Developments in plant colonization and succession on Surtsey during 1999–2008

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ABSTRACT

Plant immigration on Surtsey continued during 1999–2008 and 69 vascular plant species had colonized the island by 2008. That year 63 species were recorded, of which 32 had formed viable populations. Birds were considered the main agents of seed dispersal to the island, having dispersed 75% of the species, while 16% were wind dispersed and 9% by sea from 1965.

Plant succession was studied in permanent plots. Barren areas were starkly distinct from a gull colony area affected by breeding seagulls from 1985. Average breeding density by plots within the gull colony was 4 nests 1000 m^{-2} during 2003–2008. Species richness, plant cover and biomass remained low in the barrens. Here two communities, a *Honckenya peploides* community on tephra sand and a gravel flats community with *Silene uniflora* as the indicator species, had developed. Carbon and nitrogen content of soil in barrens was very low and pH relatively high. By 2008, plant species richness in the gull colony was considerably higher than in the barrens and average plant cover and biomass was from 10 to 40 times greater. Soil within the colony area had a relatively high C and N content, and pH was lower than in the barren area. Two forb-rich grassland communities had developed within the colony. On lava, a *Puccinellia distans/Sagina procumbens* community composed mainly of ruderal species, and a community with the perennial grasses *Poa pratensis*, *Leymus arenarius* and *Festuca richardsonii* as dominants on sand and lava. With the closing of the grassland sward, species richness had declined, reflecting developing dominance.

In 2008 the forb-rich grassland of the gull colony had expanded to about 10 ha in area. It had become a foundation of an abundant invertebrate life and a small community of land birds developing on the island from 1996. Seabirds (primarily gulls) have become increasingly important in shaping and driving the ecosystem development on Surtsey through their nutrient transfer from sea to land and by dispersal of seeds to the island. Puffins have recently started breeding on the island and they are expected to affect further development of the ecosystem.

INTRODUCTION

Colonization by vascular plants on Surtsey has been followed since the formation of the island. In the early years studies focused mainly on dispersal to the island, and the establishment and spread of the pioneer species (Einarsson 1967a,b, 1973, Fridriksson & Johnsen 1968, Fridriksson 1978, 1982, 1992). Special attention was paid to the flora and fauna of the neighbouring volcanic islands that may give an indication of the long-term development on Surtsey (Fridriksson & Johnsen 1967, Fridriksson *et al.* 1972). A study of colonization and species distribution continues to the present day. As species richness and plant cover increased over the last two decades, permanent plots were established to monitor development in more detail (Magnússon *et al.* 1996, Magnússon & Magnússon 2000). These plots have also been used for studies of the invertebrate fauna and ecosystem functions (Ólafsson & Ingimarsdóttir

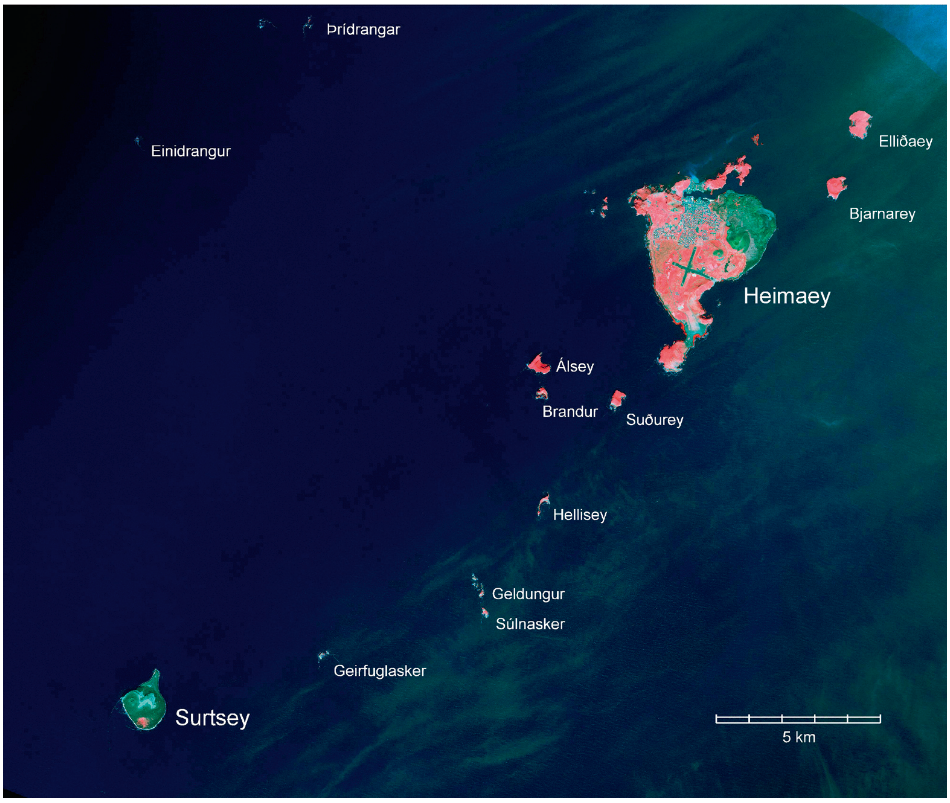

Fig. 1. Surtsey and the Vestmannaeyjar islands on an infra-red SPOT 5 image from July 16, 2003. Areas with dense vegetation appear in red colour, note the gull colony area on southern Surtsey. The Eldfell-volcano and the dark lava from the 1973 eruption give a striking contrast on Heimaey.

2009, Sigurdsson 2009, Sigurdsson & Magnússon 2009).

The importance of seabirds in ecological functions has been increasingly acknowledged in recent years. They can be viewed as chemical and physical engineers that affect terrestrial vegetation through nutrient transport from sea to land, seed dispersal and physical disturbance (Ellis 2005, Ellis *et al.* 2006, Sekercioglu 2006). Breeding seagulls have had great influence on plant colonization and vegetation development on Surtsey since 1985 (Magnússon & Magnússon 2000, Magnússon & Ólafsson 2003).

In the present paper, we provide an account of plant colonization and succession on Surtsey over the last 10 years and the changes that have occurred from earlier years. To our previous study in permanent plots (Magnússon & Magnússon 2000) we have added regular measurements of plant biomass and gull nesting density and their results are presented. We summarise main steps in ecosystem development on the island.

STUDY AREA

Surtsey formed during a volcanic eruption that lasted from November 1963 to June 1967. At the end of the eruption, the island had reached 2.7 km^2 in total area. During the eruption, large tephra cones were built up on the middle of the island by the two main craters. The cones were gradually transformed into denser palagonite tuff as years passed. The highest point on the island is 155 m above sea level. The southern part of Surtsey was formed by lava flows that descended from the craters. The rough lava has, to a large extent, been filled in by drifting tephra and sand from the hills above. The lava on the south-eastern-most part of the island remains mostly free of sand but airborne dust has filled hollows and fissures. The northern-most part of Surtsey is a low spit formed by eroded coastal sediments deposited leeward of the island. In occasional heavy winter storms, the spit has been flooded by extreme surf. Coastal erosion has taken its toll of the island and by 2004 it had been reduced to 1.4 km^2 (Jakobsson *et al.* 2007).

Surtsey is the southern-most of the Vestmannaeyjar islands, which are 7–33 km off the south coast of Iceland (Fig. 1). The climate in the area is mild

Table 1. Mean annual temperature and mean total precipitation at Heimaey weather station (Stórhöfdi) during 1961 – 2006 (Icelandic Meteorological Office).

Period	Temperature (°C)	Precipitation (mm)
1961–1970	5,0	1455
1971–1980	4,8	1713
1981–1990	4,7	1598
1991–2000	5,0	1473
2001–2006	5,8	1718
1961–2006	5,0	1580

and oceanic. At the Heimaey weather station, 19 km from Surtsey, the mean annual temperature during 1961–2006 was 5.0 °C and the mean annual precipitation 1580 mm (Icelandic Meteorological Office). A warming trend has been experienced in the area over the last few years as in other parts of Iceland, while precipitation has remained relatively high (Table 1). The Vestmannaeyjar area is generally frost free from the first week of May until the middle of October (Einarsson 1976).

METHODS

Plant colonization and survival

During the study period covered in this paper, annual visits to the island during mid-July continued. During each visit, all portions of the island were thoroughly searched to update survival and colonization of vascular plant species. Since 1998, the location of the first individuals of species new to Surtsey was recorded by GPS. It has also been useful to mark locations of earlier colonists that are limited to a single or very few individuals. Field markers have been left next to plants that are hard to relocate. From this work, an unbroken record on colonization and survival of vascular plant species on Surtsey exists from 1965 when the first plant was found.

Permanent plots study

The study of plant succession in permanent plots that began in 1990 on the island has been continued. Twenty-five plots, 10x10 m in size, were initially established and completed by 1995. The location of the plots was chosen subjectively with respect to substrate type and influence of gulls on vegetation development on the island (Magnússon *et al.* 1996, Magnússon & Magnússon 2000). A few of the plots have been decommissioned and new ones established because of plot destruction or revision of the sampling method. After establishment the whole set of plots was sampled for the first time in 1996 and every second year after that. In 2008, there were 25 plots in active sampling on the island (Fig. 2, Table 2). In all years, the sampling has been carried out in the middle of July.

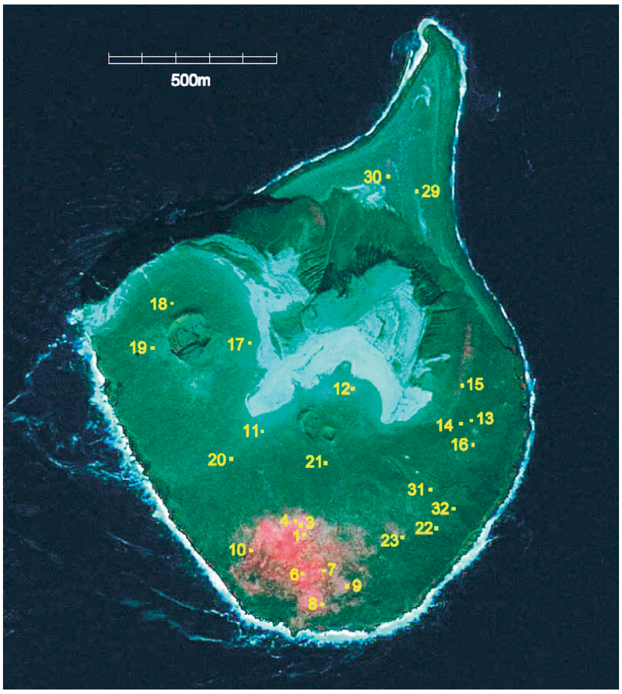

Fig. 2. Location of permanent plots on Surtsey, infra-red SPOT 5 image, July 16, 2003. Gull colony area on the southern island appears in red colour.

Vegetation

The permanent plots were sampled with line-transects (Magnússon & Magnússon 2000). Five 10 m transects were laid across each plot, parallel at 1, 3, 5, 7 and 9 m from their reference edge. Plant cover was determined by line-intercept method. All vascular plant species intercepting the line were recorded separately for each meter along the line, as well as the total cover of mosses, lichens and bare ground. Additional vascular species within the plots not intercepted by the line were also recorded. In the analysis, they were given the lowest possible intercept value of 1 cm equivalent to 0.02% cover.

Table 2. Permanent plots on Surtsey in use in 2008, year of establishment, substrate type, number of sampling and relative influence of breeding gulls.

Plot no.	First sampled	Substrate type	No. of samples	Influence of gulls
1,3,4	1990	sand-filled sheet lava	10	high
6–10	1994	sheet lava	8	high
11–14, 16, 18,19	1994	sand-filled sheet lava	8	low
15,17	1994	tephra hill site	8	low
20,21	1995	sand-filled sheet lava	8	low
22,23	1995	sheet lava	8	moderate
29,30	2005	coastal sand	3	low
31,32	2008	block lava	1	low

Soil

In 2008, soil sampling was carried out in the plots as in 1998 (Magnússon & Magnússon 2000). Four random samples were taken in each plot with a 7 cm wide soil corer down to a 10 cm depth. The samples were mixed in the field to make a composite sample for each plot. In the laboratory, the samples were dried at room temperature and sieved through a 2 mm mesh, for determination of pH, carbon (C) and nitrogen (N). pH was measured in a mixture of 5 g of dried soil and 25 ml of deionzied water after 2 hours shaking, following the methods of Blakemore *et al.* (1987). C and N content of soils was measured in a Vario MAX CN – Macro Elementar Analyzer (Elementar Analysensysteme GmbH), using 1.5–4 g samples depending on the organic matter content. The samples were ground in a ball mill and dried at 105 °C before the analysis. All soil analyses were done by the Keldnaholt chemical laboratory. The analytical methods differed and the limits of quantification were lower for C and N than in 1998 (Magnússon & Magnússon 2000).

Plant biomass

In 1999, vegetation was harvested for the first time at the permanent plots for determination of plant biomass. The sampling was repeated in 2003 and 2007. As the sampling was destructive, it was carried out in a 10x10 m area adjacent to each permanent plot. Four samples were harvested at random coordinates within the plots. The vegetation was cut at ground level along a 2 m line, using electric grass clippers with a 7.5 cm wide cut. All vegetation, live and standing dead, was collected. In the laboratory, the samples were dried at 60 °C to a constant oven dry weight.

Density of gull nests

To get an indication of the influences of the breeding seagulls on plant succession on the island a nest count in and around the permanent plots was started in 2003 and then repeated annually. This was done by inspecting carefully a 1000 m^2 circular plot with a centre in the middle of a permanent plot. A team of 4–5 researchers, spread out a long the 17,85 m long radius line, walked in a circle within the nest-counting plot. All gull nest bowls that appeared to have been occupied in the current season were counted. A record was also kept of older nests. It is the great black-backed gull (*Larus marinus*), herring gull (*L. argentatus*) and lesser black-backed gull (*L. fuscus*) that breed in great numbers upon the island (Magnússon & Magnússon 2000, Magnússon & Ólafsson 2003, Petersen 2009). Their nests have been counted but they were not separated to a species as the chicks had left the nests when the counting was carried out (mid July). A few fulmar nests (*Fulmarus glacialis*) were also encountered within the surveyed plots and they were also included.

Data analysis

We used DECORANA-ordination (Hill 1979a) to investigate vegetation similarity between individual plots and trends in plant succession. Data from the different sampling years was included for all the 25 plots in use in 2008, which gave a total of 182 plots and 26 plant species for the different sampling years. A square root transformation was performed on the cover data and downweighting of rare species was selected in the ordination procedure. A TWINSPAN-classification (Hill 1979b) was also carried out using only the 2008 data from the plots. This left 23 plant species in the analysis. The square root values were also used and the cut levels were set as 0, 1, 2, 4 and 7. The ordination and classification were run in the PC-ORD 5-package (McCune & Mefford 2006).

RESULTS

Plant colonization and survival

In 2008, the number of vascular plant species found on Surtsey from the first colonization in 1965 had risen to 69. Of those species 63, or 91%, were found alive in that season (Fig. 3, Appendix 1). The first decade of plant colonization on the island was characterised by shore plants. Survival of entering species was high and most of them formed viable populations within a few years. This period was in comparison followed by a relative stagnation during the next decade, 1975–1984, when relatively few new species entered the island and survival dropped. This was to change after 1985, following the sharp increase in number of gulls and formation of a dense breeding colony on the southern part of the island. The gulls facilitated a wave of new plant invasion and survival on the island that is still in force. From 1990–1998 there was a steady

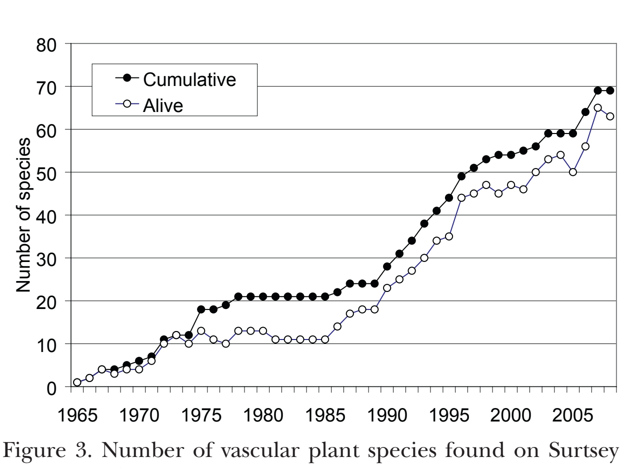

Figure 3. Number of vascular plant species found on Surtsey during 1965–2008.

Table 3. Vascular plants recorded on Surtsey from 1965 and their status in 2008. Species were considered to have formed viable populations if they had spread on the island and were found in at least 5 locations.

			Species status in 2008		
		First colonization	Alive	Viable population	Within permanent plots
Pterydophytes					
1	*Equisetum arvense*	1975	X		
2	*Cystopteris fragilis*	1971	X	X	
3	*Gymnocarpium dryopteris*	2007	X		
4	*Polypodium vulgare*	1996	X		
Monocots					
	grasses				
5	*Agrostis capillaris*	1992	X	X	X
6	*Agrostis stolonifera*	1987	X	X	X
7	*Agrostis vinealis*	1993	X		
8	*Alopecurus geniculatus*	1992	X	X	
9	*Alopecurus pratensis*	2007	X		
10	*Anthoxanthum odoratum*	1996	X		
11	*Calamagrostis stricta*	2007	X		
12	*Deschampsia beringensis*	1993	X		
13	*Festuca richardsonii*	1973	X	X	X
14	*Festuca vivipara*	2006	X		
15	*Leymus arenarius*	1966	X	X	X
16	*Phleum pratense*	1994	X		
17	*Poa annua*	1987	X	X	X
18	*Poa glauca*	1994	X		
19	*Poa pratensis*	1975	X	X	X
20	*Puccinellia distans*	1972	X	X	X
	sedges and rushes				
21	*Carex maritima*	1972	X	X	
22	*Eleocharis quinqueflora*	1993	X		
23	*Juncus alpinus*	1995	X		X
24	*Juncus arcticus*	1991	X		
25	*Luzula multiflora*	1990	X		
26	*Luzula spicata*	1997	X		
	orchids				
27	*Platanthera hyperborea*	2003			
Dicots					
	forbs				
28	*Achillea millefolium*	2007	X		
29	*Alchemilla vulgaris*	1990	X		
30	*Angelica archangelica*	1972	X		
31	*Armeria maritima*	1986	X	X	X
32	*Atriplex longipes*	1977			
33	*Atriplex sp.*	2006	X		
34	*Cakile arctica*	1965	X	X	
35	*Capsella bursa-pastoris*	1990			
36	*Cardaminopsis petraea*	1978	X	X	X
37	*Cerastium fontanum*	1975	X	X	X
38	*Cochlearia officinalis*	1969	X	X	X
39	*Epilobium collinum*	2007			
40	*Epilobium palustre*	1990	X		
41	*Euphrasia frigida*	2001	X	X	
42	*Galium normanii*	1995			
43	*Galium verum*	2003	X		
44	*Honckenya peploides*	1967	X	X	X
45	*Leontodon autumnalis*	1996	X	X	
46	*Matricaria maritima*	1972	X	X	X
47	*Mertensia maritima*	1967	X	X	X
48	*Montia fontana*	1994	X		X
49	*Myosotis arvensis*	1997	X		
50	*Oxyria digyna*	1998	X		
51	*Plantago lanceolata*	2004	X		
52	*Plantago maritima*	2002	X		
53	*Polygonum aviculare*	1991			
54	*Potentilla anserina*	1996	X	X	
55	*Ranunculus acris*	1992	X	X	
56	*Rhodiola rosea*	2006	X		
57	*Rumex acetocella*	1978	X	X	X
58	*Rumex acetosa*	1991	X	X	X
59	*Rumex longifolius*	1996	X	X	
60	*Sagina procumbens*	1986	X	X	X
61	*Saxifraga caespitosa*	2006	X		
62	*Silene uniflora*	1991	X	X	X
63	*Stellaria media*	1970	X	X	X
64	*Taraxacum spp.*	1991	X	X	X
	shrubs				
65	*Empetrum nigrum*	1993	X	X	X
66	*Salix herbaceae*	1995	X	X	
67	*Salix lanata*	1999	X		
68	*Salix phylicifolia*	1998	X		
69	*Thymus praecox*	2006	X	X	
			63	32	23

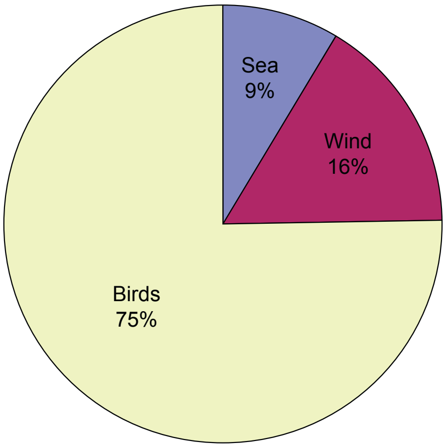

Figure 4. Probable route of dispersal by colonizing species found on Surtsey in 1965–2008.

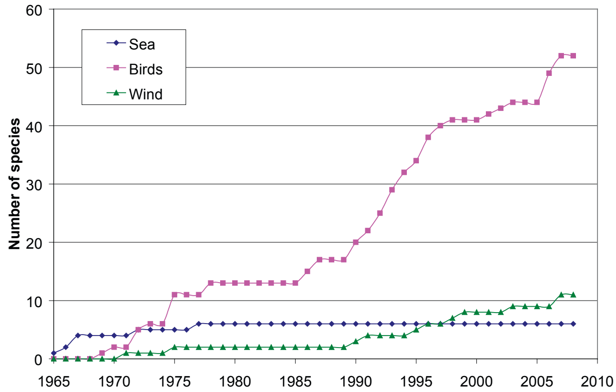

Figure 5. Cumulative curves of dispersal routes to Surtsey considered used by the different vascular plant species during 1965 – 2008. Based on dispersal-mode spectra of the flora and sites of establishment on the island (see also Appendix 1).

increase with 2–5 new species entering every year. During 1999–2005, colonization declined to 0–3 species per year indicating that it was levelling off. This was however followed by a sharp increase in 2006 and 2007 with 5 new species found on the island each year. In addition, a few species, which had been unsuccessful colonizers on the island in the past, have invaded the island again (Fig. 3).

The colonization sequence and location of first encounter of the different species indicates that about 9% were brought by sea currents to the island, 16% by wind and 75% by birds (Fig. 4. Appendix 1). The six species brought in by the sea are all coastal plants adapted to sea dispersal, e.g. *Cakile arctica, Leymus arenarius* and *Honckenya peploides*. They were the first species appearing on the sandy, northern shores. The eleven species considered wind dispersed are all adapted to that mode of transportation. They have small spores or light, hairy seeds easily carried by wind. Examples of these are the fern *Cystopteris fragilis, Taraxacum* sp., the three *Salix* species found on the island and the first orchid *Platanthera hyperborea*. The remaining 52 species were probably brought by birds to the island, either internally or externally. The first encounter of most of these species has been upon the island within or at the edge of the gull colony indicating birds as carriers. The first species considered carried by birds to the island was *Cochlearia officinalis* (Appendix 1). During the first decade dispersal by sea was most important but has not added significantly to the flora after that. Bird dispersal became important a few years later and has continued as the main gateway. Wind dispersal has on the other hand gained increasing importance after 1990 (Fig. 5).

Table 4. Viable plant populations within the main plant taxonomic groups on Surtsey in 2008 in proportion to the number of colonizing species of each group.

Plant group	Viable populations %
Pterydophytes	25
Grasses	56
Sedges & rushes	17
Forbs	51
Shrubs	60

Of the 69 colonizing species during 1965–2008, there were 4 pterydophytes, 16 grasses, 6 sedges and rushes, 1 orchid, 37 dicot forbs and 5 shrubs (Table 3). All species of these groups were alive in 2008 except the orchid and 5 species of dicot forbs, which was by far the largest group. Of the colonizing species, 32 had spread on the island and formed viable populations in 2008 (Table 3). Looking at the assemblage of plants in 2008 grasses, forbs and shrubs were relatively successful in establishing on the island while pterydophytes and the sedges and rushes met greater obstacles (Table 4). Thus, *C. fragilis* was the only pterydophyte widely distributed in 2008 and of the sedges and rushes, only *Carex maritima* had a viable population (Table 3).

The key players in plant colonization on Surtsey during the first two decades were mainly species adapted to relatively infertile habitats along the sandy shores and barren inland areas. Examples of these species are *H. peploides, L. arenarius, Mertensia maritima, C. maritima, Festuca richardsonii* and *Rumex acetosella,* which all became established and started spreading within a few years of first colonization. All are clonal perennials and stress tolerant species with relatively large seeds. The species assemblage changed considerably after 1985. With improved soil conditions came denser vegetation in the area affected by gulls. Plant species that were more nutrient demanding or had more complex requirements for establishment came to dominate. Thus *Poa annua, P. pratensis, Sagina procumbens, Stellaria media, Rumex acetosa, Ra-*

Table 5. Results of analysis of soil samples taken in permanent plots in Surtsey in 2008. Plots 1–10 and 23 were within the gull colony but plots 11–22 and 29–32 were outside it. Averages ± se. are shown below for each set of plots. C and N: total content in oven dry wt.

Plot	pH	C %	N %	C/N
1	7.25	1.26	0.098	12.93
3	7.31	0.56	0.051	10.84
4	7.40	0.49	0.047	10.49
6	6.43	4.28	0.302	14.16
7	6.51	4.72	0.400	11.81
8	7.14	2.28	0.189	12.06
9	7.33	1.79	0.163	10.94
10	7.40	0.95	0.076	12.42
11	8.64	0.03	0.004	7.63
12	8.55	0.05	0.006	7.62
13	8.25	0.03	0.005	5.19
14	8.14	0.02	0.004	4.74
15	7.92	0.02	0.004	4.36
16	7.87	0.06	0.007	7.57
17	8.52	0.03	0.005	5.47
18	8.15	0.03	0.004	6.25
19	7.83	0.03	0.006	5.82
20	8.62	0.03	0.005	6.00
21	8.39	0.02	0.004	3.81
22	6.84	0.27	0.028	9.57
23	7.07	0.24	0.025	9.64
29	8.95	0.01	0.001	8.33
30	9.39	0.03	0.003	8.67
31	7.59	0.08	0.009	9.01
32	7.73	0.19	0.019	10.05
Average:				
1–10 & 23	7.09 ± 0.12	1.84 ± 0.55	0.150 ± 0.043	11.7± 0.46
11–22, 29–32	8.24 ± 0.15	0.05 ± 0.02	0.007 ± 0.002	6.88±0.48

nunculus acris, and *Taraxacum* sp. became firmly established in the wake of the gull invasion. Among latecomers into the developing plant community in the last 15 years were a hemiparasitic species, *Euphrasia frigida,* and an orchid, *Platanthera hyperborea.* The recent invasion of shrubs to the island (Table 3) is also of interest. The three *Salix* species that occur, all wind dispersed, reached the island in 1995–1999.

PERMANENT PLOT STUDY

Density of gull nests

Gull nests were found at 9 of the 25 permanent plots from 2003 (Fig. 6). Most of the plots with nests were within the gull colony on the southern part of the island (plots 1–10) or at its expanding fringe (plot 23) (Fig. 2). In 2006 a nest was also encountered at plot 16 that was outside the main gull colony. A few scattered nests of the great black-backed gull have been on that part of the island and out to the northern spit since 1974. At plot 7 within the gull colony, 1–2 fulmar nests were found in 2003–2008 and they were included with the gull nests.

A total of 27–50 nests were found at the plots in the different years, with a low in 2003 and a high in 2008. The average number was 3.0–5.6 nests 1000 m^{-2} in a year and 4.1 nests 1000 m^{-2} over the whole period, by plots where they were encountered. The highest nest density throughout the period was at plots 9 and 10 (Fig. 6) that were at the fringe of the gull colony when they were set up. In the older part of the colony (plots 1–7), nest density was on the other hand lower.

Soil

A considerable difference was found in soil pH, C and N between plots in 2008. The pH was determined in the range of 6.4–9.4, C content 0.01–4.72%, N content 0.001–0.400 and C/N ratio 4.5–14.2 (Table 5). The soil was poorly developed

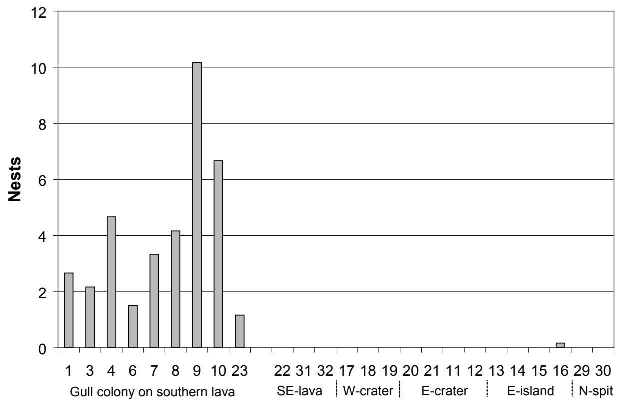

Figure 6. Average number of gull nests counted at permanent plots in 2003–2008. Nests were counted in a 1000 m^2 circle area around each plot. Plots are grouped according to location, from the gull colony on the southern lava, south eastern lava, area around the western crater, eastern crater, eastern part of the island to the northern spit, see also Fig. 2.

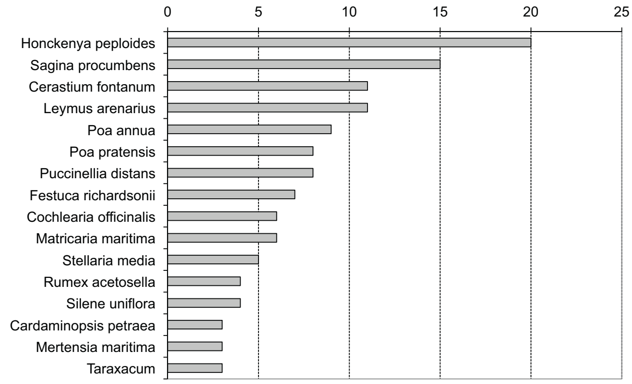

Figure 7. Relative frequency of vascular species in the 25 permanent plots in Surtsey in 2008. Species occurring in ≥ 2 plots are shown, other species occurring were *Rumex acetosa, Agrostis stolonifera, A. capillaris, Armeria maritima, Empetrum nigrum, Juncus alpinus* and *Montia fontana.*

in the barrens outside the gull colony and had a very low C and N contents, and C/N ratio and a relatively high pH (Table 5). In this area the soil was poorest (C < 0,02%) in plots 14, 15, 21 and 23, which all had a very sparse cover of *H. peploides* on coarse sand substrate. Soil from plots within the gull colony had distinctly lower pH and higher C and N contents and C/N-ratio (Table 5). In that area the soil from plots 6 and 7 was highest in C and N content and had the lowest pH. Both plots were on sheet lava and had dense grass cover and root mats. In plots 1–4, which were also in the centre of the gull colony, the soil had, on the other hand, higher pH and a lower C and N contents although their vegetation cover and biomass was comparable. These plots were in an area of sand-filled lava with high content of coarse ash in the upper soil.

Species richness and plant cover

Twenty-three vascular plant species were recorded within the permanent plots in 2008. The most frequent species were *H. peoploides, S. procumbens, Cerastium fontanum* and *L. arenarius*, all found in over 10 plots (Fig. 7). There was a great difference between plots as species richness varied from 1 to 16 (Fig. 8). In the barrens outsite the gull colony area 1–7 species were found per plot. There species richness was highest in plots 18 and 19, by the western crater (Fig. 2, 8), where species like *Armeria maritima, Cardaminopsis petraea, Rumex acetosella* and *Silene uniflora* had spread during the study period. The poorest plots (17 and 21) of the barrens still contained only one species in 2008. They were covered in tephra sand and had a very sparse cover of *H. peploides*. Within the gull colony area (plots 1–10, 23) species richness was relatively high by comparison, or 4–16 species per plot. In plots (1–6) in the centre of the colony species richness had declined in the last few years as their vegetation had become very dense. In plots (7–10, 23) along the edge of the colony, species richness had on the other hand increased. Species richness was highest in plot 10 (Fig. 8), which had a mixture of rough lava surfaces and sandy depressions within it, creating more diverse conditions than generally found in the other plots.

There was almost a two hundred-fold difference in plant cover between plots with the lowest and highest cover in 2008, as the cover range was 0.6–116% (Fig. 9). Development of cover in plots in the barren areas was very limited and in most of them it remained extremely low. In all the plots cover was less 30% in 2008, but the average cover was 7%. In the barrens cover was highest in plots (29 and 30) on the northern spit that had large patches *H. peploides*. In the two plots (31 and 32) set up in the block lava on the eastern part of the island in 2008, vascular plants were very scarce. There *Stereocaulon* lichens and *Racomitrium* mosses were most prominent and made up the cover (Fig. 9). In plots within the gull colony the average cov-

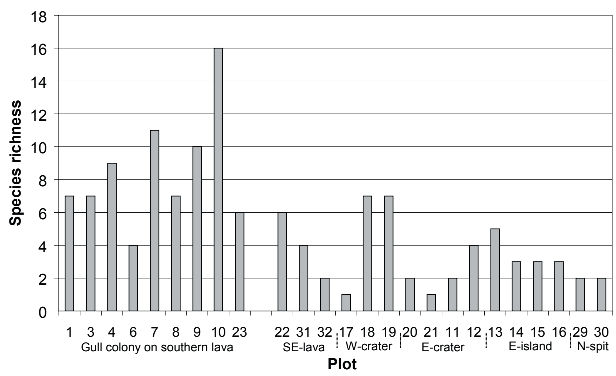

Figure 8. Species richness of vascular plants in permanent plots in 2008.

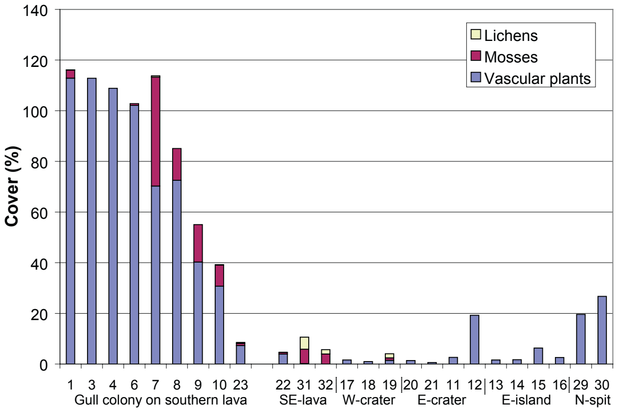

Figure 9. Total cover of vascular species, mosses and lichens in permanent plots in 2008.

er had reached 83% in 2008. In plots (1–7) in the centre of the colony the cover had reached 100% or more while it was lower in plots (8–23) at the fringe where the vegetation development had not gone as far (Fig. 9).

Plant biomass

In 2007 plant biomass within the permanent plots ranged from 0.3 to 856 g m^{-2}. Biomass was very low in plots in the barren areas and a trend in its development was not observed during 1999–2007. The average biomass of the barrens was 10 g m^{-2} and 9 g m^{-2} in 1999 and 2007 respectively, for plots measured in both years. In 2007 biomass in these areas was highest in plots (29, 30) on the northern spit which reflected their relatively high cover (Fig. 9, 10). Plant biomass was high in plots within the gull colony and there was a steady increase from the first sampling in 1999 (Fig. 10). This reflected the development in plant cover (Fig. 9). In 1999 the average biomass in plots within in the colony was 146 g m^{-2} and it had risen to 401 g m^{-2} by 2007. The biomass was highest in plots 1–6 (Fig. 9) in the centre of the colony where lush grassland had de-

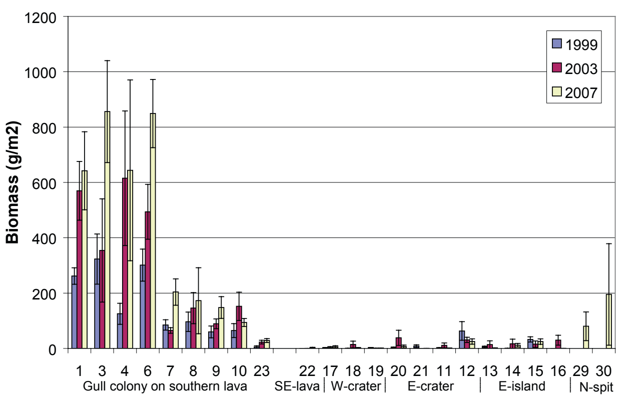

Figure 10. Average plant biomass (± s.e.) within permanent plots in 1999, 2003 and 2007. Living green and standing dead material, dry weight.

veloped. The biomass was markedly lower in plots near the fringe of the colony (Fig. 10).

Plant succession and communities – multivariate analysis

Ordination

The indirect ordination results revealed the relative vegetation changes which had occurred in the permanent plots since they were set up. On the first axis (eigenvalue 0.627) there was a separation of plots with sand as main substrate to the left of the axis and lava plots without sand on the right (Fig. 11). In the middle of the axis was plot 10 that had both types of substrate as previously described. The second axis (eigenvalue 0.371) was related to temporal vegetation change and indicated the main trends in the plant succession. At the bottom of the axis were the oldest bare lava plots representing the first stages of colonization whereas plots with more developed vegetation were higher up on the axis. Sitting highest on the second axis was plot 6 that had become an outlier in the last sampling years indicating a relatively abrupt change in vegetation composition.

The main cluster of plots to the left of the ordination diagram represented sand plots outside the gull colony. In these plots plant colonization and succession was very slow over the sampling period and limited changes in vegetation composition occurred. All the plots to the right of the cluster on the diagram were from the gull colony where significant changes occurred both on sand and lava substrate (Fig. 11). The difference and changes in species composition, plant cover and species richness of the plots in space and time explained the main trends further (Fig. 12, 13).

The key species in colonization of tephra sand areas, *Honckenya peploides*, was present in all plots in the main cluster, in most cases in a low abundance (Fig. 12, 16). With the influence of gulls in these areas *H. peploides* responded by increasing greatly in cover. This change was followed in plots 1–4 from 1990 and onward (Fig. 11,12). *H. peploides* continued increasing in cover until 2000 but declined thereafter with increased abundance of other species colonizing the plots. The first followers were the annuals *Poa annua* and *Stellaria media* along with *Cerastium fontanum*. These species also declined after 2002 when the perennial grasses *Poa pratensis* and *Leymus arenarius* became dominant in these plots (Fig. 12, 13, 18). *Matricaria matitima* increased in the gull colony after 2000 both on sand and lava. It had a rather scattered distribution and its abundance was relatively low within permanent plots (Fig. 7, 12). *Mertensia maritima*, a shore species and early colonizer of Surtsey, as *H. peploides* and *L. arenarius*, did not respond to the gull invasion.

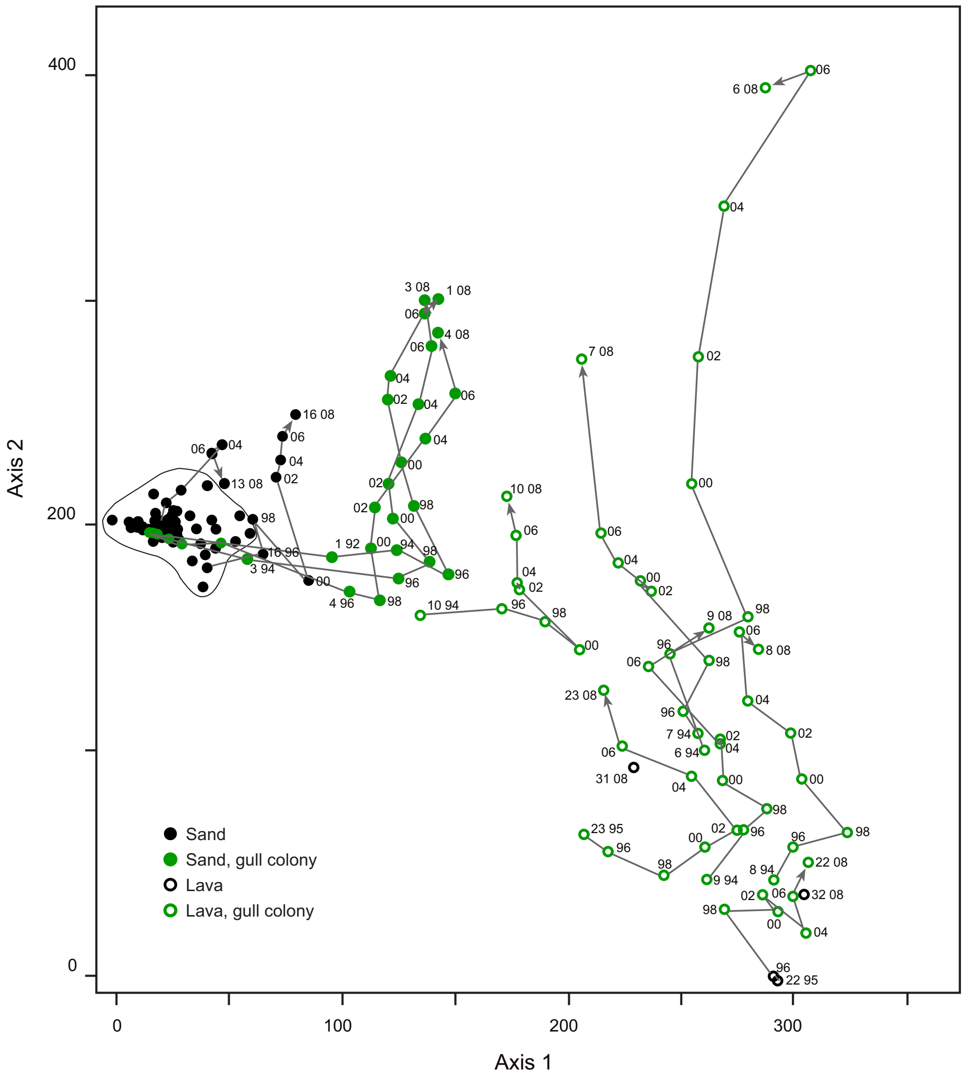

Figure 11. DECORANA-ordination results for permanent plots in the different sampling years. Lines connect the same plots and indicate relative vegetation changes and their direction between sampling years. The cluster to the left represents mainly plots 11–21 and 29–31 in the different years and plots 1, 3 and 4 at their earliest stages.

Its abundance has remained low and distribution limited (Fig. 7, 12). With the gradual rise in plant cover following the gull invasion, species richness in the sand plots increased to start with and peaked around 2000 (plots 1–4). After that it has declined with the closing of bare ground and dominance of the perennial grasses in recent years (Fig 13, 14).

On the lava within the gull colony area the key species of the first colonizing stages were different from the sand areas (Fig. 17). There *Sagina procumbens* was the first colonizer followed by *Puccinellia distans* and *Cochlearia officinalis* (Fig. 12). The species were able to grow on the sheet lava and did not require deep soil for root establishment. In the centre of the gull colony, where changes had gone furthest (plots 6–9), the abundance of these species declined with the colonization and increase of the grasses *P. pratensis* and *Festuca richardsonii* (Fig 12, 14). *P. annua, C. fontanum and Matricaria maritima* also colonized these plots (Fig. 12) and a few other species in low abundance. Plot 6 was positioned in the centre of the gull colony, at the site where the first small patch of vegetation was found in the breeding area in 1986. At the time a crust of moss (*Bryum argenteum)* with *S. procumbens* was found in the patch. When the plot was set up in 1994 there were 8 species recorded within it and *P. distans* and *P. annua* were dominant with 26% and 15% cover respectively. In that year *F. richardsonii* was found within the plot and was registered with the lowest cover of 0.02%. From that time the cover increased year by year by vegetative expansion and it formed a dense, continuous mat. In 2000 *F. richardsonii* had become dominant in the vegetation and gained 49% cover, and in 2006 the cover had reached 99% that the species maintained in 2008 (Fig. 12, 14, 19). A decline in abundance and a loss of other species occurred at the same time in the plot. The species richness peaked at 9 species in 1996–2000 but in 2008 it had declined to 4 species with the gradual overtaking by perennial grasses in the lava plots as in the sand plots. These changes were evident in the ordination results (Fig. 11–13.). Examples of species changes within selected plots occurring under the different substrate conditions and gull influence are given in Fig. 14.

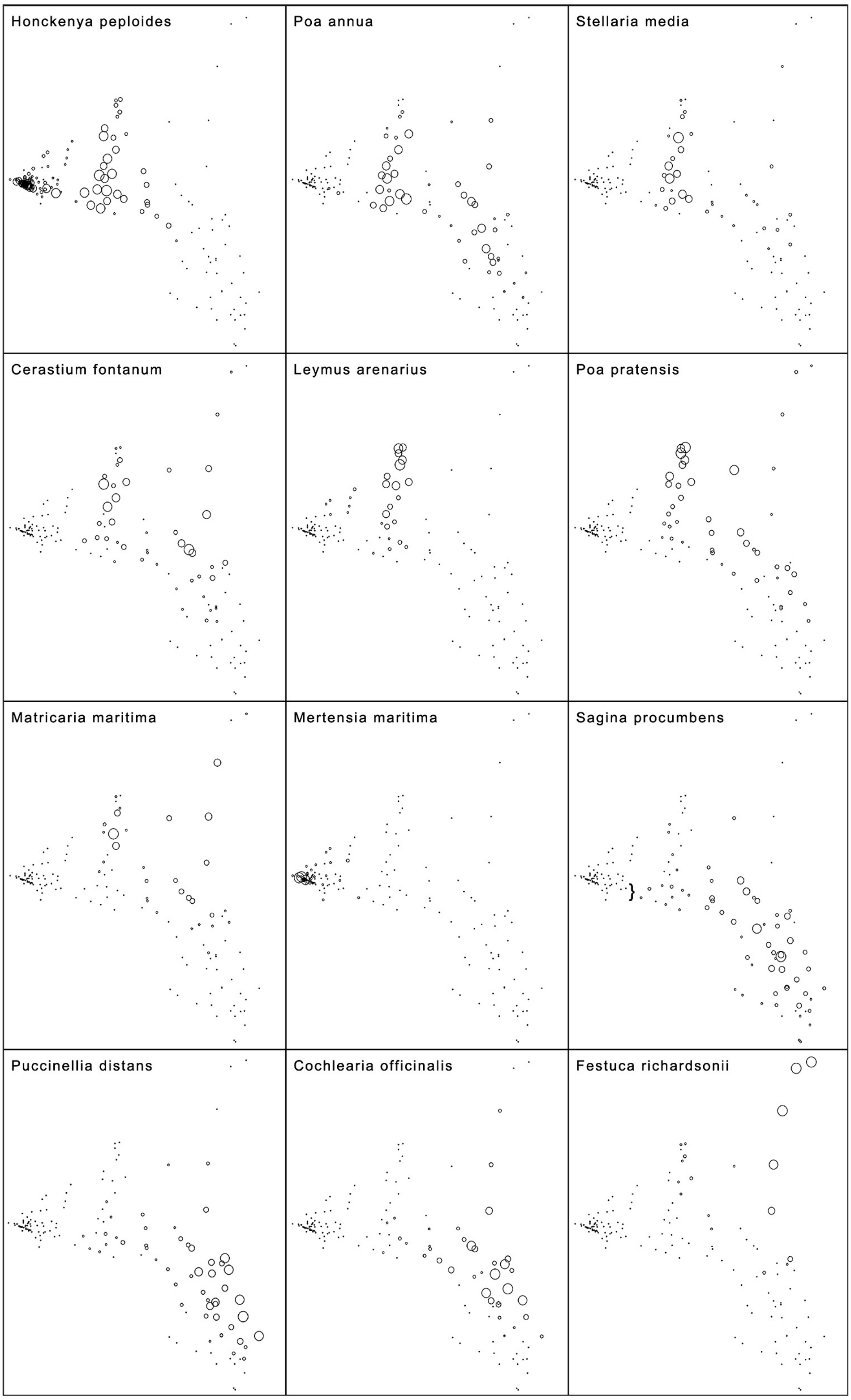

Figure 12. Relative abundance of selected species in permanent plots on Surtsey shown in relation to ordination results. Plots have the same position as shown in fig. 11; horizontal axis separated plots from sand and lava areas while main successional changes occurred along vertical axis. Bubble size reflects species cover, dots absence of species.

Classification

In a divisive polythetic classification (i.e. Twinspan) of the permanent plots data from 2008, four groups were formed (Fig. 15), and further classification is not shown. In the first division all lava plots and plots within or at the edge of the gull colony area (groups I & II) were separated from the sand plots outside the area (groups III & IV). *Poa pratensis* and *Puccinellia distans* were indicator species in the division and present in plots in groups I and II. *Honckenya peploides* was the most abundant species in plots in groups III and IV but was not confined to them. In the second division lava plots at an early succession stage (group I) separated from plots at a later stage and positioned in the centre of the gull colony area (group II). *P. distans* was the

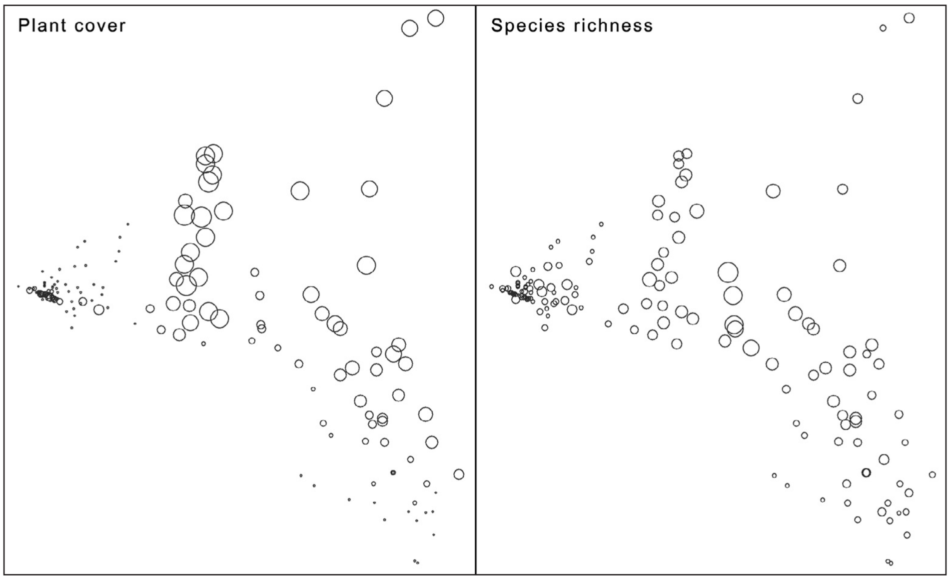

Figure 13. Relative plant cover and species richness in permanent plots on Surtsey shown in relation to ordination results. Plots have the same position as shown in fig. 11.

main indicator for group I but *Festuca richardsonii, Leymus arenarius* and *Poa pratensis* for group II. In the third division of plots outside the gull colony, a separation of plots occurred with the pioneer *H. peploides* as the only or dominant species (group III) and plots with more diverse vegetation (group IV). *Silene uniflora* was the indicator species of the division and it occurred in plots in group IV. *Cardaminopsis petraea*, *Rumex acetosella* and *Armeria maritima* were also among the species in the group.

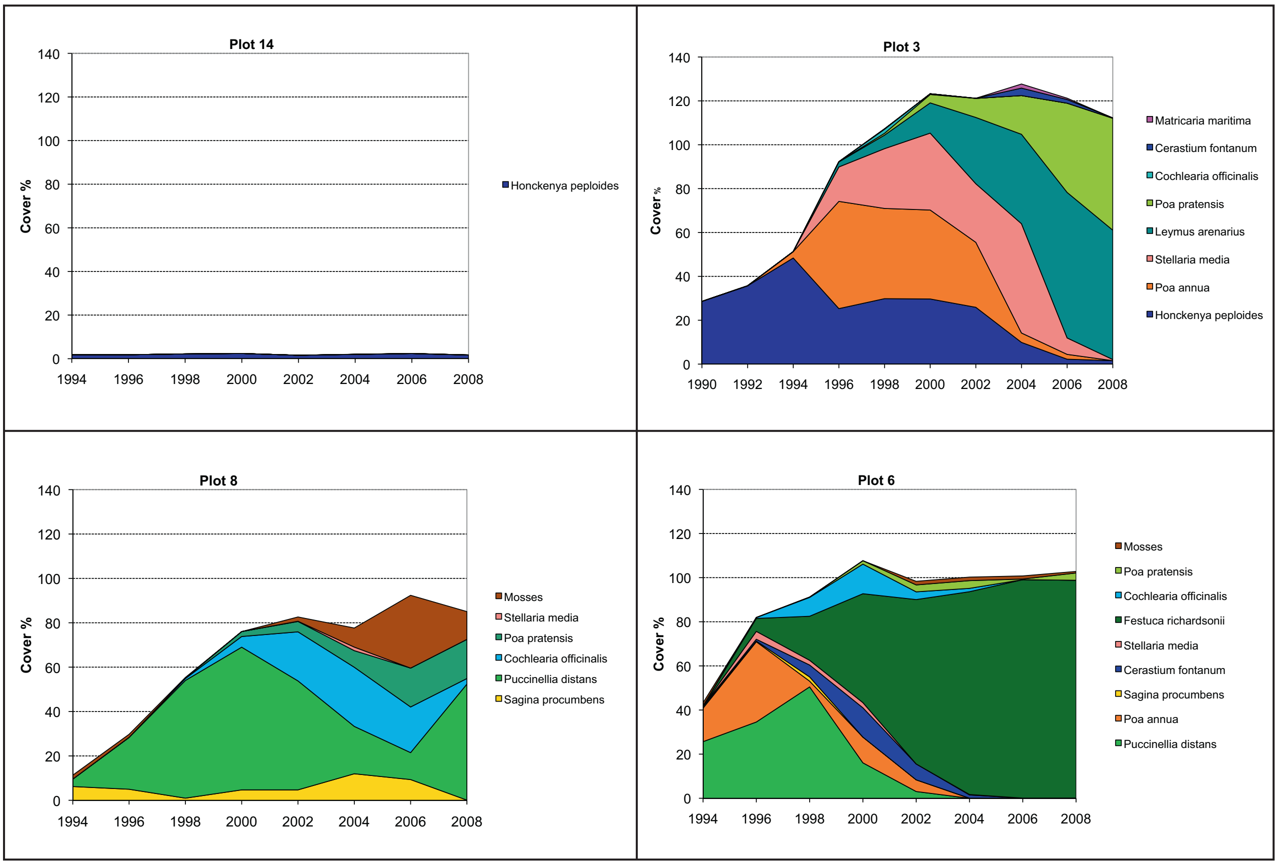

Figure 14. Examples of changes in species cover in selected permanent plots (14, 3, 8 and 6) over the study period 1990/1994–2008. Plots 14 and 3 were on sand-filled lava outside and inside the gull colony area respectively. Plot 8 and 6 were on lava pavements inside the gull colony are. Only species with > 1% cover area shown on the diagrams.

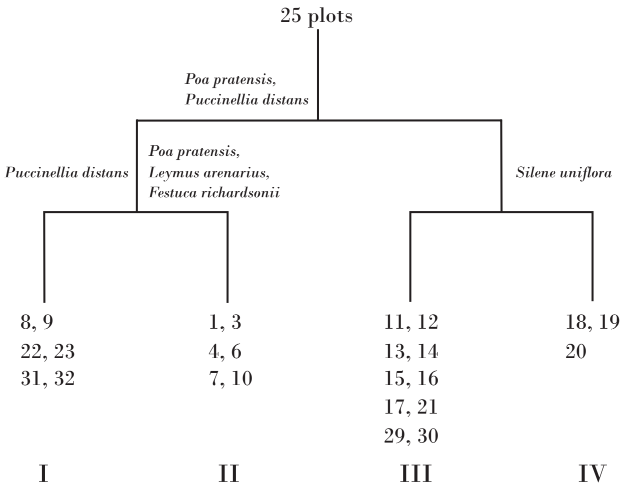

Figure 15. A TWINSPAN-classification of permanent plots based on vegetation composition in 2008. Species most decisive (indicators) of each division are shown.

DISCUSSION

Colonization

The second wave of invasion on Surtsey by vascular plant that followed the formation of a gull colony in 1985 (Magnússon & Magnússon 2000) was still in progress during this study period. In 2008 there were 63 plant species found alive on the island. Most of the species are common elsewhere on Vestmannaeyjar islands, the likely source of most species colonizing Surtsey (Fig. 1). The Icelandic mainland has every plant species that has been found on Surtsey. While Surtsey is the southernmost island of Iceland and in the pathway of migratory birds, there has been no indication of species colonizing the island from distant sources. The vascular flora of Heimaey, the largest of the Vestmannaeyjar islands (13,4 km^2), contains some 160 species (Eythor Einarsson, personal communication). Other islands, on the other hand, harbour only 2–30 species, corresponding to their area, which ranges from 0.01–0.46 km^2 (Fridriksson & Johnsen 1967). All the species recorded on the smaller islands with the exception of two (*Ranunculus repens* and *Saxifraga rivularis*), had colonized Surtsey by 2008 and most of them had formed viable populations. Two species (*Eleocharis quinqueflora* and *Gymnocarpium dryopteris*) present on Surtsey in 2008 have not been recorded elsewhere on the islands but are both found upon the mainland

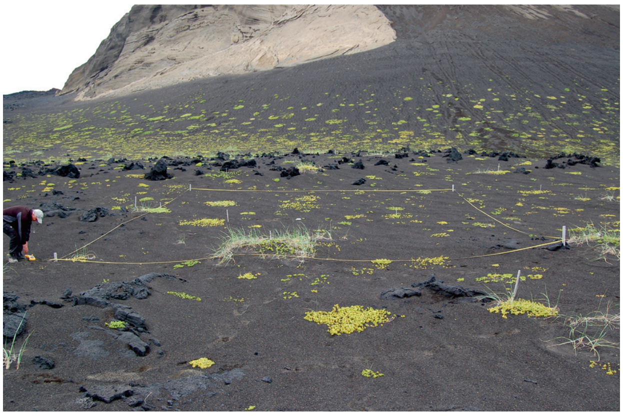

Fig. 16. *Honckenya/Leymus*-community on tephra sand in 2008, plot 14.

Fig. 18. *Leymus/Poa*-grassland on sand within gull colony in 2008, plot 3.

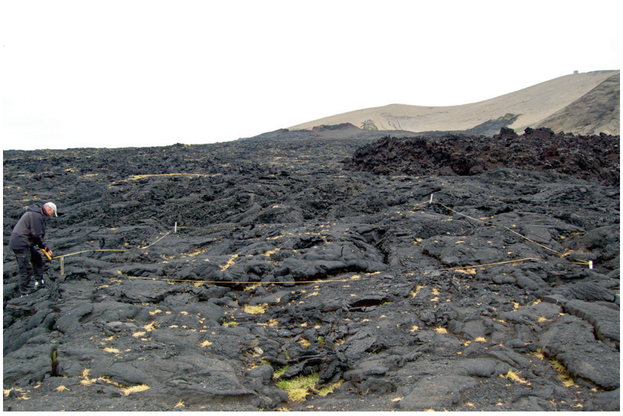

Fig. 17. *Puccinellia/ Sagina*-pioneer community on lava in 2008, plot 22.

Fig. 19. *Festuca*-grassland on lava within gull colony in 2008, plot 6.

(Kristinsson 1986). The number of species growing on Surtsey has long surpassed that of the smaller neighbouring islands. This may be explained by Surtsey's considerably larger size and its greater diversity of habitats compared to the other volcanic islands, which are much older and more eroded. It is likely that total species richness of Surtsey will continue increasing during the next few decades and peak at about 80–100 species, after which it is expected to decline with the continual erosion, shrinking of the island and increasing dominance by a few species.

Our study indicates that transport of birds has by far been the most important pathway of new vascular plant introductions to Surtsey. The lesser black-backed gull and the herring gull in particular appear to have played a major role as can be seen by the sudden rise in new colonization after their invasion of the island (Magnússon & Magnússon 2000, Magnússon & Ólafsson 2003). These species visit and feed more frequently in inland areas than the great black-backed gull does, which depends more on marine food (Götmark 1982). The lesser black-backed gull and the herring gull are therefore more likely to carry seeds. Dispersal of seeds by gulls and other birds to islands and other distant areas has been reported in several other studies (Gilham 1956, Morton & Hogg 1989, Nogales *et al.* 2001, Ellis 2005, Abe 2006) and it has also been demonstrated that predatory birds may act as secondary seed dispersers (Nogales *et al.* 2002). Snow buntings (*Plectrophenax nivalis*) have bred on Surtsey since 1996. The species feeds mostly on insects during summer when insects are abundant but on seeds during the rest of the year. The snow buntings may therefore have carried new plants to Surtsey (Fridriksson & Sigurdsson 1968). In addition, the graylag goose (*Anser anser*) bred on the island for the first time in 2002 and may be in a position to import new species. Ravens (*Corvus corax*) have frequented Surtsey from the early years and may have dispersed seeds of upland species as well.

Other factors than increased visits by birds on Surtsey have probably also played part in maintaining the high rate of plant colonization and survival on the island in recent years. The gradual warming in Iceland in the last 10 years and relatively high precipitation (Björnsson *et al.* 2008) may have positively affected the continued colonization of Surtsey and ecosystem development. However, the improved nutrient conditions of soil on the island and expansion of vegetation in the gull colony has been of the greatest importance. In the colony, the platform with favourable growing conditions for new colonists has increased in area year by year. The fungal succession is also of interest here. Studies of the fungi of Surtsey and the colonizing vascular plants indicate developmental stages from non-dependent to facultative or dependency on arbuscular mycorrhizal fungi (AMF) in the early years (Greipsson & El-Mayas 2000) to the presence of ectomycorrhizal fungi in later years (Eyjólfsdóttir 2009). A development similar to that described during succession on Mount St. Helens (del Moral *et al.* 2005). The late establishment of *Salix* species on Surtsey may have been caused by the lack of ectomycorrhizal soil fungi in the earlier years. The same applies to the orchid, *Platanthera hyperborea,* found on the island for the first time in 2003. As discussed by Thornton (1997) the minute orchid seeds are very light and widely dispersed. The small seeds have no food reserve and require mycorrhizal fungi for germination and establishment. In 2001 *Euphrasia frigida,* the first hemiparasitic species, was found on Surtsey. It has spread in the grassland in the gull colony and established a viable population. The species is a facultative root hemiparasite and plants are known to connect to a variety of hosts, including grasses (Seel & Press 1993, Nyléhn & Totland 1999).

With a record of plant colonization on Surtsey extending over more than 40 years a clear pattern of dispersal routes and their relative importance in time has emerged (Fig. 5). It has similarities to the dispersal pattern obtained in long-term studies of the colonization of Krakatau after the explosion in 1883 (Whittaker et al. 1992, Thornton 1997). There dispersal by sea was important in the early years but then stabilized, as has been found on Surtsey. In addition, dispersal by animals on Krakatau got a later start than sea dispersal. This was attributed to lack of vegetation that attracted animals, which is similar to the experience from Surtsey. On both islands animal dispersal has continued. The main difference in the pattern is wind dispersal which was important from the beginning on Krakatau and has been the most effective of the three main dispersal routes. On Surtsey on the other hand wind dispersed species were scarce in the flora over the first 30 years but have been increasing from that time. This difference probably reflects the contrasting floras and climate of the two areas. In the cool sub-arctic climate of Iceland soil and ecosystem development is very slow in comparison to the tropical environment of Krakatau. Seeds of common wind dispersed species have probably landed on Surtsey throughout the history of the island. However, conditions for establishment were not favourable until after the gull invasion of the island. Wood & del Moral (1987) demonstrated in experiments in the early years of their research on Mount St. Helens that high-dispersal species had low tolerances on the barren substrates and apparently required site amelioration prior to establishment.

Density of gull nests and soil conditions

The distribution and density of gull nests were reflected in the soil and vegetation development on Surtsey. The overarching influence of gulls and other seabirds on environment within their breeding colonies has been emphasised (Sobey & Kenworthy 1979, Hogg & Morton 1983, Mizutani & Wada 1988, Ellis 2005). At their breeding sites the birds deposit faeces and regurgitate pellets, fish and marine invertebrates are spilled on the ground during feeding of chicks and corpses of birds that die within the colony decompose. Nest material may also be brought into the sites. The most significant of these in the soil enrichment and vegetation development are the faeces that have a relatively high content of nitrogen, phosphorus, potassium and minerals (Sobey & Kenworthy 1979), which are of great importance in primary succession.

We have not attempted to measure the nutrient input from the gulls into their breeding area on Surtsey but it is substantial as indicated by the vegetation development and biomass. Nutrient loading in freshwater habitats from water birds has been estimated for the Netherlands using excretion and food models (Hahn *et al.* 2007). A seasonal estimate of a family unit (parents and offspring) for the lesser black-backed gull and the herring gull was around 0.6 kg N season^{-1} and 0.12 kg P season^{-1}. If these values are used to estimate nutrient inputs in the gull colony area on Surtsey, they give about 25 kg N ha^{-1} and 5 kg P ha^{-1} in a season, based on the nest counts at the permanent plots in 2003–2008 (4 nests 1000 m^{-2} or 40 nests ha^{-1} on the average). Taking into account the variation in nesting density between plots during 2003–2008 (1–10 nests 1000 m^{-2}) the nutrient input would be estimated as 6–60 kg N ha^{-1} and 1.2–12 kg P ha^{-1}. This is a conservative estimate because a correction is not made for the great black-backed gull which is the largest of the gulls on Surtsey and a substantial part of the breeding population with the other two species (Petersen 2009).

The results of the soil sampling in the permanent plots in 2008 indicated that C and N content of soil within the gull colony area had increased from 1998 (Magnússon & Magnússon 2000). In the barrens outside the area the contents remained extremely low. In mature, freely drained grassland soils in Iceland organic carbon is commonly in the range of 5–15% (Helgason 1968). According to Arnalds (2004) the brown andosols (BA) of Iceland have a carbon content of 2–7% in the in the top 50 cm. The highest carbon values (4.3–4.7%) determined in Surtsey in 2008 are therefore approaching levels encountered in mature soils. The results from Surtsey show clearly the importance of nutrient input for the ecosystem development.The role of the gulls on Surtsey is in many ways comparable to that of the nitrogen-fixing *Lupinus lepidus* in the plant succession on Mount St. Helens following the eruption in 1980 (del Moral & Rozzell 2005, del Moral 2009).

Plant succession and community development

The substrate conditions of the sand and lava areas on Surtsey differed greatly (Fig. 16, 17). However, similarities can be seen in the succession. In the centre of the gull colony area where plant succession has gone furthers it was mainly ruderal species (Grime *et al.* 1988) that responded to the increased nutrient input to start with and gained high abundance in the vegetation. Examples of these were *Poa annua*, *Stellaria media*, *Sagina procumbens*, *Puccinellia distans* and *Cochlearia officinalis* (Fig. 12). At the fringe of the expanding colony this stage in the vegetation development is still represented on the island and will probably be for the next few decades. With further development the ruderal species however lost ground to more competitive species that responded more slowly to start with but have become dominant in the last few years. The most prominent of these are the perennial grasses *Leymus arenarius, Poa pratensis* and *Festuca richardsonii* that have become dominant in the grassland in the centre of the gull colony area (Fig. 18, 19). They have all formed mats of relatively dense canopy of leaves by extensive lateral spread above and below ground, a character of competitive species (Grime *et al.* 1988). Mixed in the grassland are forb species like *Cerastium fontanum* and *Matricaria maritima* that are more competitive and stress tolerant than the pioneer, ruderal species.

The plant biomass, in the densely vegetated grassland plots within the gull colony area in 2007 was very high (642–856 g m^{-2}, Fig 10). It had reached similar or higher levels than lowland grasslands in Iceland where plant biomass is commonly in the range of 100 – 300 g m^{-2} in autumn but may reach ~500 g m^{-2} in the productive *Deschampsia caespitosa*-grasslands (Magnússon & Magnússon 1990, Magnússon *et al.* 1999). Further substantial increases in plant biomass in the most densely vegetated plots on Surtsey are not expected to continue as the dominant grasses have reached full cover.

The vegetation within the gull colony of Surtsey is in floristic composition and species dominance becoming more and more similar to that of the neighbouring islands (Fig. 1). On the other islands lava and sand areas along with their habitats and flora no longer exist. Most of the bedrock consists of palagonite tuff and remains of craters overgrown with vegetation. Seabirds are very abundant on the islands. Puffin (*Fratercula arctica*) is most numerous and nests in the grassland on top of the islands while guillemots, kittiwakes and fulmars inhabit the cliffs. On the islands Fridriksson & Johnsen

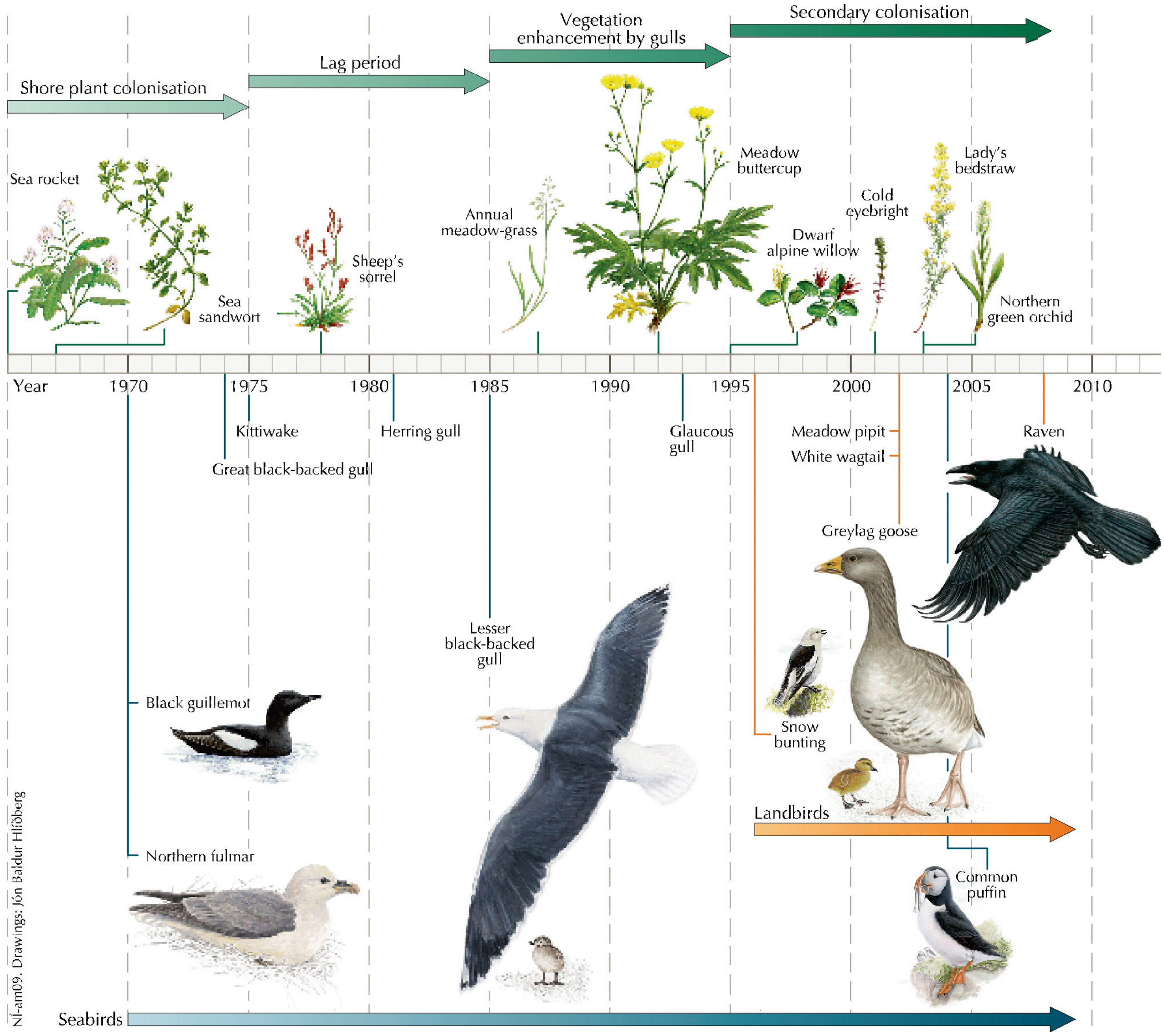

Figure 20. Main steps in species colonisation and ecosystem development of plant communities and birdlife on Surtsey. A large increase in the number of breeding seagulls on the island following 1985 improved soil nutrient status and facilitated dispersal of new plant species to the island. This was followed by enhanced development of vegetation and invertebrate communities, enabling land birds to settle on the island ten years later. Diagram made by Anette Th. Meier; drawings of plants and birds by Jón Baldur Hlídberg.

(1966) described three main plant communities: a) The puffin colony vegetation with *Festuca rubra (= richardsonii)* as the dominant species; b) Dry meadow land vegetation with *F. rubra* and *Poa pratensis* as dominants; c) The coastal cliff vegetation with *Puccinellia maritima* and *Cochlearia officinalis* as the most predominant. In general the vegetation of the larger islands was dominated by grasses, especially *F. rubra*. The vegetation development on Surtsey in recent years indicates very clearly a formation of a grassland community within the gull colony. The key players are the same species as on the neighbouring islands and so are most of the associated species.

Ecosystem development

The colonization and ecosystem development of terrestrial biota on Surtsey has been followed for 45 years (Fridriksson 1975, 2005, Magnússon & Ólafsson 2003, Jakobsson *et al.* 2007). Throughout the period new colonizers have been discovered on the island. The simple ecosystem of the early years has become more complex with the formation of communities, food webs and species interactions. The different studies of recent years indicate that the island is still going through a colonization phase that will prevail for the next few decades. This is evident for the vascular plants, lichens (Kristinsson & Heidmarsson 2009), fungi (Eyjólfsdóttir 2009), invertebrates (Ólafsson & Ingimarsdóttir 2009) and birds (Petersen 2009). Surtsey has shed a light on the formation of the neighbouring volcanic islands and their fate caused by oceanic erosion. On Surtsey we are also witnessing how they were colonized and the rise and fall of their ecosystem.

The initial colonization of shore plants on Surtsey during the first decade was followed by a lag period (Fig. 3) during which few new species colonized the island and survival was low. Further development was limited by infertility of the young soil and low rate of dispersal and colonization. With the large gull invasion of the island starting in 1985, the barrier to succession was breached and the development lepted forward. From that time forward, the gulls have been the driving force behind the changes and will probably continue to be for the near future. The gull case from Surtsey is a good example of the effects marine birds can have on terrestrial ecosystems (Ellis 2005, Ellis *et al.* 2006) and the varied roles birds can play in ecological functions (Sekercioglu 2006). On Surtsey the most important functions have been nutrient input from sea to land and seed dispersal. In the stepwise colonization and ecosystem development of Surtsey the initial importance of the shore plants should not be downplayed. They were the pioneers that later attracted the birds to breed upon the island. We see the main periods and most important steps in the development as follows (Fig. 20, 21):

- **1965–1974. Shore plant colonization:** Shore plants invade the northern shore and expand onto the sand-filled lava on the eastern part of the island. *Honckenya peploides* is most successful, forms small patches and starts producing seeds. The first pair of great black-backed gulls (GBBG) breeds on the island towards the end of the period and uses *H. peploides* plants as the main nesting material.
- **1975–1984. Lag period:** Vascular plant invasion slows, survival of colonizers is poor. Further establishment and expansion of shore plants, mainly *H. peploides* and *Leymus arenarius.* Gradual increase in nesting gulls (GBBG), nest and seek shelter in developing patches of shore plants and enhance their growth. First pair of herring gulls (HG) breeds on the island.
- **1985–1994. Gull invasion and vegetation enhancement:** The lesser black-backed gull (LBBG) invades the island. A dense gull colony is formed on the barren southern lava. The moss *Racomitrium* is the main nest material as nest material is scarce. Rapid increase in gull population with over 100 breeding pairs of LBBG, HG and GBBG at the end of the period. Gull invasion is followed by a great increase in new plant colonizers that are mainly dispersed by the gulls to the island. Arbuscular mycorrhizal fungi (AMF) are found, colonizing plant species are non-dependent, facultative or dependent on AMF. A great increase in cover of established species and fast colonization and spread of ruderal species, e.g. *Poa annua, Stellaria media* and *Sagina procumbens,* within the gull colony where the first extensive patches of vegetation are formed. Vegetated area on southern lava covers 3 ha at the end of the period.
- **1995–2008: Secondary plant colonization and establishment of land birds:** Continued colonization of new plant species and expansion of vegetation driven by the gulls, while several wind dispersed species also colonize the island. Development of a forb-rich grassland with *Poa pratensis*, *Festuca richardsonii* and *L. arenarius* as dominants. Vegetated area on southern lava occupies about 10 ha at the end of the period. Marked increase in soil organic matter and plant biomass within the gull colony. Willows establish on the island, as do a hemiparasitic species (*Euphrasia frigida)* and the first orchid (*Platanthera hyperborea*). Several ectomycorrhizal fungi are found in association with willows. Increase in number of invertebrate species

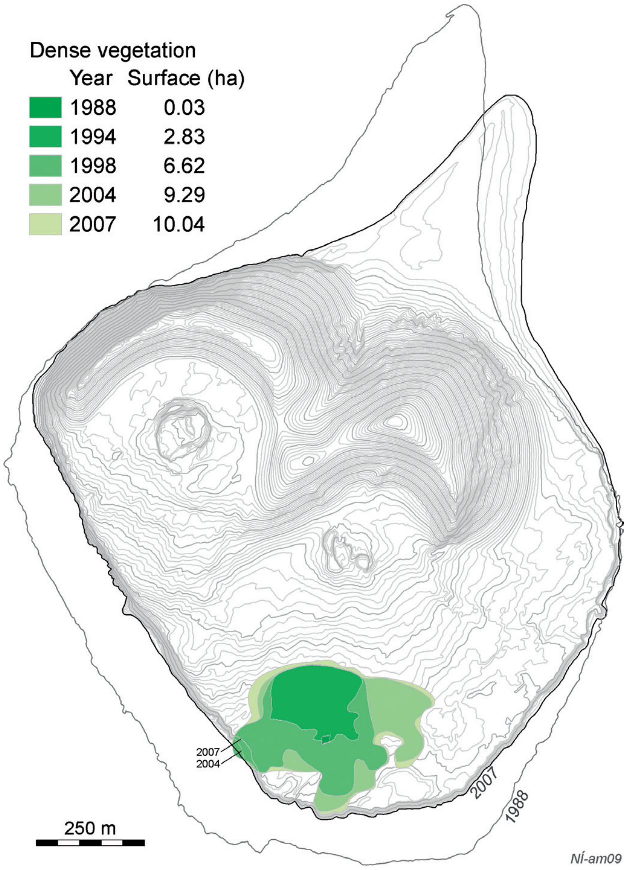

Figure 21. Expansion of dense vegetation within gull colony on Surtsey during 1988–2007. Approximation from aerial photographs, drawn by Anette Th. Meier. Note erosion of the island over the period.

and abundance on the island. Snow bunting, the first land bird species, starts breeding on the island, followed by the white wagtail and the meadow pipit, all passerine species that feed their young on insects. Greylag geese start nesting, grazing on the grassland in the gull colony. The first pairs of puffins start breeding in the cliffs. Increase in breeding gulls and expansion of colony. Ravens breed on the island at the end of the period. This omnivorous bird and a top predator, feeds its chicks mainly on eggs and the young of fulmars, gulls and kittiwakes.

We predict that during the next few decades the development on Surtsey will continue along these lines, with an increase in species richness of plants and birds, though at a slower rate. Expansion of vegetated areas will continue with associated soil development, invertebrate- and bird-life. The puffin is the most numerous and characteristic birds of the Vestmannaeyjar islands where it breeds in great numbers in the grasslands upon the islands. In the grasslands it acts as an ecosystem engineer (Sekercioglu 2006) with its burrowing activity and transfer of nutrients from sea to land. The puffin has recently started breeding in hollows and cracks in the cliffs of Surtsey. It is still confined to the cliffs but prospecting burrows have been found in the developing grassland. We expect the puffin to start breeding in the grassland within two decades and become a key species in further ecosystem development. In the longer run the erosion of the island, with a loss of habitats and encroachment of vegetation will lead to a decline in overall species richness of plants and animals and the ecosystem will become similar to that of the neighbouring islands. *Cakile arctica* was the first plant to colonize the shores of Surtsey in 1965. Of the established plant populations on the island it might also become the first victim of extinction with the disappearance of the northern lowland spit.

ACKNOWLEDGEMENTS

The Surtsey Research Society has provided logistic support for the study and transport to the island was carried out by the Icelandic Coastguard. The initiation of the project was funded by the Icelandic Research Council. Toyota Iceland supported biological research on Surtsey in 2007 and 2008. Anette Th. Meier, Sigurdur K. Gudjohnsen and Olga Kolbrún Vilmundardóttir made diagrams and maps, drawings of birds and animals were made by Jón Baldur Hlídberg. Roger del Moral and Bjarni D. Sigurdsson made valuable comments and corrections on the manuscript.

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Appendix 1. Record of vascular plant species found on Surtsey during 1965–2008 (65–08). Probable route of dispersal (D) is shown in third column. S: sea, B, b: birds, W, w: wind; capital letter denotes that species is adapted to the dispersal, but lower case that the dispersal route was most probable.

	Species	D
1	*Cakile arctica*	S
2	*Leymus arenarius*	S
3	*Honkenya peploides*	S
4	*Mertensia maritima*	S
5	*Cochlearia officinalis*	B
6	*Stellaria media*	b
7	*Cystopteris fragilis*	W
8	*Angelica archangelica*	S
9	*Carex maritima*	b
10	*Puccinellia distans*	b
11	*Matricaria maritima*	b
12	*Festuca richardsonii*	b
13	*Cerastium fontanum*	b
14	*Equisetum arvense*	W
15	*Silene uniflora*	b
16	*Juncus arcticus*	b
17	*Poa pratensis*	b
18	*Sagina procumbens*	b
19	*Atriplex glabriuscula*	S
20	*Rumex acetosella*	b
21	*Cardaminopsis petraea*	b
22	*Armeria maritima*	b
23	*Poa annua*	b
24	*Agrostis stolonifera*	b
25	*Alchemilla vulgaris*	b
26	*Epilobium palustre*	W
27	*Capsella bursa-pastoris*	b
28	*Luzula multiflora*	b
29	*Taraxacum*	W
30	*Rumex acetosa*	b
31	*Polygonum aviculare*	b
32	*Agrostis capillaris*	b
33	*Alopecurus geniculatus*	b
34	*Ranunculus acris*	b
35	*Deschampsia beringensis*	b
36	*Empetrum nigrum*	B
37	*Agrostis vinealis*	b
38	*Eleocharis quinqueflora*	b
39	*Phleum pratense*	b
40	*Montia fontana*	b
41	*Poa glauca*	b
42	*Juncus alpinus*	b
43	*Salix herbacea*	W
44	*Galium normanii*	b
45	*Potentilla anserina*	b
46	*Anthoxanthum odoratum*	b
47	*Leontodon autumnalis*	b
48	*Rumex longifolius*	b
49	*Polypodium vulgare*	W
50	*Luzula spicata*	b
51	*Myosotis arvensis*	B
52	*Salix phylicifolia*	W
53	*Oxyria digyna*	b
54	*Salix lanata*	W
55	*Euphrasia frigida*	b
56	*Plantago maritima*	b
57	*Platanthera hyperborea*	w
58	*Galium verum*	b
59	*Plantago lanceolata*	b
60	*Thymus praecox*	b
61	*Saxifraga caespitosa*	b
62	*Rhodiola rosea*	b
63	*Festuca vivipara*	b
64	*Atriplex sp.*	b
65	*Achillea millefolium*	b
66	*Alopecurus pratensis*	b
67	*Calamogrostis stricta*	b
68	*Gymnocarpium dryopteris*	W
69	*Epilobium collinum*	W