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**Plant colonization, succession and ecosystem development on Surtsey
with reference to neighbouring islands**

B. Magnússon¹, S. H. Magnússon¹, E. Ólafsson¹ and B.D. Sigurdsson²

[1]{Icelandic Institute of Natural History, Urriðahóltsstræti 6-8, P.O. Box 125, 220 Garðabær, Iceland}

[2]{Agricultural University of Iceland, Hvanneyri, 311 Borgarnes, Iceland}

Correspondence to: B. Magnússon (borgthor@ni.is)

1 **Abstract**

2 Plant colonization and succession on Surtsey volcanic island, formed in 1963, have been closely
3 followed. In 2013, a total of 69 vascular plant species had been discovered on the island; of these
4 59 were present and 39 had established viable populations. Surtsey had more than twice the
5 species of any of the comparable neighbouring islands and all their common species had
6 established on Surtsey. The first colonizers were dispersed by sea, but after 1985 bird-dispersal
7 became the principal pathway with the formation of a seagull colony on the island and
8 consequent site amelioration. This allowed wind-dispersed species to establish after 1990. Since
9 2007 there has been a net loss of species on the island. A study of plant succession, soil
10 formation and invertebrate communities in permanent plots on Surtsey and on two older
11 neighbouring islands (plants and soil) has revealed that seabirds, through their transfer of
12 nutrients from sea to land, are major drivers of development of these ecosystems. In the area
13 impacted by seagulls dense grassland swards have developed and plant cover, species richness,
14 diversity, plant biomass and soil carbon become significantly higher than in low-impact areas,
15 which remained relatively barren. A similar difference was found for the invertebrate fauna.
16 After 2000, the vegetation of the oldest part of the seagull colony became increasingly
17 dominated by long-lived, rhizomatous grasses (*Festuca*, *Poa*, *Leymus*) with a decline in species
18 richness and diversity. Old grasslands of the neighbouring islands Elliðaey (puffin colony, high
19 nutrient input) and Heimaey (no seabirds, low nutrient input) contrasted sharply. The puffin
20 grassland of Elliðaey was very dense and species-poor. It was dominated by *Festuca* and *Poa* and
21 very similar to the seagull grassland developing on Surtsey. The Heimaey grassland was
22 significantly higher in species richness and diversity, and had a more even cover of dominants
23 (*Festuca/Agrostis/Ranunculus*). We forecast that with continued erosion of Surtsey, loss of

1 habitats and increasing impact from seabirds a lush, species-poor grassland will develop and
2 persist, as on the old neighbouring islands.

3 **1 Introduction**

4 The frequent volcanic eruptions in Iceland cause regular disturbance and ecosystem regression
5 (Arnalds, 2013). In the more severe eruptions, existing biota and ecosystems are lost and new
6 surfaces created; thereafter, colonization and primary succession commence. The numerous lava
7 flows around Mt. Hekla in the south of the country have provided excellent opportunities for
8 chronosequence studies of plant colonization and community development (Bjarnason, 1991;
9 Cutler et al., 2008; Cutler, 2010), comparable to studies around active volcanoes in temperate
10 and tropical regions. The 1963 submarine eruption and birth of Surtsey island off the south coast
11 of Iceland was, however, a surprise. The volcanic origin of the Vestmannaeyjar islands was
12 known, but the previous eruptions in the system had occurred over 5.000 yrs ago (Sigurðsson
13 and Jakobsson, 2009). The Surtsey eruption, soon followed by the Heimaey eruption in 1973, set
14 a new focus on the islands and extensive geological and biological research was initiated
15 (Lindroth et al., 1973; Friðriksson, 1975; Friðriksson and Magnússon, 1992; Jakobsson et al.,
16 2007; Svavarsdóttir and Walker, 2009). Only a few volcanic islands have recently emerged,
17 including Anak Krakatau (1927) in Indonesia, Tulumán Island (1953) in New Guinea, Surtsey
18 (1963) and Motmot (1968) in Lake Wisdom on Long Island in New Guinea (Thornton, 2007).
19 Surtsey is a crucial example because of the unbroken record of monitoring and strict protection
20 of the island which has minimized human interference (Svavarsdóttir and Walker, 2009). The
21 studies on Surtsey are comparable to the long-term monitoring at Mount St. Helens volcano in
22 Washington, U.S.A., following the eruption of 1980 (Dale et al., 2005; del Moral, 2009; del
23 Moral and Magnússon, 2014). More recent eruptions around the world have evoked interest and

1 new studies of their ecological effects and recovery have commenced. These include those of
2 Kastatochi in the Aleutian Islands, which erupted in 2008 (DeGange et al. 2010).
3 The Vestmannaeyjar islands are very young on geological and evolutionary timescales. Aside
4 from their volcanic origin they have little in common with island complexes commonly cited in
5 island biogeography (Whittaker et al., 2008). However, the recent Surtsey and Heimaey
6 eruptions and their neighbouring islands with different degrees of erosion and ecosystem
7 development give a unique opportunity to understand the rise and fall of oceanic islands. The
8 rate of development on Surtsey has been faster than anticipated. From its birth the island has lost
9 half of its area due to heavy oceanic erosion (Jakobsson et al., 2007). In the colonization of the
10 island seagulls have come to play a key role in seed dispersal and nutrient transfer from sea to
11 land, essential for ecosystem development (Magnússon et al., 2009; Sigurdsson and Magnusson
12 2010; del Moral and Magnússon, 2014; Leblans et al., 2014). These islands harbour some of the
13 largest seabird colonies of the North Atlantic (Hilmarsson 2009; Hansen et al., 2011) which
14 greatly affect the vegetation and ecosystem structure. On Surtsey it has been possible, for the
15 first time, to follow the initial steps of colonization and primary succession of these subarctic
16 volcanic islands. As outlined by Svavarsdóttir and Walker (2009), the detailed studies carried out
17 on Surtsey are of particular value due to their long-term data, detailed demographic data,
18 information on species interactions and responses to nutrient inputs, opportunities to test of
19 island biogeography concepts, and more.

20 In this paper we describe plant colonization of Surtsey starting with the discovery of the first
21 plant in 1965, and report a permanent plot study initiated in 1990. This study is among the very
22 few to comprehensively follow the simultaneous development of vegetation, soil and
23 invertebrate communities. Then we present results from permanent plots newly established on

1 neighbouring islands. The general objectives of our studies are to follow plant colonization and
2 ecosystem development on Surtsey under different nutrient loads from seabirds and compare to
3 the biotas and ecosystems of the several thousand years older neighbouring islands.

4

5 **2 Methods**

6 **2.1 Study area**

7 Surtsey (63°18'N, 20°36'W) is in the Vestmannaeyjar archipelago which consists of 18 small
8 islands (from 0.001 – 13.4 km² in size). They are within a small area of 25 x 25 km and only 7–
9 35 km from the south coast of Iceland (Fig. 1). These islands form a young volcanic system with
10 the oldest rock formations dating from 40.000 years B.P.. During the Holocene, volcanism has
11 remained at a low frequency in the Vestmannaeyjar system (Sigurðsson and Jakobsson, 2009).
12 Surtsey, the southernmost of the islands, was formed during a volcanic eruption that lasted from
13 November 1963 to June 1967, when the island had reached an area of 2.7 km² and a height of
14 175 m a.s.l.. During the eruption large tephra cones were formed in explosive phases of the two
15 main central craters. The cones were gradually transformed into denser palagonite tuff
16 (Jakobsson et al., 2000). The southern part of Surtsey consists of lava flows from the craters.
17 Following the eruption the rough lava was gradually filled in by drifting tephra from the craters,
18 except for the south-easternmost part of the island where airborne dust has settled. The northern
19 part is a low spit formed by eroded coastal sediments deposited on the leeward site. The spit is
20 flooded by surf in extreme winter storms. Coastal erosion has taken a heavy toll of the island and
21 by 2012 it had been reduced by half, to an area of 1,3 km². The most extensive erosion has
22 occurred on the southern and south-western part where high seacliffs have been cut into the lava
23 shield and palagonite tuff (Jakobsson et al., 2007). Surtsey is still the second largest island after

1 Heimaey. Following Surtsey in size are Elliðaey (0.46 km²) and Bjarnarey (0.32 km²) to the
2 northeast and leeward of Heimaey. Erosion will probably leave Surtsey to resemble the
3 unprotected neighbouring islands of Geirfuglasker, Súlasker, Geldungur and Hellisey (0.02 –
4 0.13 km²) that also lie unsheltered in the open ocean (Fig. 1).

5 The climate of the Vestmannaeyjar area is mild and oceanic. At the Heimaey weather station, the
6 mean annual temperature during 1963–2012 was 5.1 °C and the mean annual precipitation 1599
7 mm (Icelandic Meteorological Office). Waters off the south coast of Iceland are productive and
8 rich in marine life (Astthorsson et al., 2007) and seabirds are particularly abundant (Hilmarsson,
9 2009). The Vestmannaeyjar islands are the home to large breeding populations of Atlantic
10 puffins (*Fratercula arctica*), northern fulmars (*Fulmarus glacialis*), manx shearwater (*Puffinus*
11 *puffinus*), storm petrels (*Hydrobates pelagicus*), Leach's petrels (*Oceanodroma leucorhoa*),
12 gannets (*Morus bassanus*), kittiwakes (*Rissa tridactyla*), common guillemots (*Uria aalge*),
13 razorbills (*Alca torda*) and black guillemots (*Cepphus grylle*); bird nomenclature follows British
14 Ornithologists' Union (BOU), 2013. The seabirds impact the vegetation with their nutrient
15 transfer from sea to land, burrowing, nest building and other activities. A few species of
16 heathland birds also breed on the islands but their density is low (Hilmarsson, 2009).

17 The vascular flora of the Vestmannaeyjar islands contains some 160 species and all but a few
18 occur on Heimaey. The other old islands harbour only 2–28 species, corresponding to their size.
19 The most diverse vegetation is also found on Heimaey, which has beach, heathland, herb slope,
20 dry meadow, seabird grassland and coastal cliff communities. On the other islands lush seabird
21 grasslands and cliff communities are the main vegetation types. The dominants of the grasslands
22 are the rhizomatous grasses *Festuca rubra* and *Poa pratensis*. Among common species of the

1 cliffs are *Cochlearia officinalis*, *Puccinellia capillaris* and *Armeria maritima* (Friðriksson and
2 Johnsen 1967; Friðriksson, 1975); plant nomenclature follows Kristinsson, 2008.

3 Heimaey has been impacted by human inhabitation and livestock grazing since the 9th century.
4 The larger surrounding islands and some of the smaller have also been grazed by sheep since
5 early times (Eyjólfsson, 2009).

6 **2.2 Plant colonization and survival on Surtsey**

7 Surtsey has been studied by biologists annually since 1964. During each visit all portions of the
8 island are thoroughly searched to update survival and colonization of vascular species. This
9 provides an unbroken and unparalleled record of plant colonization from 1965, when the first
10 plant was found on the island, to the present. Exact locations of first colonists are known, as are
11 their probable routes of dispersal, propagation and spread of survivors (Friðriksson, 1975, 2000;
12 Magnússon et al., 2009). Separate studies of lichen (Kristinsson and Heiðmarsson, 2009) and
13 bryophyte (Magnússon and Friðriksson 1974; Ingimundardóttir et al., 2014) colonization have
14 also been conducted.

15 **2.3 Study in permanent plots**

16 Plant succession has been studied in permanent plots on Surtsey since 1990 when the first plots
17 were established. The location of the plots was chosen subjectively with respect to substrate type
18 and influence of seagulls on vegetation development on the island. The first plots were set out in
19 the center of the developing gull colony, on bare and sandy lava. Following that plots were also
20 established under comparable substrate conditions on other parts of the island, in areas where
21 there were signs of plant colonization. Plots were not established in areas where no colonization
22 had occurred at the time, e.g. on the solid palagonite ridges (Magnússon et al., 1996; Magnússon

1 and Magnússon, 2000). The plots are sampled in alternate years. A few plots have been
2 abandoned and new ones established due to loss to erosion or revision of methods (see
3 Magnússon et al., 2009). In 2012 there were 25 plots operational on the island (Fig. 2).
4 In 2013 the study was extended to two of the older volcanic islands of the archipelago, Elliðaey
5 and Heimaey (Fig. 1). The aim was to investigate old grassland communities of the islands under
6 different nutrient inputs from seabirds as these grasslands are indicative of the future
7 development on Surtsey. Two accessible islands and areas with limited human disturbance were
8 selected. The number of plots was determined by the available time and manpower and was
9 considered as an absolute minimum for a comparison to the Surtsey plots. Permanent plots,
10 identical to the Surtsey plots, were established on each island and sampled in the same way in the
11 middle of July. The four Elliðaey plots were set up within puffin colonies with high nutrient
12 inputs from sea to land (Table 1), where soil depth was > 1 m on a south-facing palagonite tuff
13 slope (one plot) and north- or south-facing cinder crater slopes (three plots) dating from 5000–
14 6000 years ago (Sigurðsson and Jakobsson, 2009). Similarly, four plots were set up on Heimaey,
15 on west- (two plots) and north-facing (two plots) palagonite tuff slopes with > 1 m soil depth, in
16 an a small enclosed valley on the southern part of the island (Fig. 1). The eruption in which the
17 valley was created also dates from 5000–6000 years ago. Since the valley is not open out to the
18 ocean it has probably never been a seabird breeding site and thus it was not expected to be
19 impacted by high nutrient input from seabirds as are the Elliðaey plots (Table 1).

20 21 **2.4 Vegetation, soil and plant biomass**

22 The permanent plots are 10 x 10 m in size, and were sampled with line-transects (Magnússon et
23 al., 2009). Five parallel 10 m transects were laid across each plot, at 1, 3, 5, 7 and 9 m from their

1 edge. Plant cover was determined by line-intercept method, all vascular plants were recorded
2 separately for each metre along the line. Additional species within the plots not intercepted by
3 the lines were also recorded and given an intercept value of 1 cm, equal to 0.02% cover.

4 Soil was sampled within the Surtsey plots in 1998 and again in 2008 (Magnússon et al., 2009). In
5 the latter sampling, four random samples (7 cm dia x 10 cm depth) were taken in each plot and
6 mixed for a composite sample. In the laboratory the samples were sieved through a 2 mm mesh
7 for determination of pH, total organic carbon (C) and nitrogen (N), carried out by the Centre of
8 Chemical Analyses (Efnagreiningar Keldnaholti), ICETEC, Reykjavik, Iceland. Details are
9 further described in Magnússon et al. (2009). Soil samples of plots in Elliðaey and Heimaey
10 were sampled to 10 cm depth in three locations per plot. The samples were sieved through 2 mm,
11 ground to powder and total C and N analysed by dry combustion with an NC2100 C/N analyser
12 (Carlo Erba Instruments, Italy) at Univ. of Antwerp, Belgium. Only the C data from Surtsey
13 2008 and Elliðaey and Heimaey in 2013 is dealt with here.

14 Plant biomass has since 1999 been harvested from the Surtsey plots every fourth year
15 (Magnússon et al., 2009), the last sampling occurring in 2011. The sampling was destructive and
16 carried out in a 10 x 10 m area adjacent to each permanent plot. Four samples were harvested at
17 random coordinates, the vegetation was cut at ground level a long a 2 m line, using electric grass
18 clippers with a 7.5 or 9.5 cm wide cut. All vegetation was collected. The samples were dried at
19 60 °C to constant oven dry weight.

20 **2.5 Density of seabird nests**

21 Since 2003 density of seabird nests (mainly seagulls) around the permanent plots on Surtsey has
22 been determined annually. A 1000 m² circular plot with a centre in the middle of a permanent

1 plot was inspected and nest bowls occupied in the current season counted. The lesser black-
2 backed gull (*Larus fuscus*), great black-backed gull (*L. marinus*) and herring gull (*L. argentatus*)
3 breed in substantial numbers upon the island. A few fulmar nests (*Fulmarus glacialis*) have also
4 been encountered in the surveys and they were included (Magnússon et al., 2009). The plots on
5 Elliðaey were within dense breeding colonies of puffins (*Fratercula arctica*). Nesting density
6 was estimated according to methods of Hansen et al. (2011). The number of puffin burrows was
7 counted in four 4 x 4 m randomly placed subplots within or by each permanent vegetation plot.
8 Average burrow occupancy rate of 66% for Elliðaey in 2013 (Hansen, personal communication)
9 was used to calculate nesting density.

10 **2.6 Invertebrates on Surtsey**

11 Invertebrate studies started on Surtsey in 1965 and were continued annually until 1984. Sampling
12 was sporadic from 1985 to 2002 after which it recommenced and became an integral part of the
13 biological studies. Sampling included pitfall trapping, netting and direct picking for different
14 taxa. Most of the pitfall trapping was conducted in the permanent vegetation plots to relate the
15 invertebrate communities to the vegetation and plant succession directly. In this paper, we used
16 data of invertebrate catches in pitfall traps in the permanent plots on Surtsey from 2002 to 2008
17 (Ólafsson and Ingimarsdóttir, 2009).

18 **2.7 Data analysis**

19 Vegetation data (vascular plants only) sampled in the permanent plots in 2012 (Surtsey) and
20 2013 (Heimaey and Elliðaey) were analysed with detrended correspondence analysis (DCA;
21 indirect ordination) and two-way indicator species analysis (TWINSPAN; classification, Hill
22 1979a;b). The cover data were transformed (log+1) prior to analysis. In the ordination rare

1 species were downweighted. In the classification cut levels were set to 0, 0.05, 0.1, 0.2, 0.5, 1.0
2 and 1.5 after data inspection. The Shannon index of species diversity was calculated for all
3 plots. Multivariate analyses were conducted with PC-ORD 6 (McCune and Mefford, 2011). One
4 way ANOVA on log-transformed values was used to determine significance of parameters for
5 plots outside and inside the gull colony on Surtsey (JMP 6.0 package; SAS Inst., 2006). The
6 variables were seabird nesting density, plant cover, species richness, plant diversity, plant
7 biomass, soil carbon, invertebrate species richness, and invertebrate and Acari/Collembola
8 catches. The same test was used to compare these characteristics of the TWINSPAN vegetation
9 classes: plant cover, species richness, plant diversity, plant biomass and soil carbon.

10 **3. Results**

11 **3.1 Plant colonization on Surtsey**

12 The first species to colonize Surtsey in 1965 was the sea rocket (*Cakile maritima*), dispersed to
13 the island by sea currents. The most recent colonizer is a wind dispersed moonwort (*Botrychium*
14 *lunaria*) first found in 2011. The total number of plants that have established on the island at any
15 time is 69 species. In the 2013 expedition to the island 59 of these were found (Fig. 3), but only
16 39 species appeared to have viable populations (Appendix A), defined as a population that has
17 expanded or which occurs in at least five locations. The plant colonization curve for the island
18 over the first 50 years can be divided into four main periods (Fig. 3). The initial colonization of
19 plants occurred during the first decade. These were mainly shore plants (Fig. 4) resulting from
20 ocean dispersal and establishing on the infertile and sandy volcanic substrate of the island (e.g.
21 *Cakile maritima*, *Leymus arenarius*, *Honkenya peploides*, *Mertensia maritima*). During this
22 period the first bird-dispersed (*Cochlearia officinalis*) and wind-dispersed species (*Cystopteris*

1 *fragilis*) also colonized the island (Fig. 4). Most of the species were able to survive on the
2 pristine island and start propagation. In the second period, approx. 1975–1985, colonization
3 slowed and survival of newcomers was considerably lower than previously (Fig. 3). They were
4 less well adapted to the harsh conditions than the pioneers. Only two of the species (*Cerastium*
5 *fontanum* and *Rumex acetosella*), colonizing during this period, gained roothold and established.
6 In the third period, approx. 1986–2007, a second wave of plant colonization occurred and
7 survival of plants improved greatly. This was triggered by the establishment of a seagull
8 breeding colony on the southern part of the island. The colony, which soon grew to 200–300
9 breeding pairs, became the locus of plant colonization. The gulls not only improved the nutrient
10 status of the soil but also acted as agents of seed dispersal. Plants with higher nutrient demands
11 now started to flourish and expand (e.g. *Cochlearia officinalis*, *Stellaria media*, *Sagina*
12 *procumbens*, *Tripleurospermum maritimum*, *Cerastium fontanum*, *Festuca rubra*, *Poa pratensis*,
13 *P. annua*, *Ranunculus acris*). Several years into this period, there was a pronounced increase in
14 colonization of wind dispersed species (Fig. 4). The soil amelioration brought about by the gulls
15 opened a window for light-seeded (or sporophytic) species with limited seed reserves (e.g.
16 *Taraxacum spp.*, *Leontodon autumnalis*, *Salix herbacea*, *S. phyllicifolia*, *S. lanata*, *Platanthera*
17 *hyperborea*, *Botrychium lunaria*) to establish. In 2007 the number of species on the island
18 peaked at 64 (Fig. 3). In the last period, 2008–2013, Surtsey suffered a net loss of plant species.
19 Only one new colonizer was recorded but all the lost species were very rare.

20 **3.2 Effects of seagulls on development on Surtsey**

21 During 2003–2012 gull nests were encountered in ten of the permanent study plots, nine within
22 the main breeding area (Table 2). The total number of nests varied from 19–50. The average

1 number of nests in the ten year period was 3.9 within the breeding area. In plots outside it only
2 one nest was ever encountered, leading to an average of 0.01 (Table 2).

3 In 2012 there were 22 plant species recorded within the 25 permanent plots (Appendix A).

4 Species with the highest relative frequency were *Honkenya peploides*, *Sagina procumbens*,
5 *Leymus arenarius* and *Cerastium fontanum*, which occurred in over 50% of the plots (Fig. 5).

6 The most notable changes since 2008 were the increases of *Arabidopsis petraea* and *Silene*
7 *uniflora*, both of which established late but had reached a spreading phase. *L. arenarius* and *C.*
8 *fontanum* had also increased considerably. *Cochlearia officinalis* had lost ground in 2012 and
9 was only found in half of the plots it was recorded in in 2008 (Fig. 5). Its main distribution was
10 near the cliffs on the southern lava within the seabird colony where grass swards and competition
11 was increasing.

12 There was a great variation in the development of the plant cover, species richness and diversity
13 in the permanent plots in 2012. This was reflected in the plant biomass and carbon status of soil
14 (Table 2), from earlier sampling. Where breeding seabirds were absent or their impact low, the
15 vegetation remained poorly developed. Average plant cover of plots outside the seabird colony in
16 2012 was 7.1% (Table 2;), but most of the plots had < 5% cover. The cover was highest in the
17 two plots with well developed shore community on the northern spit (Fig. 2). Average species
18 richness of plots outside the gull colony was 4.4 (range 1–9). The most common species were
19 *Honkenya peploides*, *Sagina procumbens*, *Leymus arenarius*, *Cerastium fontanum*, *Arabidopsis*
20 *petraea*, *Poa annua* and *Silene uniflora*. *H. peploides* had a mean cover of 5.0% and was the
21 only species which had reached over 1% cover outside the gull colony (data not shown). In the
22 plots within the gull colony the average plant cover was 90.3% (Table 2). In four of the plots the
23 canopy had closed and layering of vegetation occurred. Average species richness of colony plots

1 was 7.7 (range 7–12) in 2012. The most common species of the gull colony were *Poa pratensis*,
2 *Festuca rubra*, *Cerastium fontanum*, *Honkenya peploides*, *Leymus arenarius*, *Sagina*
3 *procumbens*, *Tripleurospermum maritimum*, *Puccinellis capillaris*, *Stellaria media*, *Taraxacum*
4 spp., *Cochlearia officinalis* and *Poa annua*. It was *P. pratensis* and *F. rubra* that had gained the
5 highest mean cover of 33.3% and 16.9% respectively. Six other species had reached over 1%
6 mean cover within the seabird colony in 2012 (data not shown). Average plant species diversity
7 (Shannon) in plots outside the seabird colony in 2012 was 0.5 but 1.0 in plots within the colony
8 (Table 2).

9 In 2011, mean plant biomass in plots outside the gull colony was 47 g dwt m⁻². Biomass was
10 highest in the northern spit plots, 29 and 30, which had dense cover of *H. peploides*. Within the
11 colony, there was an average of 221 g dwt m⁻² (Table 2). The peak biomass was in plots with
12 dense grass swards of *L. arenarius* and *P. pratensis* (plots 1, 3 and 4). Topsoil in the permanent
13 plots outside the gull colony in 2008 had average total carbon of 0.05%, but 1.84% inside the
14 colony (Table 2).

15 The invertebrate communities determined from the pitfall traps in the gull colony during 2002–
16 2006 were richer in species and density than were the barren areas (Table 2). For the invertebrate
17 groups that were identified to the species level, there were 28.3 species found on the average
18 within the gull colony plots, while only half of that in the plots outside the colony (Table 2).
19 Total catches per day for these groups was, however, similar in the two areas (Table 2). Mites
20 (Acari) and springtails (Collembola), which were dominant in the catches of the pitfall traps
21 were treated separately and joined into one group (Table 2). They were, however, not identified
22 to a species level. In the sheer number of these animals there was a great and significant

1 difference between the two areas. In plots outside the gull colony the average catch was 20.3
2 animals per day which compares to 108.4 animals per day within the colony.

3 The gradual increase and expansion of dense vegetation of the gull colony has been monitored
4 using aerial photographs and satellite images taken regularly of the island. The first signs of
5 vegetation were visible on an aerial photo from 1988, approximately three years after the first
6 nesting of the gulls. At that time the area of the gull colony was only 0.03 ha in area. By 1998 it
7 had increased to 6.6 ha and in 2012 the area had reached 12.1 ha or over 9% of the island (Fig.
8 6).

9

10 **3.3 Comparison of vegetation development on Surtsey with neighbouring islands**

11 Multivariate classification and ordination were used to analyse resemblance of the young,
12 developing vegetation of Surtsey in 2012 to the older grasslands of Heimaey and Elliðaey islands
13 sampled in 2013. Four groups were formed by TWINSpan (Fig. 7). A comparison of the groups
14 showed their floristic, soils and density of seabird density differences (Table 3). The Heimaey
15 grassland (group I), which lacks seabirds, had a moderate vascular plant cover, but it was not
16 significantly different from the Elliðaey and Surtsey seabird plots (groups II and III; Table 3).
17 The Heimaey grassland had the largest species richness and diversity. The top 10 cm soil of the
18 Heimaey plots was relatively rich in carbon and similar to the Elliðaey and Surtsey seabird
19 grasslands (Table 3). In the species-rich Heimaey grassland there was an average of 18 species in
20 each plot (Table 3). The dominant species in the cover were *Festuca rubra* (20.8%), *Agrostis*
21 *capillaris* (16.3%), *Ranunculus acris* (11.5%) and *Anthoxanthum odoratum* (8.2%).

1 The dense seabird grassland of Elliðaey and Surtsey (group II) had the highest plant cover but
2 low species richness and diversity. The average C content of soil was highest in this group
3 (Table 3). On the average six species were found in the plots of group II (Table 3). Nesting
4 density of puffins in the plots of Elliðaey was very high, 269 nests per 1000 m², which compares
5 to 5.1 gull nests per 1000 m² in the Surtsey plots of the same group (Table 3). The Elliðaey
6 puffin grassland consisted of only three species, recorded in all plots and in significant quantity.
7 The predominant species of the sward was *Festuca rubra* (67.2%), followed by *Poa pratensis*
8 (18.4%) and the annual *Stellaria media* (4.7%) which was found on the excavated soil around the
9 puffin burrows. Three Surtsey plots of this group had a similar species composition to the
10 Elliðaey grassland and a relatively high or developing cover of *F. rubra* and *P. pratensis*.

11 The third Twinspan-group consisted of Surtsey plots from within or near the gull colony (Fig. 7).
12 The vegetation of these plots was in transition from barrens to grassland. The nesting density was
13 lower than in the Surtsey plots of group II, average plant cover was slightly lower, species
14 richness and diversity a little higher, but they did not differ significantly (Table 3). C
15 concentration of the soil was considerably lower than in plots of groups I and II, but it was
16 elevated from the plots of the Surtsey barrens in group IV, and the differences were significant
17 (Table 3). The dominant species in the plots in group III were *P. pratensis* and *L. arenarius* in
18 the sandy plots, but the lava plots were more variable with *P. capillaris*, *S. procumbens*, *P.*
19 *pratensis* and *F. rubra* as the most common species (data not shown).

20 The fourth Twinspan-group consisted of Surtsey plots which were located outside the gull
21 colony and in an early or static succession (Fig. 7). The plant cover of these plots was poorly
22 developed, species richness and diversity low and the soil was very poor in C (Table 3). These
23 plots were all on sand/tephra substrate, with the exception of plots 31 and 32 on block lava (Fig.

1 2). *H. peploides* was the characteristic species of this group with an average cover of 6.7%. All
2 other species of this group had < 0.3% average cover.

3 DCA ordination separated plots with dense grasslands, regardless of location, from poorly
4 developed and barren Surtsey plots on the first axis (eigenvalue 0.791, gradient final length
5 6.172). Main separation along the second axis (eigenvalue 0.453, gradient final length 4.077),
6 was between sandy and lava plots on Surtsey (Fig. 8). The Heimaey plots formed a dense and
7 distinct cluster of points on the left of the diagram, underlining the difference in vegetation
8 composition from the Elliðaey and Surtsey plots. The Elliðaey plots were also in a dense cluster,
9 as expected, but Surtsey lava plots (6 and 7) with the best developed *F. rubra*/*P. pratensis*
10 swards were also here (Figs. 9–10). Furthest to the right and at the top of the diagram were
11 Surtsey plots that were outside the gull colony and with poorly developed vegetation (Fig. 8). On
12 the right was a cluster of plots with mainly *H. peploides*, which develop into *P. pratensis*/*L.*
13 *arenarius* grassland under the impact of seabirds and increased nutrient inputs, as shown in
14 Surtsey plots 1, 3 and 4 (Fig. 9). At the top were barren lava plots with *Sagina procubens* and
15 *Puccinellia capillaris* as pioneers, which develop towards *F. rubra*/*P. pratensis* grassland under
16 increased nutrient inputs. The ordination showed that as the succession progressed, under the
17 influence of the seabirds, the vegetation of the sand and lava areas became more similar in
18 composition than at the pioneer stages (Fig. 8).

19 **4. Discussion**

20 **4.1 Plant colonization on Surtsey**

21 The record of plant colonization of Surtsey and the probable routes of dispersal revealed, show
22 how the main vectors of immigration change during the ecosystem development on the island.

23 Of the 69 plant species found on the island since 1965, about 75% have been dispersed by birds,

1 15% by wind and 10% by the sea. During the first years shore plants dispersed by the sea were
2 the main pioneers on the island. These plants had relatively large seeds, rich in reserves, enabling
3 them to establish on nutrient poor, sandy substrates. In the case of Surtsey the distance from the
4 source on the nearby islands and the mainland is only a few to tens of kilometers so the chances
5 of floating seeds ending upon the shores of Surtsey were high. New species dispersed by the sea
6 have not been found on Surtsey after 1977 (Fig. 4). However, two of the species (*Cakile* and
7 *Atriplex*), both annuals, did not gain a foothold on the island following their first colonization
8 (Magnússon et al., 2009).

9 The decrease in rate of plant colonizatón and relative stagnation during 1975–1985, was
10 probably caused by poor soil conditions and limited influx of seeds of new plants species. The
11 sudden increase of the seagulls and formation of their breeding colony in 1985 was followed by a
12 second wave of plant colonization continuing for the next 20 years. Most of the new plant
13 species were found within or at the edges of the colony, indicating that the seeds were to a large
14 extent dispersed to the island by the gulls and that nutrient additions from the birds had brought
15 about the necessary soil amelioration for the plants to establish and spread on the island.

16 Occurrence at the margins suggested that competition from established plants inhibit
17 establishment of new arrivals. Dispersal of seeds by gulls and other birds to islands is reported in
18 several studies (Nogales et al., 2001; Ellis, 2005; Abe, 2006; Aoyama et al., 2012). Most gulls
19 are omnivorous, opportunistic feeders that use a variety of foods including earthworms, berries
20 and cereal grain. The presence of seeds in their diets is reported for many species (Calvino-
21 Cancela and Martin-Herrero, 2009; Calvino-Cancela 2011). Of the three large seagull species
22 breeding on Surtsey, it is probably the lesser black-backed gull and the herring gull that have
23 been the main agents of seed dispersal to the island. Both species are known to visit and feed in

1 inland areas of the mainland, whereas the great black-backed gull is more confined to shore areas
2 and depends more on marine food (Götmark, 1982; Magnússon et al., 2009). Other bird species
3 may also have carried seed to Surtsey, e.g. snow buntings (*Plectrophenax nivalis*), greylag geese
4 (*Anser anser*) and ravens (*Corvus corax*) that have frequented the island and bred in recent years
5 (Magnússon et al., 2009; Petersen, 2009).

6 Wind-borne seeds and spores of various plant species must have rained over the island from its
7 birth. It was, however, not until after 1990 that we saw a considerable increase in colonization of
8 wind-dispersed species, a trend that still persists. This change is attributable to the improved soil
9 conditions on the island following the gull invasion in 1985. High-dispersal wind-borne species
10 are known to have limited reserves and low tolerance of barren substrates and they often require
11 site amelioration prior to establishment (Wood and del Moral, 1987). Among the wind-borne
12 species entering Surtsey after 1990 are three species of willows (*Salix*), an orchid (*Platanthera*
13 *hyperborea*) and a small fern ally (*Botrychium lunaria*) which either grow in association with or
14 require mycorrhizal fungi for germination and establishment (Schmid and Oberwinkler, 1994;
15 Chadde and Kudray 2001; Thornton, 1996; Eyjólfsdóttir, 2009). Hence, the late establishment of
16 these species may partly have been caused by a lack of the fungi in the early years. The shifting
17 pattern of dispersal routes and their relative importance during the first 50 years of colonization
18 on Surtsey has some similarities to the plant dispersal spectra obtained from other volcanic
19 islands, e.g. Krakatau (Whittaker et al., 1992; Thornton, 1996), Anak Krakatau, (Partomihardjo
20 et al., 1992) and Long Island volcano (Harrison et al., 2001; Thornton et al., 2001). They show
21 importance of sea-dispersal at the early stages but animal- and wind-dispersal patterns are more
22 variable.

1 The halt in colonization of new species and a net loss of species on Surtsey after 2007 may
2 indicate that competition is increasing in the community with denser swards and that most of the
3 likely colonists have already arrived. A comparison of the flora of Surtsey with the other outer
4 islands of the Vestmannaeyjar archipelago (Friðriksson and Johnsen, 1967) shows that in the 50
5 years all the common species of the other islands have been dispersed and established on Surtsey
6 and that most of them have formed viable populations (Appendix A). The flora of Surtsey is by
7 far the richest of any of the islands, explicable by its larger size, greater habitat diversity, more
8 open swards and the absence of sheep grazing. Many of the plants confined to Surtsey are
9 species of open shores, sands and tephra plains that no longer occur on the older islands.

10 **4.2 Effects of seagulls on development on Surtsey**

11 This study shows that the seagulls have had pronounced effects on the vegetation and soil
12 development. This was also reflected in the invertebrate fauna. The birds have thus jumpstarted
13 the ecosystem buildup (Sekercioglu, 2006). At the nesting sites the birds deposit faeces and
14 regurgitate pellets, fish and marine invertebrates are spilled on the ground, feathers are shed and
15 corpses of birds that die decompose. Of greatest importance for the soil enrichment and
16 vegetation development are the faeces that have a relatively high content of nitrogen,
17 phosphorus, potassium and minerals (Sobey and Kenworthy, 1979; Bancroft et al., 2005), which
18 are of great importance in primary succession (Walker and del Moral, 2003). In an earlier
19 account (Magnússon et al., 2009) we estimated from nesting density and other studies (Hahn et
20 al., 2007) that annual nutrient inputs from gulls in the Surtsey colony were about 25 kg N ha^{-1} . A
21 new study of the soil development on the island, however, indicates that the average annual input
22 within the colony is 47 kg N ha^{-1} , while the background atmospheric N deposition is only ca 1.2
23 kg N ha^{-1} (Leblans et al., 2014). The nutrient enrichment of soil from the seagulls on Surtsey has

1 had cascading effects on plant populations, invertebrates and landbird colonization on the island
2 (Magnússon et al., 2009; Ólafsson and Ingimarsdóttir, 2009, Petersen, 2009), similar to the
3 nitrogen-fixing lupins on Mount St. Helens (del Moral and Rozzell, 2005; del Moral, 2009; del
4 Moral and Magnússon, 2014). These observed patterns were extended in the present study.

5 In areas of the island outside the gull colony the plant succession and soil development has
6 remained slow (Magnússon et al., 2009). A gradual buildup has occurred (Stefansdottir et al.,
7 2014) but rates of change are not comparable to the gull colony area (del Moral and Magnússon
8 2014, Leblans et al., 2014). The longterm monitoring of vegetation in permanent plots on Surtsey
9 showed that it was mainly ruderal species (sensu Grime et al., 1988) that initially responded to
10 the increased nutrient inputs from the gulls leading to an abrupt increase in species richness and
11 diversity of the vegetation (Magnússon et al. 2009). With further development these species
12 have, however, lost ground to more competitive, rhizomatous grass species of greater longevity
13 that have become dominant in the vegetation in the oldest part of the gull colony. A decline in
14 species richness and diversity has occurred during this development.

15 The invertebrate fauna of areas outside the gull colony was characterized by low species richness
16 and catches of animals. Dipterans were the majority of species caught, however, most of them
17 derived from the gull colony area (Ólafsson and Ingimarsdóttir, 2009). Within the gull colony the
18 invertebrate fauna showed a considerable change in ecosystem structure and function. The high
19 catches of mites (Acari) and springtails (Collembola) are indicative of denser vegetation and
20 greater decomposition activity (Swift et al., 1979). These animals are an important source food
21 for larger invertebrates, such as staphylinid beetles and linyphiid spiders which were abundant
22 in the gull colony (Ólafsson and Ingimarsdóttir 2009). In the dense vegetation plant feeding
23 invertebrates had colonized and started to thrive, such as root feeding dipterans, saprophagous

1 dipterans and plant feeding lepidopterans. Several species of parasitic hymenopterans had also
2 become a part of the invertebrate community of the gull colony, but their main hosts are dipteran
3 and lepidopteran larvae and aphids (Ólafsson and Ingimarsdóttir, 2009). Colonization of some of
4 the bird species on Surtsey was dependant on the developing vegetation and invertebrate fauna of
5 the gull colony. In 1996, ten years after the formation of the colony, snow bunting
6 (*Plectrophenax nivalis*) became the first landbird to breed on the island (Magnússon and
7 Ólafsson, 2003). At that time the dense vegetation of the gull colony had extended to ca. 5 ha.
8 After 2000 two other passerines, the pied wagtail (*Motacilla alba*) and the meadow pipit (*Anthus*
9 *pratensis*), also started breeding (Magnússon et al., 2009; Petersen, 2009). These three passerine
10 species are dependant on insects for raising their young and their main source of food is within
11 the gull colony (Ólafsson and Ingimarsdóttir, 2009). Studies of invertebrate colonization of
12 young volcanic islands and nunataks have shown that at the early stages allochthonous inputs or
13 littoral debris are important sources for pioneering communities consisting of heterotrophic
14 scavenging detritivores and predators (Edwards and Thornton, 2001; Sikes and Slowik 2010;
15 Ingimarsdóttir et al., 2013), not dependant on colonization by autotrophs (Hodkinson et al.,
16 2002). This was also the case in the early years on Surtsey (Lindroth et al., 1973). Plant
17 colonization and vegetation development is followed by further invertebrate colonization and
18 diversification. However it is characterised by relatively generalist species as colonization by
19 specialists of later successional vegetation stages is harder (New and Thornton, 1992) and occurs
20 on a different time scale.

21 **4.3 Vegetation development on Surtsey in comparison to neighbouring islands**

22 The vegetation of the older Vestmannaeyjar islands (> 5.000 yrs old) gives an insight into what
23 will be the outcome of long-term succession on Surtsey. Although the grassland sites sampled on

1 Heimaey and Elliðaey in 2013 are small and do not represent all the different conditions and
2 plant communities of the islands (Friðriksson & Johnsen, 1967; Friðriksson et al., 1972a), they
3 do provide a meaningful comparison and connection between the primary and mature stages in
4 plant succession on these bird impacted volcanic islands. The response of the different plant
5 species to nutrient enrichment and early dominance of grasses in the bird colony on Surtsey is
6 also of particular interest. The best developed grassland plots on Surtsey showed a strong affinity
7 with the plots sampled in the puffin colonies on Elliðaey, which were also very species-poor, of
8 low diversity and had *Festuca rubra* and *Poa pratensis* as dominant species. The high breeding
9 density of the puffins indicated that nutrient input from the seabirds on Elliðaey was several
10 times higher than in the gull colony on Surtsey.

11 All the outer islands of the Vestmannaeyjar islands are impacted by seabirds and receive external
12 nutrient inputs. Their vegetation has a greater resemblance with the puffin colonies of Elliðaey
13 than the Heimaey grassland studied (Friðriksson and Johnsen, 1967; Friðriksson et al. 1972b).

14 Our results showed that the Elliðaey puffin colonies had by far the richest soils in carbon, as well
15 as nitrogen (Leblans, unpublished data). The Heimaey grassland sampled, which has developed
16 under limited nutrient input from seabirds, had, by contrast, high species richness and diversity
17 in comparison to the Elliðaey/Surtsey seabird grassland. A study of vegetation, seabirds and the
18 impact of introduced foxes on islands in the sub-arctic Aleutian archipelago in Alaska has
19 demonstrated that at high seabird densities plant communities are graminoid dominated (Croll et
20 al., 2005). On fox-infested islands with reduced seabird populations abundance of grasses
21 declined and the vegetation developed towards tundra, due to reduced marine nutrient inputs
22 (Croll et al., 2005). Grasslands on fertile soils with high availability of nitrogen and phosphorus
23 are known to be species-poor with low plant diversity (Janssens et al., 1998). In their

1 experimental study of a *Festuca rubra* grassland in central Europe, Pavlu et al. (2012), found that
2 at high doses of N and under no P and K limitations, a substantial decline in species richness
3 occurred. The trends observed in the grassland developing on Surtsey and the contrasts between
4 the grasslands of Elliðaey and Heimaey under different seabird impacts are similar to the
5 findings of these grassland studies.

6 **5. Conclusions**

7 Over the the first 50 years, seagulls were the main agents of ecosystem development on Surtsey
8 through seed-dispersal to the island and nutrient transfer from sea to land. In areas impacted by
9 the gulls, productive, species-poor grassland has developed on relatively rich soils, high in
10 invertebrate abundance and with breeding insectivorous birds. Continued breeding of the
11 seagulls, colonization of puffins and other seabirds will lead to further development of the
12 grassland. Due to erosion the island will eventually loose its lower sandy and lava habitats with
13 the associated flora and fauna. The bird colonies will concentrate on the upper part of the island
14 where grassland will develop as on the older neighbouring islands.

15

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11 for decades and, Roger del Moral made valuable comments and improvements on the
12 manuscript.

13

1 **Appendices:**

2 **Appendix A:** Vascular plants colonizing Surtsey during 1965–2013 and species list for
 3 neighbouring Vestmannaeyjar islands. (•) denotes species that have been recorded on Surtsey but
 4 were not present in 2013; species that had formed viable populations (v.p.) in 2013 or were
 5 found within permanent plots (p.p) in 2012 are marked. The species list of the Vestmannaeyjar
 6 islands is based on Friðriksson and Johnsen 1967 and our surveys of Elliðaey and Álsey in 2010–
 7 2013.

8

	Island size (km ²)	Island			Elliðaey	Bjarnarey	Álsey	Suðurey	Hellisey	Brandur	Súlnasker	Geirfuglasker	Þrídrangar
	1.3	Surtsey 2013	Surtsey v.p. 2013	Surtsey p.p. 2012									
Surtsey order of colonization													
1	<i>Cakile maritima</i>	•	•	•									
2	<i>Leymus arenarius</i>	•	•	•									
3	<i>Honkenya peploides</i>	•	•	•									
4	<i>Mertensia maritima</i>	•	•	•									
5	<i>Cochlearia officinalis</i>	•	•	•	•	•	•	•	•	•	•	•	
6	<i>Stellaria media</i>	•	•	•	•	•	•	•	•	•	•	•	
7	<i>Cystopteris fragilis</i>	•	•										
8	<i>Angelica archangelica</i>	•			•	•	•	•					
9	<i>Carex maritima</i>	•	•										
10	<i>Puccinellia capillaris</i>	•	•	•	•	•	•	•	•	•	•	•	
11	<i>Tripleurospermum maritimum</i>	•	•	•	•	•	•	•	•	•	•	•	
12	<i>Festuca rubra</i>	•	•	•	•	•	•	•	•	•	•	•	
13	<i>Cerastium fontanum</i>	•	•	•	•	•	•	•	•	•	•	•	
14	<i>Equisetum arvense</i>	•				•							
15	<i>Silene uniflora</i>	•	•	•	•	•	•	•	•	•	•	•	
16	<i>Juncus arcticus</i>	•											
17	<i>Poa pratensis</i>	•	•	•	•	•	•	•	•	•	•	•	
18	<i>Sagina procumbens</i>	•	•	•	•	•	•	•	•	•	•	•	
19	<i>Atriplex glabriuscula</i>	•	•				•	•	•	•	•	•	
20	<i>Rumex acetosella</i>	•	•	•									
21	<i>Arabidopsis petraea</i>	•	•	•									
22	<i>Armeria maritima</i>	•	•	•	•	•		•	•				
23	<i>Poa annua</i>	•	•	•	•	•	•	•		•			
24	<i>Agrostis stolonifera</i>	•	•			•	•	•					
25	<i>Alchemilla filicaulis</i>	•											
26	<i>Epilobium palustre</i>	(•)											
27	<i>Capsella bursa-pastoris</i>	(•)											
28	<i>Luzula multiflora</i>	•	•		•	•							
29	<i>Taraxacum</i>	•	•	•	•	•	•	•	•	•	•	•	
30	<i>Rumex acetosa</i>	•	•	•	•	•	•	•	•	•	•	•	
31	<i>Polygonum aviculare</i>	(•)											
32	<i>Agrostis capillaris</i>	•	•		•	•	•	•					
33	<i>Alopecurus geniculatus</i>	•											
34	<i>Ranunculus acris</i>	•	•		•	•	•	•					
35	<i>Deschampsia beringensis</i>	•											

36	<i>Empetrum nigrum</i>	•	•	•																	
37	<i>Agrostis vinealis</i>	•																			
38	<i>Eleocharis quinqueflora</i>	•																			
39	<i>Phleum pratense</i>	•																			
40	<i>Montia fontana</i>	(•)					•	•	•	•											
41	<i>Poa glauca</i>	•																			
42	<i>Juncus alpinoarticulatus</i>	•																			
43	<i>Salix herbacea</i>	•	•																		
44	<i>Galium normanii</i>	(•)																			
45	<i>Argentina anserina</i>	•	•						•												
46	<i>Anthoxanthum odoratum</i>	•	•						•												
47	<i>Leontodon autumnalis</i>	•	•	•			•	•	•	•											
48	<i>Rumex longifolius</i>	•	•	•																	
49	<i>Polypodium vulgare</i>	•																			
50	<i>Luzula spicata</i>	•																			
51	<i>Myosotis arvensis</i>	•																			
52	<i>Salix phylicifolia</i>	•	•																		
53	<i>Oxyria digyna</i>	(•)																			
54	<i>Salix lanata</i>	•																			
55	<i>Euphrasia frigida</i>	•	•				•	•		•											
56	<i>Plantago maritima</i>	•	•				•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
57	<i>Platanthera hyperborea</i>	(•)																			
58	<i>Galium verum</i>	•																			
59	<i>Plantago lanceolata</i>	•	•																		
60	<i>Thymus praecox</i>	•	•																		
61	<i>Saxifraga cespitosa</i>	•	•				•	•	•												
62	<i>Rhodiola rosea</i>	(•)					•	•	•												
63	<i>Festuca vivipara</i>	•																			
64	<i>Achillea millefolium</i>	•						•	•	•											
65	<i>Alopecurus pratensis</i>	(•)					•														
66	<i>Calamagrostis neglecta</i>	•																			
67	<i>Gymnocarpium dryopteris</i>	•	•																		
68	<i>Epilobium collinum</i>	(•)																			
69	<i>Botrychium lunaria</i>	•																			
<i>Neighbouring islands additional species</i>																					
70	<i>Ranunculus repens</i>							•												•	
71	<i>Draba incana</i>							•													
72	<i>Juncus bufonius</i>							•													
73	<i>Epilobium hornemannii</i>							•													
74	<i>Saxifraga rivularis</i>																			•	
<i>Species total</i>		59	39	22			28	28	24	22	9	11	7	4	2						

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1 **Figure captions**

2 **Fig. 1.** Surtsey and other Vestmannaeyjar islands on an infra-red Rapid Eye image from August
3 28, 2012. Areas with dense vegetation appear in red colour, e.g. gull colony on Surtsey. Location
4 of vegetation plots sampled on Elliðaey and Heimaey in 2013 is shown in yellow.

5 **Fig. 2.** Location of permanent plots on Surtsey, infra-red Rapid Eye image from August 28,
6 2012. Note dense vegetation of gull colony (13 ha) on the southern lava and shore community (1
7 ha) on the northern spit. Plots 1, 3, 4, 6–10 and 23 are within the gull colony.

8 **Fig. 3.** Surtsey colonization curve for vascular plants during 1965–2013. Vertical, dotted lines at
9 bottom of diagram show divisions between the four main phases of colonization.

10 **Fig. 4.** Cumulative curves of dispersal routes to Surtsey most probably used by different vascular
11 plant species during 1965–2013. Based on dispersal-mode spectra of the flora and sites of
12 establishment on the island.

13 **Fig. 5.** Relative frequency of vascular species in the 25 permanent plots on Surtsey in 2008 and
14 2012. Species occurring in ≥ 2 plots are shown.

15 **Fig. 6.** Expansion of dense vegetation within the Surtsey seagull colony during 1988–2012.
16 Approximation from aerial and satellite images, by Anette Th. Meier. Island outlines indicate
17 erosion over the period.

18 **Fig. 7.** TWINSPAN-classification of permanent plots sampled on Surtsey (S), Heimaey (H) and
19 Elliðaey (E) in 2012–2013. Species most decisive (indicators) of each division are shown and the
20 four groups formed.

21 **Fig. 8.** DCA-ordination results for permanent plots sampled on Surtsey (S), Heimaey (H) and
22 Elliðaey (E) in 2012–2013. Arrows indicate direction of succession on Surtsey under nutrient
23 inputs from breeding seagulls, axes units are multiplied by 100

24 **Fig. 9.** *Poa pratensis*/*Leymus arenarius* grassland in centre of gull colony (plot 1) on Surtsey in
25 2013. Upper crater areas and palagonite ridges remain barren. Photo: BM.

26 **Fig. 10.** *Festuca rubra*/*Poa pratensis* grassland on upper parts of Elliðaey. Plot E1 was located in
27 a puffin colony on palagonite ridge above and to the right of cottage. Photo: BM, 2010.

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1 Table 1. Permanent plots on Surtsey (S) in 2012, Elliðaey (E) and Heimaey (H) in 2013, year of
 2 establishment, substrate type and influence of seabirds. The plots on Elliðaey and Heimaey have thick (>
 3 1 m), developed soils on top of substrate.

Plot no.	First sampling	Substrate type	Seabird influence
S1,3,4	1990	Sandy sheet lava	High
S6-10	1994	Sheet lava	High
S22,23	1995	Sheet lava	Moderate
S11-14, 16, 18-21	1994, 1995	Sandy sheet lava	Low
S15, 17	1994	Tephra hill slopes	Low
S29,30	2005	Coastal sand	Low
S31, 32	2008	Block lava	Low
E1-4	2013	Cinder & palagonite hill slopes	High
H1-4	2013	Palagonite hill slopes	Low

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1 Table 2. Surtsey permanent plot data. Average density of gull nests in plots on Surtsey 2003–2012 (no. /1000 m²), plant cover, species
 2 richness and diversity of vascular plants in 2012, standing biomass of vascular plants (live and dead) in 2011, and total carbon in top
 3 10 cm of soil in 2008. Invertebrate and Acari/Collembola data are pitfall traps averages for the 2002–2006 sampling seasons, catch
 4 data are individuals caught. Means ± s.e.; *p* = ANOVA level of significance, n.s. = > 0.05; * = ≤ 0.05; ** = ≤ 0.01; *** = ≤ 0.001.
 5 ^aPlots 11–22, 29–32; ^bplots 1, 3, 4, 6–10, 23; ^cinclude Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera,
 6 Thysanoptera, Araneae, Gastropoda and Oligochaeta. Invertebrates (including Acari/Collembola) were not sampled in plots 31 and 32,
 7 n=14.

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	Outside ^a gull colony n=16, 14	Inside ^b gull colony n=9	<i>p</i>
Nests no.	0.01±0.01	3.9 ±0.8	***
Plant cover %	7.1 ±2.8	90.3 ±15.2	***
Plant species richness	4.4 ±0.5	7.7 ±0.9	*
Plant diversity (Shannon)	0.5 ±0.1	1.0 ±0.2	*
Plant biomass g dw m ⁻²	46.7 ±23.9	221.2 ±75.6	**
Soil carbon %	0.05 ±0.02	1.84 ±0.55	***
Invertebrate species richness ^c	14.2±1.1	28.3±1.3	***
Invertebrate catch/day ^c	13.9±2.3	17.7±2.9	n.s.
Acari/Collembola catch/day	20.3±10.7	108.4±13.4	***

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1 Table 3. Average density of seabird nests (no. /1000 m²), plant cover, species richness and diversity of vascular plants, and soil carbon
 2 in plots sampled on islands, according to main Twinspan groupings; ^G: average density of gull nests on Surtsey 2003-2013; ^P: average
 3 density of puffin nests on Elliðaey in 2013. Means ± s.e.; *p* = ANOVA level of significance, n.s. = >0.05; * = ≤ 0.05; ** = ≤ 0.01; ***
 4 = ≤ 0.001. Means with same letter are not significantly different at *p* = 0.05.

5

Island	Presence of seabirds	Twinspan group	No. of plots	Nesting density	Plant cover %	Species richness	Plant diversity	Soil carbon %
Heimaey	-	I	4	0	69.20±16.34a	18.00±1.19a	1.90±0.22a	6.23±1.47a
Surtsey/Elliðaey	+	II	7	5.13 ^G /269 ^P	88.42±12.25a	6.00±0.90b	0.80±0.16b	9.14±1.11a
Surtsey	+	III	8	2.51 ^G	70.99±11.55a	7.13±0.84b	0.85±0.15b	1.07±1.04b
Surtsey	-	IV	14	0	7.56±8.73b	4.43±0.64b	0.54±0.12b	0.04±0.79c
<i>p</i>				n.d.	***	***	***	***

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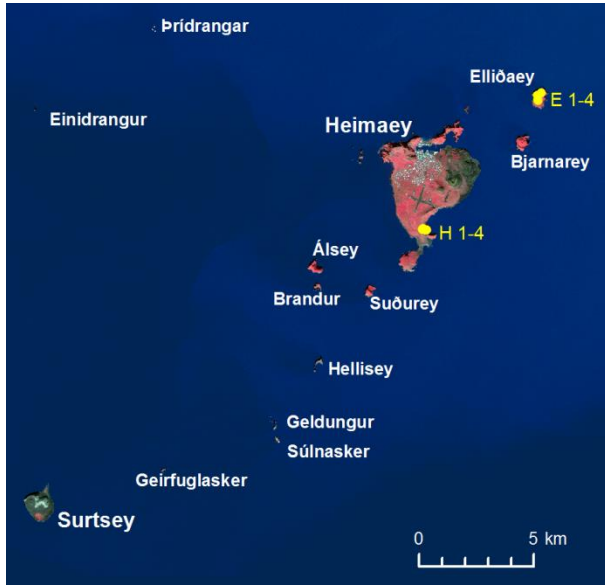
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1 **Figures**

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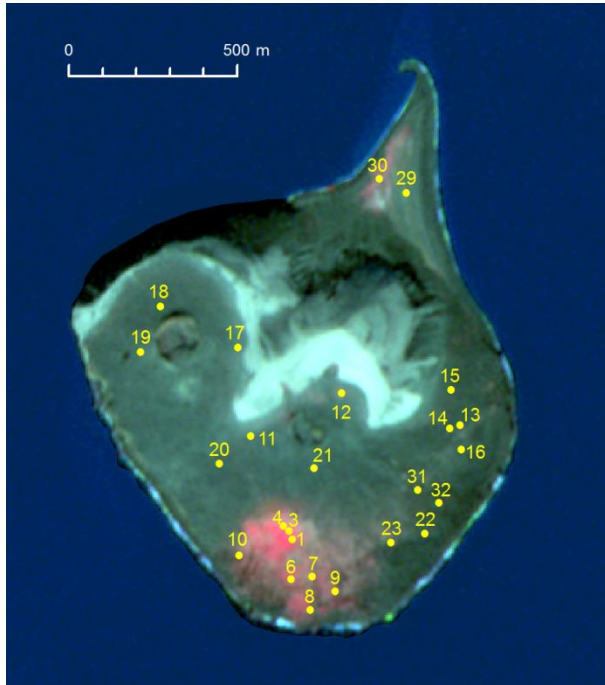
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6 Fig. 1.

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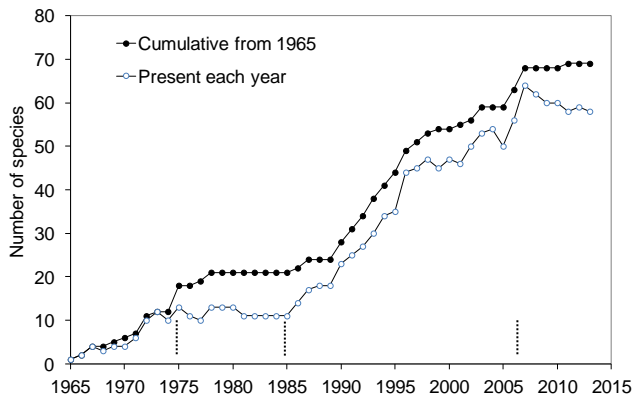


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5 Fig. 2.

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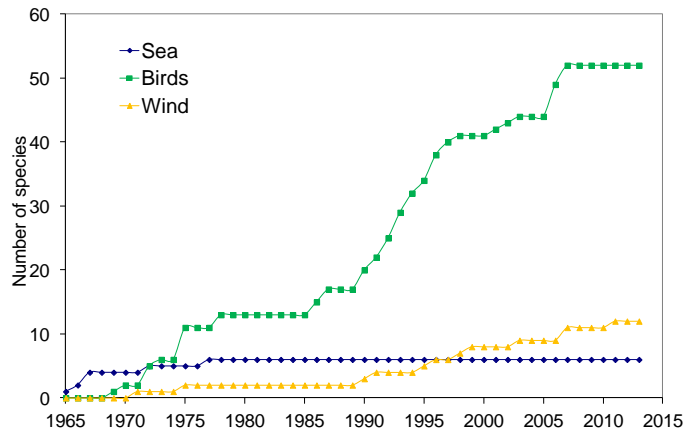
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3 Fig. 3.

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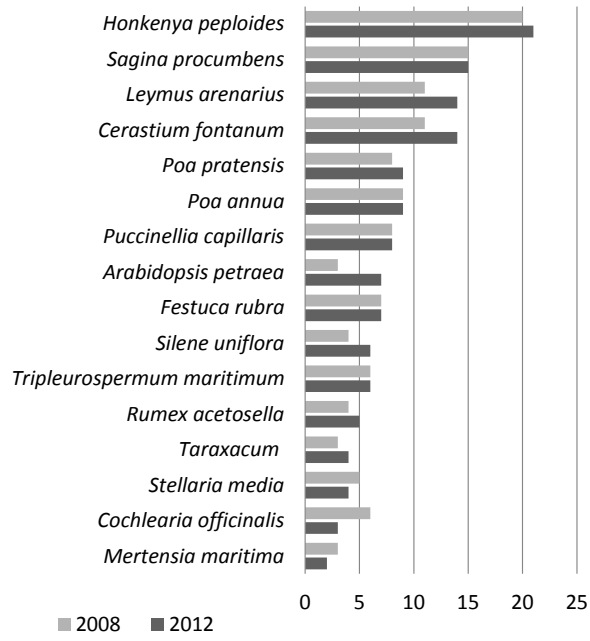


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5 Fig. 4.

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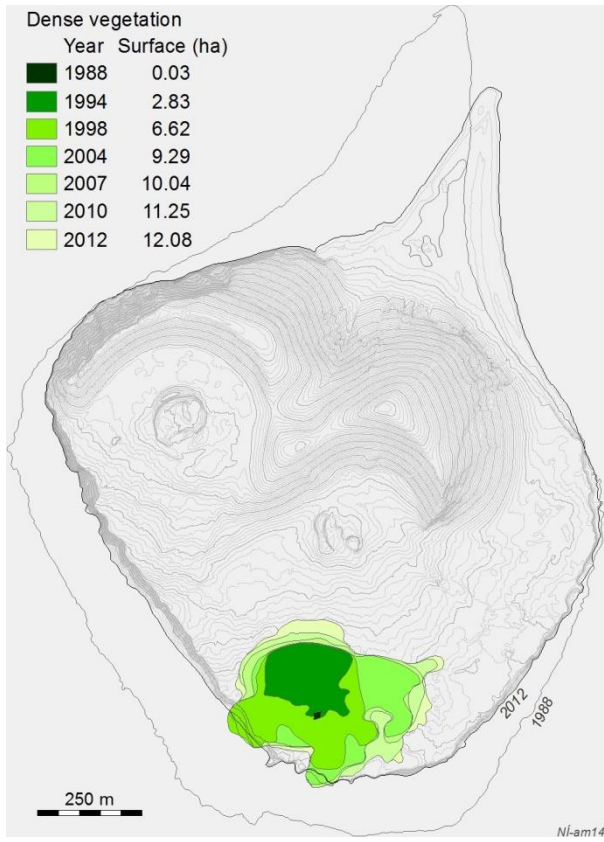
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5 Fig. 5.

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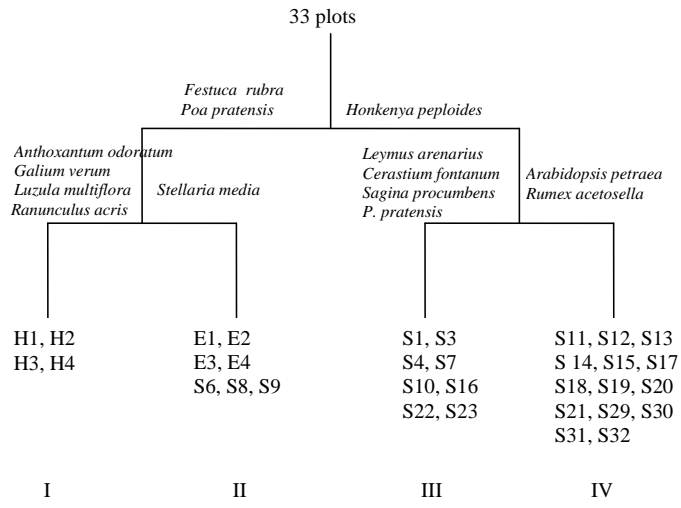
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6 Fig. 6.

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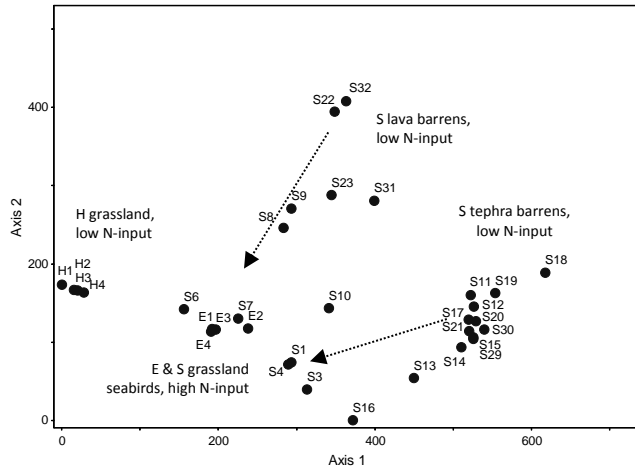
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Fig 7.

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