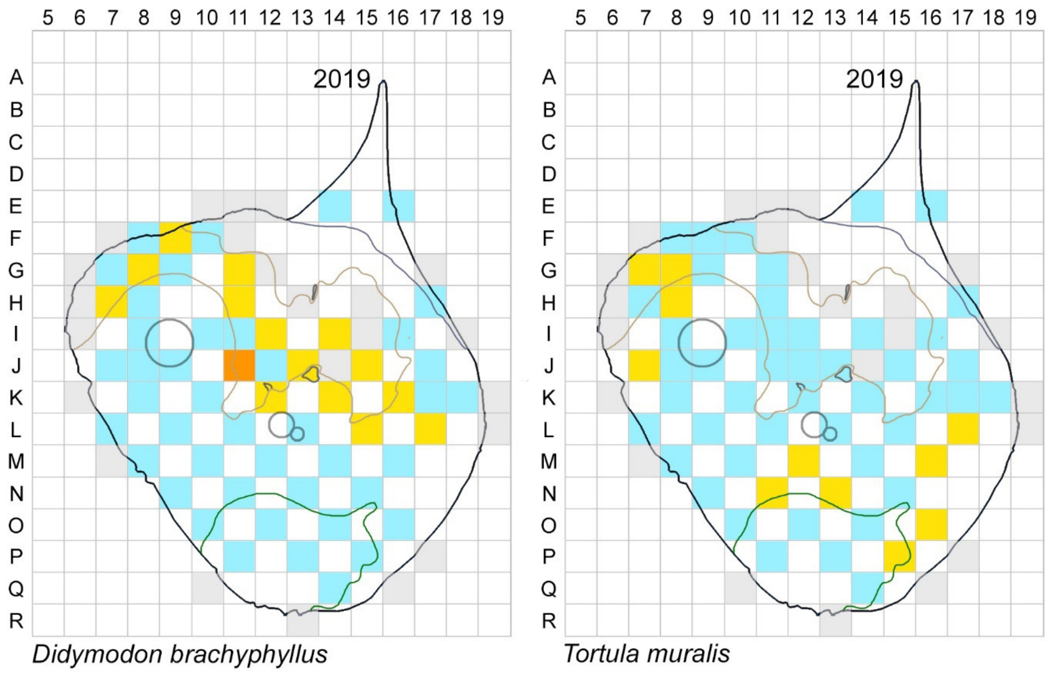

Figure 13. Distribution maps for *Didymodon brachyphyllus* and *Tortula muralis,* two of the bryophyte species that showed the greatest changes in distribution between 2008 and 2018. *D. brachyphyllus* was found in only 2 quadrats in 2008 and *T. muralis* was found in a single quadrat in 2008 (Table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

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

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

Declining species

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

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

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

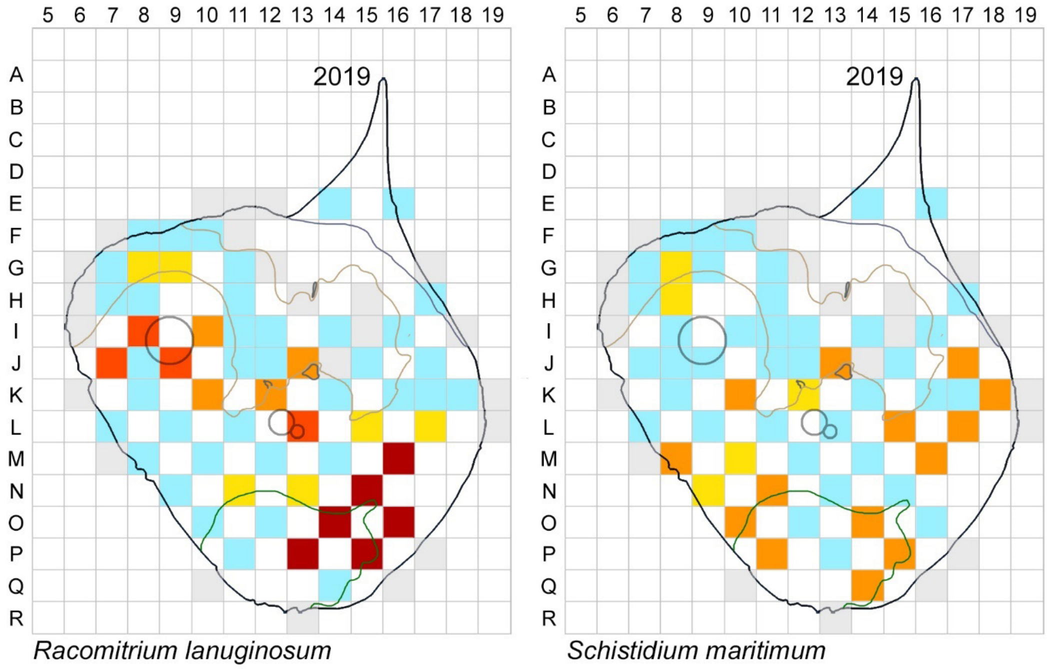

Figure 14. Distribution maps for *Racomitrium lanuginosum* and *Schistidium maritimum,* two of the bryophyte species that showed the greatest changes in distribution between 2008 and 2018. Only data from quadrats investigated in 1971, 1972, 2008 and 2018, are included. Legend: Pale blue = species not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

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

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

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

Elliðaey and comparison to Surtsey

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

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

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

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

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

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

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

CONCLUSION

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

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

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

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

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SUPPLEMENTAL INFORMATION

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

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APPENDICES

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

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

MARCHANTIOPHYTA

Anastrophyllaceae L.Söderstr., De Roo & Hedd.

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

Cephaloziellaceae Douin

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

Lophoziaceae Cavers

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

Scapaniaceae Mig.

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

Gymnomitriaceae H.Klinggr.

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

Jungermanniaceae Rchb.

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

Aneuraceae H.Klinggr.

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

Aytoniaceae Cavers

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

Marchantiaceae Lindl.

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

BRYOPHYTA

Polytrichaceae Schwägr.

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

Encalyptaceae Schimp.

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

Funariaceae Schwägr.

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

Distichiaceae Schimp.

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

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

Hymenolomataceae Ignatov & Fedosov

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

Amphidiaceae M.Stech

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

Aongstroemiaceae De Not.

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

Dicranellaceae M.Stech

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

Fissidentaceae Schimp.

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

Rhabdoweisiaceae Limpr.

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

Ditrichaceae Limpr.

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

Pottiaceae Schimp

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

Grimmiaceae Arn.

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

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

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

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

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

Bartramiaceae Schwägr.

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

Meesiaceae Schimp.

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

Bryaceae Schwägr.

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

Mniaceae Schwägr.

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

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

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

Orthotrichaceae Arn.

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

Aulacomniaceae Schimp.

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

Plagiotheciaceae M.Fleisch.

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

Amblystegiaceae G.Roth

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

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

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

Scorpidiaceae Ignatov & Ignatova

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

Brachytheciaceae Schimp.

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

Pylaisiaceae Schimp.

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

Hylocomiaceae M.Fleisch.

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

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

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

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

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