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Ecosystem respiration, vegetation development and soil nitrogen in relation to breeding density of seagulls on a pristine volcanic island, Surtsey, Iceland

B. D. Sigurdsson¹ and B. Magnusson²

¹Agricultural University of Iceland, 112 Keldnaholt, 125 Reykjavik, Iceland

²Icelandic Institute of Natural History, P.O. Box 5320, 125 Reykjavik, Iceland

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Correspondence to: B. D. Sigurdsson (bjarni@lbhi.is)

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Abstract

Since its birth in 1963 by volcanic eruption in the North Atlantic Ocean off Iceland, Surtsey has been a unique natural laboratory on how organisms colonize volcanic islands and form ecosystems with contrasting structure and function. In July, 2004, ecosystem respiration rate, soil properties and surface cover of vascular plants were measured on 21 plots distributed among the main plant communities found 40 years after the primary succession started. The plots could be divided into two groups, inside and outside seagull (*Larus* sp.) colonies found on the island. Vegetation cover of the plots was strongly related to the density of seagull nests within and around them. The occurrence of seagull nests and increased vegetation also coincided with significant increase in ecosystem respiration, soil carbon and nitrogen, and with significantly lower soil pH and soil temperatures. The ecosystem respiration was high inside the gull colonies, similar to the highest fluxes measured in drained wetlands or agricultural fields in Iceland. The most important factor for vegetation succession and ecosystem function on Surtsey seems to be the amount of nitrogen, which was mainly brought in by the seagulls.

1 Introduction

Surtsey is a volcanic island that emerged from the North Atlantic Ocean in 1963 in an eruption that lasted for three years. The island was protected in 1965, which limited the human impact to only few visits annually by scientists. Since then, Surtsey has been a unique laboratory to study how life colonizes isolated volcanic islands and how primary succession starts. The island became UNESCO World Heritage Site in July 2008 due to its unique geology and research activity during the past 45 years (Hermannsson, 2009).

Bacteria and fungi were probably the first organisms to become established on the volcanic substrate (e.g. Schwabe, 1970), but the first vascular plant was found on the

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beach in 1965 while the island was still erupting (Fridriksson, 1966). Mosses were first detected in 1968, lichens in 1970 and mushrooms in 1971 (Jóhannsson, 1968; Kristinsson, 1972; Eyjólfsdóttir, 2009).

Vascular plants have dominated the primary succession on Surtsey, and their colonization and succession has been studied intensively (e.g. Fridriksson, 1966; Magnússon et al., 1992, 2009; Magnússon and Magnússon, 2000). The first twenty years were characterised by colonization and succession of coastal plant communities, with *Honckenya peploides* and *Leymus arenarius* being the key species, forming sparse vegetation cover on sandy areas of the island (Fridriksson, 1992; Magnússon et al., 2009). In 1986 a few pairs of lesser black-backed gull (*Larus fuscus*) formed a small breeding colony on a lava plain on the southern part of the island (Magnússon and Magnússon, 2000; Petersen, 2009). This colony remained spatially well defined and grew in size over the next several years, with herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) moving in. In 2003, ca. 300 pairs of gulls bred on the island (Petersen, 2009), most of them within the colony. The establishment of the gull colony had a large effect on the rate of colonization by vascular plants. In total, 69 vascular plant species have been found on the island, whereof 63 species were surviving in 2008 (Magnússon et al., 2009), which is 16% of Iceland's native vascular plant flora.

Ecosystem function has not been studied as much on Surtsey as the ecosystem structure. In the early years Henriksson and Rodgers (1978) and Henriksson and Henriksson (1982) studied terrestrial nitrogen cycle. Magnússon (1992) studied how ecosystem respiration changed with increasing cover of *L. arenarius* and *H. peploides* on the island. He found that respiration rates were related to differences in vegetation cover and root biomass. Frederiksen et al. (2000) studied soil development on Surtsey and showed how microbial biomass served as nutrient-retaining mechanism that kept nutrients from leaching out when brought in by atmospheric deposition, sea spray, nitrogen fixing microorganisms and bird droppings. This enabled vascular plants to colonize and utilize the accumulated nutrients. Klamer et al. (2000) also studied the

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amount of microbial biomass in unvegetated and vegetated soil. Sigurdsson (2009) measured ecosystem carbon fluxes in swards of *Leymus arenarius* and *Honckenya peploides* growing within moist and dry microsites on the island. This study indicated that soil humidity could also be an important factor for ecosystem function.

5 How fast the nutrients are released from the dead organic matter depends on the activity of decomposition in the soil layer. As the organic matter is decomposed, CO₂ is released and leaves the surface as soil respiration. The second major contributor of CO₂ to the soil respiration is the metabolism of living plant roots in the soil volume. When aboveground parts of living plants are included in respiration measurements, 10 as in the present study, CO₂ from shoot metabolism is also included. Then, the process is termed ecosystem respiration (R_e). The rate of R_e depends therefore both on plant biological activity and decomposition activity of soil organisms. The R_e gives a measure of the ecosystem function and together with gross primary production (GPP) determines the annual carbon balance and the accumulation of organic matter in the ecosystem (Grace, 2001). 15

The objective of the present study was to investigate biological activity in different vegetation types and development stages on Surtsey which have been followed in a study with permanent plots initiated in 1990 (Magnússon and Magnússon, 2000; Magnússon et. al., 2009).

20 **2 Material and methods**

2.1 Site description

Surtsey is the southernmost of the Vestmannaeyjar islands, off the south coast of Iceland (63.3° N, 20.6° W). The climate is relatively mild for the 63rd latitude and oceanic, with annual mean temperature of 5.0° C and mean annual precipitation of 1576 mm during 1965–2005, as recorded on the Heimaey weather station 15 km to the northeast of Surtsey (Icelandic Meteorological Office). 25

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Surtsey emerged in an eruption that lasted from November 1963 to June 1965. When the eruption ceased the island was 2.65 km² and ca. 30% were made out of rough lava surfaces and 70% was covered by loose tephra, but its size has decreased to 1.41 km² due to sea erosion (Jakobsson et al., 2007). Weathering and erosion have also greatly changed the surface of the island. The tephra cones around the two craters (Fig. 1) have gradually transformed into dense palagonite tuff and the rough lava has been covered to large extent by a layer of drifting tephra and sand, which is this study is termed “soil”.

2.2 Measurements

Measurements of ecosystem respiration were conducted on 19–20 July 2004 in 21 permanent vegetation survey plots (Fig. 1). The plots, which are 10×10 m in area, were set up on the island in 1990–1995 to follow the impact of the developing seagull colony on the vegetation succession (Magnússon and Magnússon, 2000). Plots 1–10 were placed inside the colony while plots 11–23 were placed on different surfaces outside the colony (Fig. 1). It was evident in 2004 that plot 23 had become influenced by the seagulls and was therefore reclassified with the plots inside the gull colony.

CIRAS II infrared gas analyser and a SP1 respiration chamber (PP Systems, UK) were used to measure ecosystem respiration (R_e) in the plots. A 14 m long tape was fitted diagonally between the SW and NE corners of the plots and four respiration measurements were made per plot, generally at 1 m, 4 m, 8 m and 11 m from the SW corner. In few plots, where the respiration chamber could not be sealed due to uneven volcanic rocks, the measurements were made at next suitable surface along the tape. Soil temperature was recorded at 5 and 10 cm depth with a temperature probe placed adjacent to the respiration chamber. All measurements took place during daytime hours.

Vegetation surface cover was measured in each permanent plot during routine sampling in 2004 by line-intercept method as described by Magnússon and Magnússon (2000). Vegetation surface cover was also recorded under the flux measurement chamber at each measurement. Density of gull nests was recorded in 2004 by carefully

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inspecting a 1000 m² circular plot around each permanent vegetation plot (Magnússon et al., 2009).

The soil was sampled in the permanent plots in 2004. Four 10 cm deep soil cores were taken at random location within each plot and mixed to form a composite sample.

The samples were sieved through 2 mm mesh and dried at 80°C for 48 h and analysed at the Centre of Chemical Analyses (Efnagreiningar Keldnaholti), ICETEC, Reykjavik, Iceland. Total N was analysed by Kjeldahl wet combustion on Tecator Kjelttec Auto 1030 Analyzer. Total C was analysed by dry combustion on Leco CR-12 Carbon Analyzer and the soil pH was measured by an electrode (Orion model 920 A) in a soil/water mixture of 1:1.

3 Results

The plots inside the gull colony had on average 3.4 nests within a 1000 m² area, while no nests were found by the plots outside the colony (Table 1). Vegetation cover in the plots within the gull colony was significantly greater than in the plots outside, or on the average 78% and 5%, respectively. The increased vegetation cover in the gull colony was reflected in significantly lower soil temperatures compared to barren sand plots outside the colony. The difference was on average 4.6°C (Table 1). The average vegetation cover measured in each plot in 2004 was similar to the average cover in the four fixed measurement points for ecosystem respiration (R_e) within each plot (Table 1), indicating that four points were enough to cover the variation within each plot. There was also a significant increase in both total carbon and nitrogen in the soil in the gull colony and soil pH was significantly lower in the more vegetated soil (Table 2). Ecosystem respiration varied in a similar way as the vegetation cover, with a highly significant difference between the gull colony and the area outside it (Fig. 2). On average the R_e was 4.14 and 0.17 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ within and outside the gull colony, respectively. Plot 23, which was in an area recently colonized by the gulls, showed intermediate rates of R_e (Fig. 2).

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The most important driving factor for vegetation cover and ecosystem function appeared to be the amount of nitrogen (N) found in the soil (Fig. 3). The vegetation cover in the permanent plots had reached 100% when nitrogen content was at about 0.1% of soil DM. At soil N concentration lower than 0.1% there was a strong positive linear relationship with surface cover (ANOVA, $P < 0.001$, $r^2 = 0.78$):

$$\text{Cover} = 1455.4 \times N - 9.0 \quad (1)$$

Ecosystem respiration also showed a strong linear relationship with soil N (ANOVA, $P < 0.001$), but contrary to surface cover, there was no saturation observed with higher nitrogen concentrations (Fig. 3). Soil N explained 51% of the variability observed in R_e (ANOVA, $v0.001$, $r^2 = 0.51$):

$$R_e = 20.45 \times N + 0.62 \quad (2)$$

4 Discussion

The formation of the gull colony was a turning point in the succession of plant and animal life on Surtsey (Magnússon and Magnússon, 2000). The gulls facilitated colonization of new plant species, probably by carrying seeds to the island. Also they fertilized the sterile soil with their droppings and food brought to the nest sites from the sea. This led to an explosive development of plant and animal communities, including an ever increasing number of invertebrate (Ólafsson and Ingimarsdóttir, 2009), lichen (Kristinsson and Heidmarsson, 2009) and fungal species (Eyjólfsdóttir, 2009). In the past 15 years extensive swards of grasses and forbs have been formed within the area affected by the gulls (Magnússon and Magnússon, 2000; Magnússon et al., 2009). Vegetation development on other parts of the island have on the other hand remained slow by comparison (Magnússon et. al., 2009).

The increase in vegetation cover and number of plant species within the seagull colony has been linked to a substantial increase in available nitrogen, originating from

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the sea and brought upon the island by the birds (Magnússon et al., 1996; Magnússon and Magnússon, 2000; Frederiksen et al., 2000). Low water retention of the volcanic substrate which can lead to water stress episodes at dry spells during summer, may however also pose a barrier for plant growth on Surtsey (Sigurdsson, 2009).

5 The present results highlight how important the nutrient inputs from the seagulls have been for the biological activity on Surtsey, indicated by the rate of R_e . The R_e was 24 times higher within the seagull colony than outside. The large difference existed even if temperature sensitivity of R_e must partly have counteracted it, since the insulation from the increased vegetation cover kept the soil from warming as much within the
10 seagull colony as the sparsely vegetated areas outside. Both soil and plant respiration increase in an exponential way as temperature rises (e.g. Grace, 2001).

The R_e values measured in the gull colony were among the highest encountered in terrestrial ecosystems in Iceland (e.g. Óskarsson, 1998; Sigurdsson, 2001; Beckmann et al., 2004; Bjarnadottir et al., 2009) and compare to maximum values encountered
15 in agricultural croplands and temperate grasslands (Falge et al., 2002) or in fertile Icelandic wetlands (Óskarsson, 1998).

The present results showed a clear linear relationship between vegetation cover and the soil N in the range of 0.0–0.10% of DM and over the whole range encountered in soil N for R_e (0.0–0.35% N). Such a positive relationship between soil N and soil
20 respiration was also found by Halvorson et al. (1991), who studied how primary succession and ecosystem processes were affected by colonization of a nitrogen-fixing *Lupinus* species on pyroclastic deposits created in the 1980 eruption in Mount St. Helens, Washington state, USA.

The importance of seabirds on ecosystem functions has been increasingly acknowledged in recent years. Where they build their colonies they can be viewed as chemical and physical engineers that affect both ecosystem structure and function through
25 disturbance, seed dispersal and nutrient transport from sea to land (Ellis, 2005; Sekercioglu, 2006).

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It is useful to study how biological activity changes in the early stages of primary succession of a pristine volcanic island like Surtsey. First primary producers have to become established on the sterile surface. They accumulate atmospheric carbon (organic matter) with photosynthesis and absorb soil nutrients into their living tissues.

5 Their dead tissues create the soil organic matter and improve soil fertility, which allows more nutrient and moisture demanding species to colonize. Such a development has generally been believed to take a long time (del Moral and Wood, 1993), especially at higher latitudes where each growing season is short. The present study showed, however, how the initial steps of such a development can be much faster than previously
10 expected, with the seabirds playing the key role.

5 Conclusions

The most important factor for the rapid vegetation succession and a build-up of high ecosystem fluxes on Surtsey appears to be the amount of nitrogen, which was mainly brought in by the seagulls. The present study shows how ecosystem activity can be
15 enhanced by colonization of animals who are not dependent on the resources of the given ecosystem.

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20 Th. Meier made the 2007 elevation map of the island.

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Table 1. Site properties of permanent survey plots inside and outside a gull colony in July 2004. Cover was measured in % of surface area. T_s stands for soil temperature at ca. 10 cm depth (°C). Difference within and outside gull colony was tested with One-Way ANOVA: $ns=P>0.05$, * $P=0.05-0.01$, ** $P=0.01-0.001$, *** $P<0.001$.

No	Gull colony	Nests per 1000 m ²	Substr. type ^a	Key plant sp. ^b	Veget. cover	Flux cover 2004	Soil depth (cm)	T_s (°C)
1	+	1.0	B	Poa pra	98.8	100	28.7±7.2	14.5
3	+	0.5	B	Ste med	100.0	100	>35	12.8
4	+	2.5	B	Poa ann	86.8	100	35.0±8.9	15.0
6	+	0.5	A	Fes ric	96.9	100	6.3±1.5	13.3
7	+	4.5	A	Poa pra	86.2	100	3.5±0.5	14.4
8	+	3.0	A	Coc off	70.3	76	3.0±0.7	15.3
9	+	11.0	A	Sag pro	95.1	81	7.3±1.0	14.4
10	+	6.5	A	Hon pep	40.9	98	4.5±1.0	12.8
23	+	1.0	C	Sag pro	30.1	83	1.0±0.0	17.9
Mean±SE		3.4±1.2			78.3±8.7	93.1±3.3		14.5±0.5
11	-	0	C	Hon pep	3.3	1	>35	19.7
12	-	0	C	Hon pep	23.9	21	>35	17.9
13	-	0	B	Hon pep	3.1	0	>35	20.5
14	-	0	B	Hon pep	2.4	0	23.7±8.8	20.6
15	-	0	C	Hon pep	9.8	20	>35	19.2
16	-	0	B	Hon pep	2.0	1	5.3±0.9	20.9
17	-	0	B	Hon pep	1.7	0	>35	19.5
18	-	0	B	Car pet	4.8	0	7.3±1.0	17.8
19	-	0	B	Hon pep	1.0	3	8.0±0.6	19.7
20	-	0	B	Hon pep	3.8	1	>35	17.8
21	-	0	B	Hon pep	1.2	1	>35	20.7
22	-	0	A	Sag pro	1.0	1	2.0±0.4	15.5
Mean±SE		0±0			4.8±1.9	4.4±2.4		19.1±0.5
P		-			***	***	ns	***

^a Substrate type A = Lava (hard surface), B = partly sand-filled lava, C = sand;

^b Car pet = *Cardaminopsis petraea* (L.) Hiit., Coc off = *Cochlearia officinalis* L., Fes ric = *Festuca richardsonii* Hooker, Hon pep = *Honckenya peploides* (L.) Ehrh., Poa ann = *Poa annua* L., Poa pra = *Poa pratensis* L., Sag pro = *Sagina procumbens* L., Ste med = *Stellaria media* (L.) Vill.

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Table 2. Total carbon (C), pH and nitrogen (N), expressed in % of dry soil, sampled in permanent plots on Surtsey in 2004.. Difference within and outside gull colony was tested with One-Way ANOVA: $ns=P>0.05$, $*P=0.05-0.01$, $**P=0.01-0.001$, $***P<0.001$.

No	Gull colony	pH	Total N	Total C	C:N ratio
1	+	6.81	0.07	0.87	13.0
3	+	6.70	0.06	0.63	10.9
4	+	6.82	0.04	0.48	11.3
6	+	6.45	0.32	5.00	15.6
7	+	6.35	0.24	2.83	11.8
8	+	6.50	0.22	2.95	13.5
9	+	6.42	0.12	1.52	12.9
10	+	6.77	0.05	0.64	12.2
23	+	6.33	0.05	0.65	12.7
Mean±SE		6.57±0.07	0.13±0.03	1.73±0.52	12.7±0.5
11	-	8.02	0.01	0.04	9.1
12	-	8.03	0.01	0.05	7.3
13	-	7.73	0.01	0.04	7.4
14	-	7.64	0.00	0.02	5.1
15	-	7.62	0.01	0.05	7.0
16	-	7.31	0.01	0.04	6.2
17	-	7.85	0.01	0.03	4.3
18	-	7.44	0.01	0.02	2.5
19	-	7.39	0.01	0.03	3.1
20	-	7.95	0.01	0.04	3.2
21	-	7.75	0.01	0.02	1.4
22	-	6.76	0.02	0.10	5.8
Mean±SE		7.59±0.11	0.01±0.00	0.04±0.01	5.2±0.7
P		***	***	**	***

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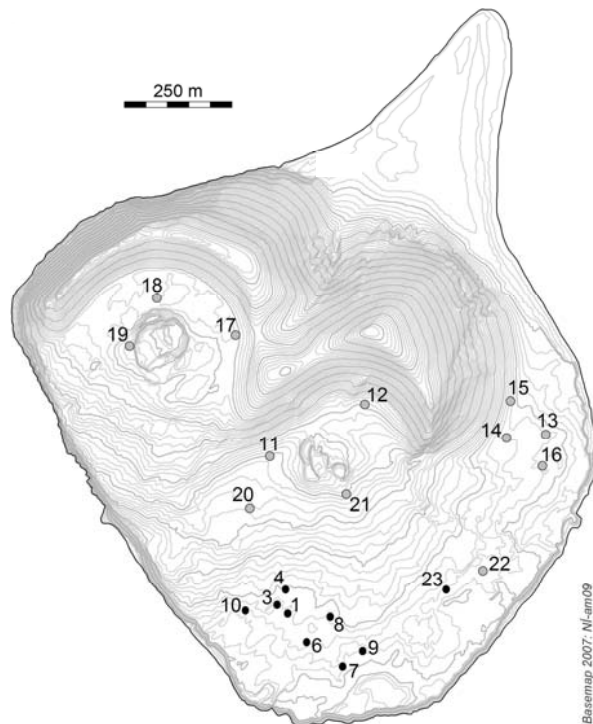


Fig. 1. Location of the 21 permanent vegetation plots on Surtsey where flux measurements were carried out in 2004, shown on a topographical map of the island from 2007. Black and gray dots indicate plots within and outside the seagull colony. Contour intervals are 2 m.

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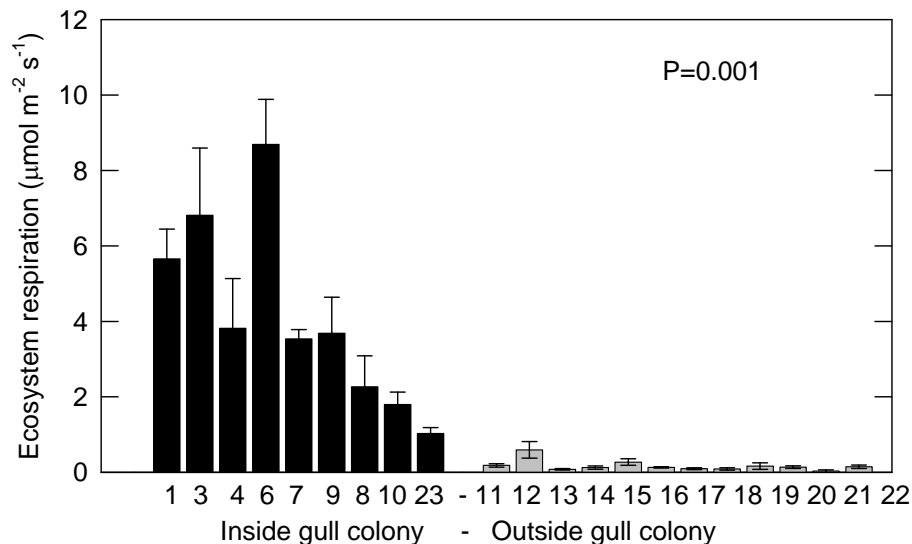


Fig. 2. Ecosystem respiration (average of $n=4 \pm \text{SE}$) in the permanent vegetation plots on Surtsey. Black and light grey bars indicate plots located within and outside the seagull colony, respectively. Numbers on x-axis are plot numbers. The P-value indicates the significance of One-Way ANOVA test on the difference between the two groups.

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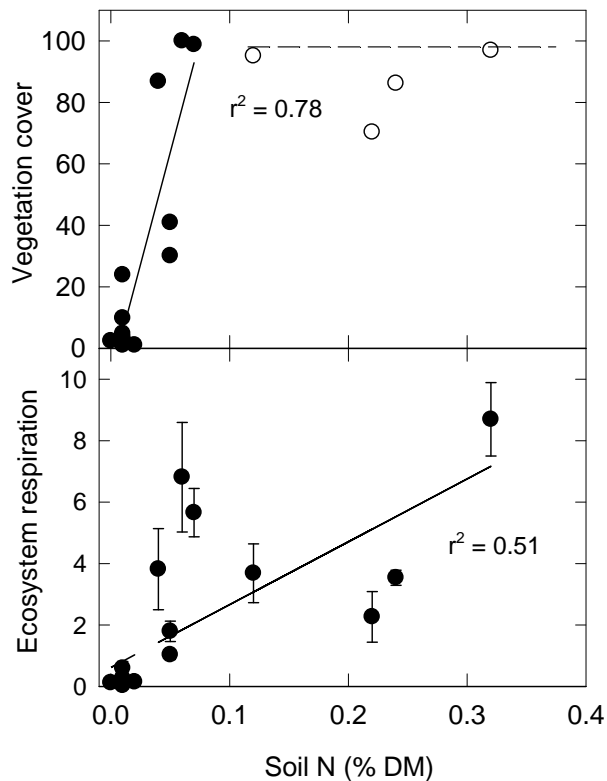


Fig. 3. Vegetation surface cover (top panel; in %) and ecosystem respiration (bottom panel; in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in the permanent plots on Surtsey as a function of soil N. Only plots with $N < 0.10\%$ were included in the regression analysis for vegetation cover (filled symbols). Each point of R_e is an average for 4 measurements \pm SE.

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