

Effects of seabird nitrogen input on biomass and carbon accumulation after 50 years of primary succession on a young volcanic island, Surtsey

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Abstract

What happens during primary succession after the first colonizers have occupied a pristine surface largely depends on how they ameliorate living conditions for other species. For vascular plants the onset of soil development and associated increase in nutrient (mainly nitrogen, N) and water availability is especially important. Here, we report the relation between N accumulation and biomass- and ecosystem carbon (C) stocks in a 50-year-old volcanic island, Surtsey, in Iceland, where N stocks are still exceptionally low. However, a 27-year-old seagull colony on the island provided nutrient-enriched areas, which enabled us to assess the relationship between N stock and biomass- and ecosystem C stocks across a much larger range in N stock. Further, we compared areas on shallow and deep tephra sands as we expected that deep-rooted systems would be more efficient in retaining N. The sparsely vegetated area outside the colony was more efficient in N retention than we expected and had accumulated $0.7 \text{ kg N ha}^{-1} \text{ y}^{-1}$, which was ca. 60% of the estimated N input rate from wet deposition. The seagulls have added, on average, $47 \text{ kg N ha}^{-1} \text{ y}^{-1}$, which induced a shift from belowground to aboveground in ecosystem N and C stocks and doubled the ecosystem 'N use efficiency', determined as the ratio of biomass and C storage per unit N input. Soil depth did not significantly affect total N stocks, which suggests a high N retention potential. Both total ecosystem biomass and C stocks were strongly correlated with N stock inside the colony, which indicated the important role of N during the first steps of primary succession. Inside the colony, the ecosystem biomass C stocks ($17\text{-}27 \text{ kg C ha}^{-1}$) had

30 reached normal values for grasslands, while the soil organic carbon stocks (SOC; 4-10 kg C ha⁻¹)
31 were only a fraction of normal grassland values. Thus, it will take a long time until the SOC stock
32 reaches equilibrium with the current primary production, during which conditions for new
33 colonists may change.

34

1. Introduction

Primary succession, the chain of processes in which an ecosystem develops on an unvegetated substrate that lacks a developed soil (Vitousek et al., 1989; Walker and Del Moral, 2003), is a complex process that depends on the interplay of numerous factors, both biotic and abiotic (Raab et al., 2012). Most studies on primary succession of volcanic islands and inland volcanos have focused on community changes in flora and fauna (e.g. Walker et al., 2003; Magnússon et al., 2009; Marteinsdottir et al., 2010), but fewer have looked into changes in underlying environmental drivers for community change (Walker and Del Moral, 2003). Yet, such drivers often play a crucial role in the onset of ecosystem development (Kögel-Knabner et al., 2013) and are also often a function of long-term ecosystem processes, such as soil development (Long et al., 2013a).

The buildup of biomass leads to the accumulation of soil organic carbon (SOC), which is an indicator of soil development (Kögel-Knabner et al., 2013). SOC greatly improves the physical and chemical properties of soil, such as water holding capacity and ion exchange capacity, thereby enhancing nutrient retention and exchange (Deluca and Boisvenue, 2012). As the successful germination, establishment and growth rate of many species strongly depends on these soil properties, the presence of well-developed soils forms an ecological threshold for many species (Long et al., 2013b). Consequently, biomass and carbon (C) accumulation form an important step in the course of primary succession that enables less stress-tolerant and often more

productive species to arrive (Grime, 1977). A positive reciprocal relationship can be expected between SOC (and its source, biomass production) and nutrient accumulation (Li and Han, 2008). On the one hand, SOC facilitates the retention of nutrients, while on the other hand improved nutrient supply has a positive effect on plant biomass in all terrestrial systems (Gruner et al., 2008), which leads to increased SOC accumulation. Therefore, we expected the amount of nutrient input to be an important determinant of biomass and C accumulation during primary succession. Once the system has reached a sufficient level of fertility for, often more productive, secondary colonizers to establish, they will enhance SOC production and a positive feedback loop between biomass production (SOC) and nutrient accumulation will initiate. Subsequently, the rate of primary succession has been shown to increase following such fertility change (Olf et al., 1993; Vitousek et al., 1993; Sigurdsson and Magnússon, 2010).

Of all nutrients, nitrogen (N) is most frequently the limiting nutrient for plant growth in high latitude terrestrial ecosystems due to the adverse effect of cold temperatures on biogeochemical processes (Aerts and Chapin, 2000; Reich and Oleksyn, 2004; Storm and Suess, 2008), and this is even more pronounced on young substrates (Vitousek et al., 1993; Vitousek and Farrington, 1997; Elser et al., 2007). Therefore, N is expected to be strongly linked with SOC accumulation during primary succession of young volcanic islands at high latitudes.

Surtsey is a volcanic island which surfaced during a submarine eruption between 1963 and 1967, and has from the very beginning been strictly protected for research (Baldurson and Ingadóttir, 2007). This makes it an exceptionally suitable location to study the natural course of successional processes. As Surtsey is still a young volcanic island, its vegetation is expected to be N limited (Vitousek et al., 1993; Vitousek and Farrington, 1997; Elser et al., 2007). Nitrogen has indeed been identified as a strong limiting factor for plant growth and succession at Surtsey (Hendriksson, 1976; Magnússon and Magnússon, 2000), and the N:P ratio of five dominant plant species on Surtsey generally indicates a strong N limitation ($N:P < 14$; Aerts and Chapin, 2000) (Thuys et al., 2014).

The importance of nutrients became very visible after the establishment of a seabird colony in 1986 (mainly lesser black backed gull, *Larus fuscus*) on the SW side of the island (Magnússon and Magnússon, 2000) (Fig. 1). Seabirds are known to transfer nutrients, primarily ammonium and nitrate, from sea to land (Polis and Hurd, 1996; Anderson and Polis, 1999; Ellis et al., 2006; Nie et al., 2014). The effect of enhanced nutrient inputs has been studied by comparing surfaces that were unaffected by seabirds with the seabird-colonized area (Magnússon and Magnússon, 2000; Magnússon et al., 2009; Sigurdsson and Magnússon, 2010). In the seabird colony, the rapid increase in soil N elicited subsequent increases in plant cover and species richness. These earlier studies did, however, not attempt to quantify the rate of N accumulation or study the development of the whole ecosystem biomass, C or nutrient stocks.

Within the seabird colony at Surtsey, the earlier studies have revealed diverging successional trajectories of vascular plant communities between areas with deep tephra sand or with surfacing lava rocks (Magnússon and Magnússon, 2000). This has become even more pronounced during the past decade (Del Moral and Magnússon, 2014), showing faster development of species richness and plant cover in seabird colony plots on deep tephra sand.

The main goal of this study was to quantify the rate of N accumulation in different permanent study plots on Surtsey and investigate how this compared to changes in the whole ecosystem biomass and C stocks. Despite the fact that earlier studies have revealed drastic effects of the seabird-derived N input on the ecosystem structure and functions on Surtsey (Magnússon and Magnússon, 2000; Kristinsson and Heidmarsson, 2009; Magnússon et al., 2009; Petersen, 2009; Sigurdsson and Magnússon, 2010; Del Moral and Magnússon, 2014; Thuys et al., 2014) no data exist on the annual N input coming from seabirds, except from a coarse estimate of (Magnússon et al., 2009), who combined excretion and food models for the lesser black-backed gull (*Larus fuscus*) and the herring gull (*Larus argentatus*) derived from Hahn et al. (2007), and nest counts on Surtsey. We therefore attempted to obtain a more precise approximation of the seabird derived N input by measuring total N stocks and correcting for the total colonization time. Our null hypothesis was that the annual net N accumulation rate inside the seabird colony amounts to ca. 30 kg N ha⁻¹ as was estimated by Magnússon et al. (2009).

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110 Further, we tested four hypotheses in detail:

111 (i) Atmospheric N deposition is the main N source outside the seabird colony. As we do not
112 expect that this sparsely vegetated area is very efficient in N retention, large amounts of N can be
113 lost due to leaching during large rain events. Field observations in different ecosystems with low
114 N input rates, as is the case outside the colony, revealed an average N retention of 75% (Thomas
115 et al., 2013). Therefore, we hypothesized that total N stocks outside the seabird colony would
116 approximate 75% of the total estimated accumulated atmospheric N deposition during the past 50
117 years.

118 (ii) Among similar vegetation types, those with deeper root systems were shown to be more
119 effective in avoiding N leaching losses than their shallower rooting equivalents (Bowman et al.,
120 1998). On Surtsey, most N that leaches through the upper substrate layer is removed from the
121 system by seeping into cracks and fissures in the lava bedrock. Therefore, we hypothesized that
122 plots on deep tephra sand show higher N retention compared to plots on shallow tephra sand.

123 (iii) Nutrient rich systems are known to invest relatively more in aboveground plant growth than
124 nutrient poor systems (e.g. Warembourg and Estelrich, 2001; Wang et al., 2008; Gao et al., 2011;
125 Zhou et al., 2014). Therefore we expected to find a shift from belowground to aboveground
126 biomass, C and N stocks inside the seagull colony, compared to outside the colony.

127 (iv) An important factor in the process of soil development, the process in which bedrock
128 material is transformed into a soil with defined horizons by a combination of climate, biota,
129 topography, parent material and time, is the accumulation of SOC (Kögel-Knabner et al., 2013).
130 As SOC is a product of biomass degradation, we hypothesized that the increased productivity
131 within the seagull colony enhances the rate of soil development.

132

2. Material & Methods

2.1. Site description

Samples were collected on Surtsey (63°18'11"N 20°36'17"W) in mid July 2012 and mid July 2013. The island surfaced during an eruption between 1963 and 1967 and was 1.41 km² in 2004. Surtsey is the youngest island of the Vestmannaeyjar archipelago, which is located on the insular shelf 32 km off the south coast of Iceland. The archipelago constitutes a separate volcanic system, which initiated activity around 100.000 years BP (Jakobsson, 1979). Climate conditions on the archipelago are humid sub-arctic. Winter and summer average temperatures between 1971 and 2000 were 1.5-2 °C and 10 °C, respectively (Icelandic Meteorological Office). Total annual precipitation during the same period was on average 1600 mm and fell mainly between October and March. The prevailing wind direction is East, and wind speed exceeds hurricane force ($>32.7 \text{ m s}^{-1}$) on average 15 days per year (Icelandic Meteorological Office). The bedrock of the higher parts of Surtsey consists of basalt tuff, whereas in its lower parts it is made out of basaltic lava (Jakobsson, 1968). The island is still too young to have well developed soils. The lava is partly filled with tephra sand and silt, which originates from the eruption, from erosion of the bedrock material and by aeolian transport from the mainland. The vegetation on these sandy areas is dominated by *Honkenya peploides* and *Leymus arenaria* (Magnússon et al., 2014; Stefansdottir et al., 2014). In 1986, a seabird colony of lesser black backed gulls (*Larus fuscus*) was established in a confined area on the SW edge of the island (Petersen, 2009), and has been expanding in size

ever since. The dominant plant species inside the seagull colony are *Poa pratensis*, *P. annua* and *Festuca richardsonii* (Magnússon et al., 2009).

2.2. Sample sites

Between 1990 and 1995, permanent 10x10 m plots were established on Surtsey to survey ecosystem changes in and outside the seabird colony (Fig. 1). Out of these plots, we selected 18 representative plots inside and outside the seabird colony, partly on deep (≥ 30 cm deep) and partly on shallow tephra sand (< 30 cm deep). Ten plots were situated outside the colony (of which six were sampled in 2012 and four in 2013) and eight plots were situated inside the colony (of which four were sampled in 2012 and four in 2013). In every case, half of the plots were located on shallow and the other half on deep tephra sand. We placed three subplots (20x50 cm) for destructive sampling 0.5 m outside the southern edge of each permanent plot ($n_{\text{outside colony}} = 30$; $n_{\text{inside colony}} = 24$).

2.3. Vegetation & soil sampling

During the two expeditions to Surtsey, all vascular plants were cut in each subplot (20x50 cm) and subsequently separated into species in the field. Next, the litter layer was collected from the same plots, except in the more vegetated seabird colony, where it was collected from a 20x20 cm subplot within the harvest plot. Soil was then sampled from where the litter had been removed using a hand-driven soil corer (8.67 cm diameter). Consecutive soil samples of 5 cm depth were

taken down to 30 cm depth or until the bedrock was reached. All samples were air dried awaiting further analyses.

2.4. Sample preparation and chemical analysis

Fine roots (all roots were of diameter < 2 mm) were picked manually from soil samples in the laboratory, for maximum 60 minutes per sample. In case where litter was found during the sorting process, it was added to the litter sample. The root-free soil was sieved through a 2 mm sieve in order to separate the coarse soil fraction (> 2 mm) from the sand, silt and clay particles (< 2 mm). All fractions (1) roots, (2) soil particles < 2 mm and (3) soil particles > 2 mm) were dried for 48 h at 40 °C. The coarse fraction was assumed to contain only a marginal amount of organic C or N. In few cases where the sample weight was too small for analysis (< 1 g dry weight), samples from the same layer were merged by neighboring subplots within the same plot. The basaltic tephra sand in Surtsey does not contain any carbonates (mineral C), and inorganic N was assumed to be negligible compared to the total SON (soil organic nitrogen) stock (Ponnameruma et al., 1967), and was therefore not measured.

After drying all biomass samples for 48 h at 40 °C, dry mass of (1) all aboveground vascular plants (separated in monocotyledons, eudicotyledons and ferns and horsetails), (2) moss, (3) litter and (4) fine roots (in 0-5, 5-10, 10-20 and 20-30 cm depth layers) was weighed.

187 For each sample, 1 g dry mass (DM) was milled using a ball mill (Retsch MM301 Mixer Mill,
188 Haan, Germany) and then total C and N concentrations were analysed by dry combustion on
189 Macro Elementary Analyzer (Model Vario MAX CN, Hanau, Germany). C and N concentration
190 was determined for (1) all aboveground vascular plant parts together, (2) litter, (3) moss, (4) roots
191 and (5) soil particles (< 2 mm) per aforementioned soil layers. Soil samples were then dried at
192 105 °C for 48 hours and weighed again to get the correct DM.

193 *2.6. C and N stocks and accumulation rates*

194 Carbon- and N stocks in (1) aboveground vascular plant biomass, (2) litter and (3) moss were
195 estimated by multiplying total DM with the respective concentrations and were expressed per unit
196 area. Carbon- and N stocks in (1) roots and (2) soil particles (< 2 mm) per unit area were
197 calculated per soil layer by multiplying total DM < 2mm of the soil layer with the respective
198 concentrations.

199 For the plots outside the seabird colony, N accumulation rate was calculated by dividing the total
200 N stock by the number of years since the start of accumulation (from 1963, the year of the
201 surfacing of the island), assuming a constant N accumulation rate. For the plots inside the seabird
202 colony, a separate estimate was made for the N accumulation rate of seabird derived N. Therefore
203 the total N stock of plots inside the colony was first subtracted by the amount of total N stock
204 outside the colony, assuming that this equals the non-bird N input over the whole island.

Subsequently, the remaining N stock was divided by the years since seagulls started to breed within 1000 m² of each plot; information that was available from (Magnússon and Magnússon, 2000; Magnússon et al., 2009).

2.7. Data analyses

Differences in ecosystem N stocks, biomass and C stocks were tested with generalized linear models in the R software (R Development Core Team, 2012), with seabird colony (yes – no) and tephra depth (deep-shallow) as fixed variables, and plots and sampling year (2012 and 2013) as random variables. Random factors were excluded whenever insignificant. Differences in N accumulation rate and in proportional distribution of SON and root N per soil depth layer were tested in the same way. The correlations between (1) biomass stocks, (2) ecosystem C stocks and (3) root/shoot ratios (R/S ratios) and ecosystem N stocks were tested separately for plots within and outside the seagull colony. Therefore, we used a correlation test, applying the “Spearman” method, whenever the assumptions of homoscedasticity (tested with residual plot) or linearity (tested with the runs test (Turlach, 2011; Trapletti et al., 2012; Zeileis et al., 2012)) were not met. Null hypotheses were rejected when $p < 0.05$.

3. Results

3.1. Ecosystem N stock and distribution

The total N stock outside and inside the seabird colony after 50 years of island development and ca. 26-27 years after the first lesser black backed gull colonization differed significantly, by a factor of approximately 30 (Fig. 2, Table 1). Soil depth had no significant effect on total accumulated N stock (in biomass and soil), neither outside nor inside the seabird colony. Also, the N stock of the living compartment (shoots, roots and moss together) and of shoots, roots and moss separately did not differ between deep and shallow tephra sand. However, inside the seagull colony, the N stock of the dead OM (organic material) compartment (litter and SON combined), and of the litter and SON separately, was significantly higher in deep tephra sand than in shallow tephra sand on lava (Fig. 2, Table 1).

Of the total N stock outside the colony, approximately 96% of the N was stored belowground in roots and SON, while within the colony this was reduced to about 78 and 88% in deep and shallow tephra sand, respectively (Fig. 2).

The amount of N stored as SON was 24 (on deep tephra sand) and 11 (on shallow tephra sand) times higher inside than outside the colony (Fig. 2, Table 1). Despite this drastic effect on absolute SON stocks, the seagull colony did not change the relative distribution of SON through the upper 30 cm of the soil profile. Irrespective of the bird influence, about 35% of the total SON

in deep tephra sands was located in the upper 5 cm, and decreased gradually to about 5% at 25-30 cm depth (Fig. 3, Table 2).

3.2. Nitrogen accumulation rate

The average rate of total N accumulation (in both living and dead compartments) over the 50 years of island succession was $0.7 \text{ kg ha}^{-1} \text{ y}^{-1}$ outside the seagull colony and the effect of tephra depth was not significant (Fig. 4, Table 1). In sharp contrast, the seabirds accelerated the N accumulation rate, with a factor of almost 50 - 100, to 36 and $58 \text{ kg ha}^{-1} \text{ y}^{-1}$ on shallow and deep tephra sands, respectively (Fig. 4). Within the seabird colony the difference in N accumulation was significantly different with tephra depth (Table 2).

3.3 Ecosystem biomass and C stocks and SOC concentrations

The area inside the colony contained 50 times more biomass than the plots outside of the bird colony, irrespective from tephra depth. For C, the area inside the colony contained 29 times more C than the area not affected by the seabirds on deep tephra sand, and 16 times more C on shallow tephra sand (Fig. 5, Table 1).

The seabird colony increased all individual stocks of biomass and C, both belowground as aboveground (Fig. 5, Table 1). The living biomass stock was over 50 times larger ($0.7 \text{ vs } 36 \text{ kg ha}^{-1}$ outside and inside the colony, respectively), and the living biomass C stock was almost 70 times higher ($0.19 \text{ vs } 13 \text{ kg ha}^{-1}$ outside and inside the colony, respectively) (Fig. 5). The

proportion of C stored in living biomass compared to SOC also shifted drastically; from a 24:76 distribution outside the colony, to a 68:32 distribution inside the colony.

Tephra depth, however, had only an effect inside the colony. There, the plots on deep tephra sand stored more litter, litter C, SOC and total C than those on shallow sand layers (Fig. 5, Table 1). The SOC stock in deep tephra sand (10 kg C ha^{-1}) was more than twice as large than on shallow tephra sand (4 kg C ha^{-1}) (Fig. 5).

On deep tephra sand, the seabird colony had a pronounced effect on the relative distribution of the roots (Fig. 3). Outside the colony, the roots were evenly distributed throughout the upper 10 cm of the soil. Inside the colony, however, the roots were concentrated in the top 5 cm (57% of the total root weight within 30 cm depth), and declined to a fraction of only 4% between 20 and 30 cm depth.

The SOC concentration in the upper 5 cm of the tephra sand outside the colony was 0.12 ± 0.02 % (error is SE; data not shown). Inside the colony, there was a significant depth effect on SOC concentration in the upper 5 cm of the tephra sand. On deep tephra sand, the SOC concentration was 0.9 ± 0.3 %, whereas it was as high as 4.6 ± 0.4 % on shallow tephra sand (errors are SE's; data not shown).

3.4. Impacts of ecosystem N stock on biomass and C stocks

There was a highly significant positive linear relationship within the seagull colony between total ecosystem biomass and C stock on the one hand and total ecosystem N stock on the other hand (Fig. 6), while almost half of the N and C was located in the soil (50 and 40% on deep and shallow soils respectively), and was therefore not directly related to the biomass. An increase of one g of N could support extra 32 g biomass and 20 g of ecosystem C. Outside the colony, neither biomass nor C showed a significant correlation with total N stock (here approximately 80% of N and C was located in the soil), but for one g N, a median of 17 and 12 g of biomass or C stock were found (Fig. 6). There was no significant correlation between R/S ratio and ecosystem N stock, outside, neither inside the colony (Fig. 7). The variation in the measured R/S ratio was large. The values ranged from 0.1 to 194 outside the colony and from 1.8 to 96 inside (Fig. 7). The median R/S ratios were 18 and 5, outside and inside the seabird colony, respectively.

4. Discussion

4.1. Nitrogen accumulation outside the seabird colony

The mean N accumulation rate in soil and biomass outside the seabird colony during 50 years since Surtsey first emerged ($0.7 \text{ kg ha}^{-1} \text{ y}^{-1}$, Fig. 4), represents about 50-60% of the estimated annual atmospheric N deposition rate in Iceland corrected to 1600 mm annual precipitation ($1.3 - 1.4 \text{ kg N ha}^{-1} \text{ y}^{-1}$) (Gislason et al., 1996; Sigurdsson et al., 2005). This estimate of 50-60% retention is somewhat low compared to the average N retention in systems under low N input (75%, Thomas et al., 2013) and even more so compared to the >80% N retention in bare dune habitats reported by ten Harkel et al. (1998). This could be explained by the initial lack of plants on the island, resulting in higher leakage during the first years. After establishment of the primary colonizers in the 1970s and 1980s, the total aboveground vegetation cover outside the colony has remained low and stable ($3.0\% \pm 0.3$) since the start of detailed measurements in 1994 (Magnússon, unpublished data). Despite the very sparse aboveground vegetation cover, it became evident during sampling that the unvegetated tephra sand areas were fully colonized by roots. Another study, which took place on and around *Leymus* dunes in the same area outside the seagull colony, but not within our permanent study plots, found similar dense root distribution (Stefansdottir et al., 2014). Therefore, we can assume that after vegetation establishment the N

303 retention on Surtsey has increased and is now close to the 75-80% reported for ecosystems with
304 low N inputs (Thomas et al. 2013).

305 We assume atmospheric deposition to be the main source of N outside the seabird colony.
306 Additional mechanisms of N input could be: (1) N inputs from volcanic processes, (2) chemical
307 weathering of N-containing bedrock, (3) N input from overflying birds, (4) symbiotic N₂ fixation
308 (5) free living N₂ fixation and (6) N fixation by lichens and biological soil crusts (BSC).

309 Mechanisms (1) and (2) can be largely rejected, since Ponnameruma et al. (1967) showed that the
310 tephra sands of Surtsey did not contain any organic N and very little inorganic NH₄ and NO₃; the
311 latter probably mostly originating from rainfall during the first 4 years since the eruption started.

312 This study did report some inorganic N in recently deposited tephra, which could indicate
313 volcanic N sources (cf. Huebert et al., 1999). However, the concentrations were lower in the
314 older tephra layers, probably indicating leaching due to initial lack of biological activity to retain
315 the NO₃. Further, we argue that N deposited by overflying birds (3) was of minor importance,
316 because, as was stated above, total plant cover did not increase between 1994 and 2012 in any of
317 the permanent plots outside the seabird colony (Magnússon, unpublished data). A steady increase
318 of vegetation cover after 1986 (the establishment of the colony) would be expected if overflying
319 birds added a substantial amount of N. Also N input mechanisms (4) and (5) were probably of
320 lesser importance as well, since to date no plant species known to have N₂-fixing symbionts have
321 colonized Surtsey (Magnússon et al., 2014), and because the low water retention of the tephra

sand and the low soil temperatures would not support large populations of free-living N₂ fixing microbes (Zielke et al., 2005; Sorensen et al., 2006). The mean annual soil temperature and volumetric water content were 7.5 °C and only 8.4%, respectively, at 5 cm depth during 2010-2012 (unpublished data). Mechanism (6), N-fixation by lichens or biological soil crusts, must be occurring on Surtsey, because Kristinsson and Heidmarsson (2009) found known N₂-fixing species on the island. However, these species had a very limited distribution on the island, and their N input to the ecosystem is therefore assumed to be negligible for the island as a whole.

4.2. Nitrogen accumulation inside the seabird colony

The SON values from Surtsey ranged from 0.03 to 0.65 ton ha⁻¹, and span the whole range that Lin et al. (2000) modeled for Iceland (0.0 - 0.5 ton ha⁻¹). This shows well the large effect the seabirds have had on the N stock on Surtsey in only 27 years. The apparent lack of other major N inputs on Surtsey, which typically complicate the quantitative estimation of seabird-driven N input rates, enabled us to calculate a reliable estimate of N input rates by seabirds from the measured N stocks and seabird colonization duration.

The seabirds increased the ecosystem N-stock 30-fold during 26-27 years, compared to the area outside the seagull colony, equivalent to an input rate of 47 kg ha⁻¹ y⁻¹ averaged across both substrate types. This value was much higher than we originally hypothesized, but it corresponded

almost exactly with the estimate of Bancroft et al. (2005) ($50.9 \text{ kg ha}^{-1} \text{ y}^{-1}$) for a Wedge-tailed Shearwaters (*Puffinus pacificus*) colony on Rottnest Island (West-Australia), who used guano traps to estimate seabird-derived N deposition. We are not aware of other studies that attempted to estimate seabird N input rates, but our own calculations, based on a study of Breuning-Madsen et al. (2010), who measured the N stocks in a 24-years old Cormorant colony in the Horsens Fjord (Denmark), resulted in even higher N input rates (an average of $292 \text{ kg ha}^{-1} \text{ y}^{-1}$). The SON concentration in the upper 10 cm of soil inside the bird colony at Surtsey ($2.5 \text{ mg g}^{-1} \text{ DM}$) was higher than what was found by Ligeza and Smal (2003) in perennial colonies of piscivorous birds in northern and eastern Poland ($\sim 0.6 \text{ mg g}^{-1} \text{ DM}$), but was very similar to that reported by Anderson and Polis (1999) for seabird colonies on hyperarid, naturally nutrient-poor islands in the Gulf of California ($\sim 2 \text{ mg g}^{-1} \text{ DM}$). It must be noted that both these studies investigated longer-lived bird colonies. Given the high organic-matter retention capacity of the andosols at Surtsey, it might be that SON concentrations increase even further, but this remains speculation..

4.3. Effect of tephra-layer depth on N retention

Even if SON and litter N accumulation were significantly higher at the deeper tephra sands within the seagull colony, we did not find a significant effect of tephra-layer depth on total N

stock, when biomass-N was included. This suggests a high N retention potential in the upper centimeters of the tephra sand. This finding contradicts with our second hypothesis, that deeper substrates would positively affect N retention, as was shown by Selman et al. (2014). Faster succession rates on the deeper tephra sands in Surtsey (Magnússon and Magnússon, 2000; Del Moral and Magnússon, 2014) can therefore not be explained solely by increased N accumulation rates.

4.4. Shifts from belowground to aboveground plant biomass

Despite the fact that the median R/S ratio outside the colony (18) was almost three times higher than the upper extreme for cool temperate deserts reported by (Mokany et al., 2006), it corresponded closely with the mean ratio of 19 reported by (Stefansdottir et al., 2014) for the *Leymus* area outside the seabird colony. For the grassland inside the colony, the median R/S of 5 did not differ much from the median reported by Mokany et al. (2006) for cool temperate grasslands without bird colonies. Given the more severe nutrient limitation expected for cool temperate grasslands compared to grasslands in a seabird colony, this similar R/S was unexpected. We therefore assume that the low water retention capacity of the sands on Surtsey caused frequent droughts and that the positive impact of drought on R:S offset the negative effect of seabird-driven nutrient inputs (see discussion below).

Changes in nutrient availability can often be detected by looking at R/S ratios (Levang-Brilz and Biondini, 2003; Chu et al., 2006), as increased nutrient availability promotes investment in aboveground plant parts. Therefore, we hypothesized (hypothesis iii) a decrease in R/S ratio with increasing ecosystem N stock. Despite the fact that previous research has shown negative correlations between R/S ratio and nutrient availability in grassland ecosystems (Levang-Brilz and Biondini, 2003; Chu et al., 2006), no such relationship was found on Surtsey, neither inside, nor outside the colony. Outside the seabird colony, such a potential relationship might be concealed by the patchiness of the aboveground vegetation, the homogeneous root distribution (Stefansdottir et al., 2014) and the relatively small size of the measurement frames. The combination of these three factors probably explains why we measured several unrealistically high R/S ratio's, ranging up to 194. Inside the seabird colony, the lack of relationship between R/S and N stock is possibly due to other factors, such as limiting water availability, overruling the effect of N availability on the R/S ratio. Drought has been reported to be an important determinant of R/S ratios (Donkor et al., 2002; Gianoli et al., 2009; Dreesen et al., 2012) and water infiltration in Andosols is rapid compared to most other soils (Basile et al., 2003), especially when the carbon content is below 12% as is the case on Surtsey (Arnalds, 2008). Therefore, we attribute the absence of a clear nutrient influence on R/S to an overruling effect of drought in all occurring nutrient situations.

395 *4.5. Shifts from belowground to aboveground N and C and 'N use efficiency'*

396 The clear shift in both N and C from belowground to aboveground stocks inside the colony
397 agrees with our hypothesis iii that the increase in nutrient availability inside the colony would
398 stimulate the system to invest more in aboveground growth. This relationship between nutrient
399 availability and growth investment confirms many earlier studies (e.g. Warembourg and
400 Estelrich, 2001; Wang et al., 2008; Gao et al., 2011; Zhou et al., 2014). This shift from below- to
401 aboveground was accompanied by a doubling of the N use efficiency; the grassland inside the
402 colony supported ~ 2 times more biomass and biomass-C per g N, compared to the almost
403 unvegetated area outside the colony. This large increase in the 'N use efficiency' indicated a
404 positive feedback between N stock and the storage of both biomass and C. This increase was
405 caused by the drastic shift in C distribution: from a 76:24 towards a 32:68 proportion in SOC and
406 biomass, respectively. The C/N ratio of SOC was smaller than that of biomass (10.4 ± 0.6 vs.
407 39.1 ± 2.3 (mean \pm SE)), in line with the C/N ratios for undisturbed soils reported by Chapin et
408 al. (2011) (~14) and for leaves reported by Sterner and Elser (2002) (~36). Hence, the overall
409 C/N ratio of ecosystems with most C stored in SOC (such as the non-colonized area) is typically
410 smaller than the overall C/N ratio of ecosystems with a high fraction of C stored in living
411 biomass (such as in the seabird colony).

The reason why higher N-stocks can support more biomass and C per unit N remains to be better explored. Several studies on immature volcanic soils in New Zealand, Chile and Japan have found a positive relationship between total N-stock and net N-mineralization rates (and consequently plant available N) (Parfitt et al., 2005; Hirzel et al., 2010; Yamasaki et al., 2011). In the last study, the increased N-mineralization following N-addition was proved to be correlated with the inhibition of microbial N-immobilization (and consequently decreased competition between plant and microbial N-uptake). This inhibition of N uptake by microbes was proposed to result from (1) nitrification-induced acidification, (2) increased soil osmotic potential to toxic values and (3) an inhibition of ligninolytic enzyme production. The significant acidification inside the seabird colony on Surtsey (Sigurdsson and Magnússon, 2010) supports this hypothesis, however, further study is needed to investigate the role of microbial N-immobilization in N-availability for plants on Surtsey.

4.6. Seabird effect on biomass and C stocks

Aboveground biomass outside the colony ($0.13 \pm 0.08 \text{ ton ha}^{-1}$) was very small and has almost not changed since the first measurements of aboveground biomass in the permanent plots in 1999 (0.1 ton ha^{-1}) (Magnússon et al., 2009). This invariable aboveground biomass probably also indicates relatively little changes in belowground biomass. As biomass degradation is an

important source of SOC (Kögel-Knabner et al., 2013), the low biomass production rates outside the seagull colony explain largely the quasi constant SOC concentration and the lack of soil formation. Since 1986, the seabird influence caused an over 50-fold increase of total biomass, from 0.7 to 36 ton ha⁻¹, which corresponds to a shift from values typical for deserts (0-20 ton DM ha⁻¹) to values typical for grassland ecosystems (20 to 50 ton DM ha⁻¹) (Larcher, 2003). This large increase in only 25 years can largely be attributed to seabird N input, as there was a strong positive relationship between total ecosystem biomass stock and N stock (as proxy for available N) inside the seabird colony.

The aboveground biomass has been increasing nearly linearly from 1.4 ton ha⁻¹ in 1999 to 4.1 ton ha⁻¹ in 2007 (Magnússon et al., 2009) to 5.9 ± 0.9 ton ha⁻¹ (error = SE) in 2012-2013. This steady increase indicates that aboveground limitations on growth, such as competition for light and space, were minor compared to the belowground limitations for water and nutrients. This could be expected in a natural grassland ecosystem with relatively low nutrient levels (Kiaer et al., 2013). This was also supported as well by the strong link between biomass and N stock.

The C stock in living biomass showed a clear shift as well, from a typical desert C stock outside the colony (0.19 ton ha⁻¹; desert ecosystems: 0-10 ton ha⁻¹; Larcher, 2003) to a stock typical for grassland ecosystems inside the colony (13 ton ha⁻¹; grassland ecosystems: 10-25 ton ha⁻¹; Larcher, 2003). However, despite the fact that biomass and living C-stock both have been

developing from desert to grassland, the SOC accumulation was lagging behind, and remained far below the average for temperate grassland soils according to (Schlesinger, 1997) (see also 4.7).

4.7. Did the N accumulation accelerate soil development?

Outside the colony, the soil development has been proceeding very slowly, as the SOC concentration, which is a reliable indicator of soil development (Kögel-Knabner et al., 2013), had only increased slightly since 1986 in the upper 5 cm of the tephra sand ($0.12 \pm 0.02\%$ SOC vs. $0.10 \pm 0.02\%$ SOC; errors are SE's) (Arnalds, unpublished data). When Surtsey had just emerged, the SOC concentration was $0.012 \pm 0.009\%$ (error is SE) (Ponnameruma et al., 1967).

Inside the colony, the SOC concentration has been increasing with a factor of 10 to 60 since the establishment of the colony, from 0.08% (taking the 1986 value as baseline SOC concentration as this was the first year of permanent seabird colonization) to $0.9 \pm 0.3\%$ on deep tephra sand and $4.6 \pm 0.4\%$ on shallow tephra sand (errors are SE's). This large increase agrees with (Stockmann et al., 2013) who hypothesized that priming effects, such as N addition, might stimulate SOC accumulation in grasslands with a high R/S. However, Stockmann et al. (2013) reported that grassland soils typically contain more than 1 - 3% SOC. Yang et al. (2014), for instance, measured a SOC concentration of 28 up to 58% in an arid grassland in North China. So despite

466 the rapid buildup, the area inside the bird colony has not yet been lifted to a SOC concentrations
467 that are typical for grassland ecosystems. Also the current stock of SOC of about 4 (shallow) to
468 10 (deep) ton ha^{-1} is still marginal compared to the average SOC stock in temperate grassland
469 soils of 192 ton ha^{-1} according to Schlesinger (1997). This indicates that the soil development at
470 Surtsey is still in its first phase. Therefore, we expect that the SOC content will continue to
471 accumulate for many centuries before it reaches an equilibrium with the aboveground
472 productivity.

473

5. Conclusion

The calculated annual N accumulation rate outside the seabird colony amounted to ca. 50-60% of the estimated atmospheric N deposition during the past 50 years. This shows that the tephra sand was much more efficient in N retention than expected. The seabird derived N input was higher than was expected based on earlier estimates for Surtsey. There was no difference in N retention between shallow and deep tephra sands, when total N stocks in biomass and soil were compared. Different succession rates on deep tephra sands within the seagull colony can therefore not be explained by increased N retention there. There was a clear shift from belowground to aboveground biomass, C and N inside the colony. Consequently, the R/S decreased from very high values outside the colony to more moderate values inside. Further, the 'N-use efficiency' or the amount C fixed per g N, was twice as high inside the colony. The accumulation of SOC, which is an indicator of soil development, was enhanced inside the seabird colony. However, despite the fact that the biomass and C stock of living material reached the typical range of grasslands, the SOC stock remained still small compared to SOC stocks in well-developed grasslands. Therefore we expect that the SOC stock will continue to increase for many centuries until it reaches an equilibrium with the litter production.

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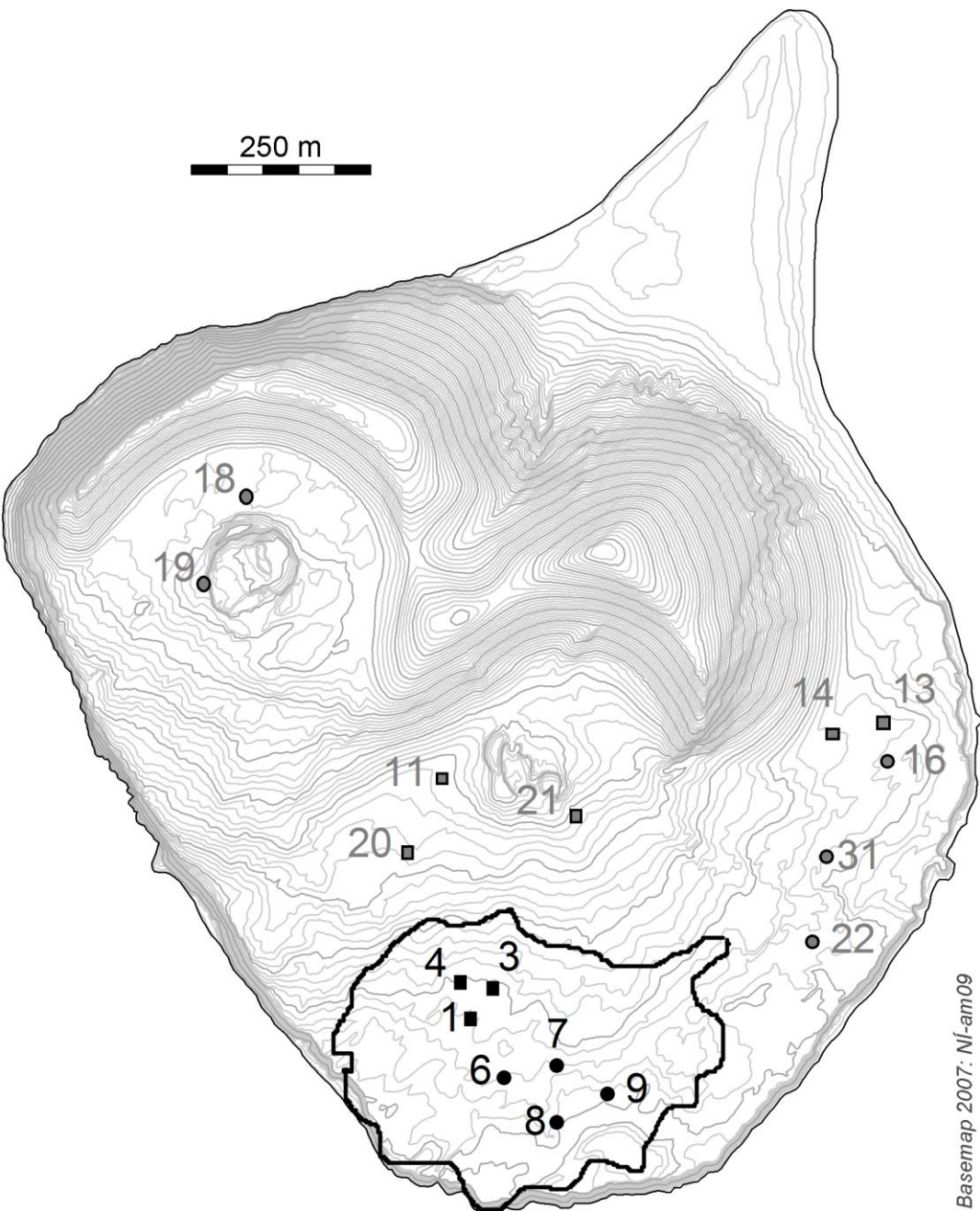
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691
692 **Fig. 1.** Location of the permanent study plots on Surtsey that were used in this study, shown on a
693 topographical map from 2007. Contour intervals are 2m, the highest point on the island is 152m
694 a.s.l.. The Eastern crater is located close to plots 18 and 19, the Western crater is located close to
695 plot 21. North of the craters, a high rim of palagonite tuff was formed. The dense vegetation

within the seabird colony in 2012 is marked with a black line (Approximation from aerial and satellite images, by Anette Th. Meier; Magnússon et al., 2014). Grey = Outside seabird colony; Black = Inside colony; Squares = Deep tephra sand; Circles = Shallow tephra sand.

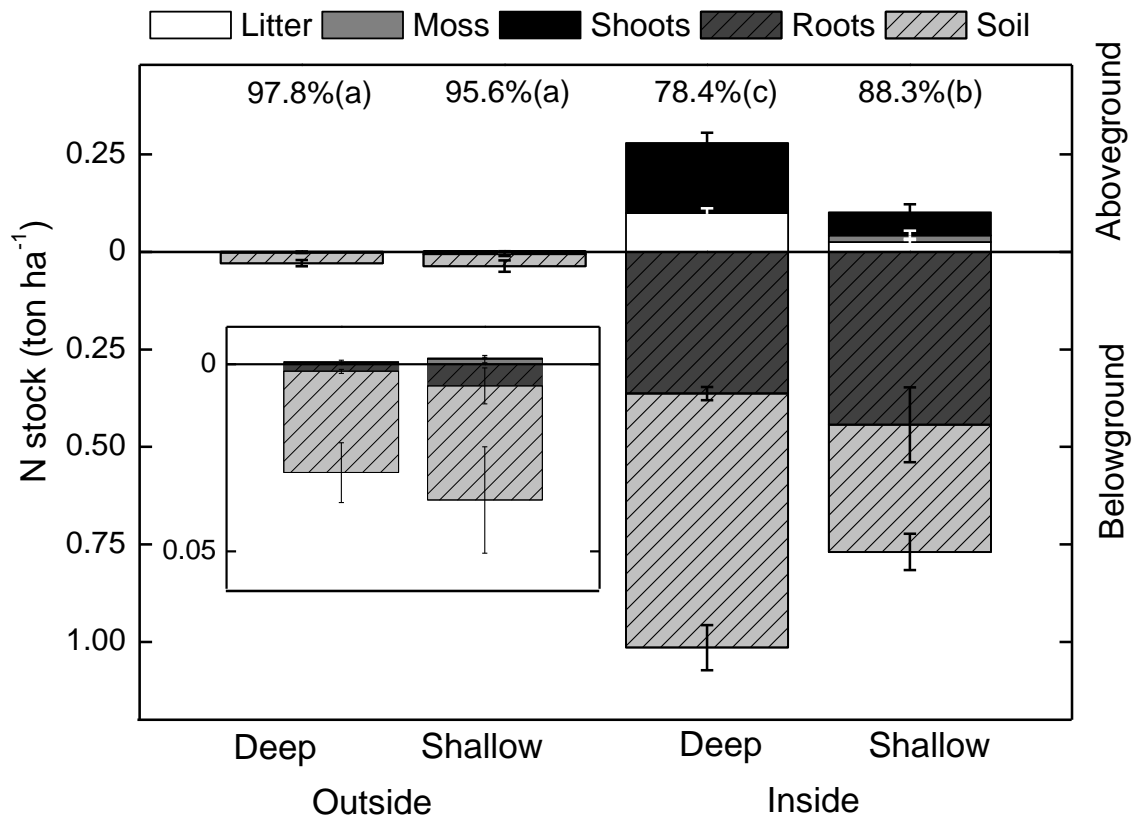


Fig. 2. Mean (\pm SE) values of the nitrogen (N) stocks in litter, shoots, roots (to 30 cm depth) and soil organic nitrogen (SON) (to 30 cm depth) in four ecosystem types on Surtsey. The inserted graph gives the small N stock outside the colony in more detail. ‘Shoots’ include all aboveground living plant parts. Statistical results for are given in Table 1. Percentages above the graph indicate the % of total N that is located belowground. Letters show statistical differences.

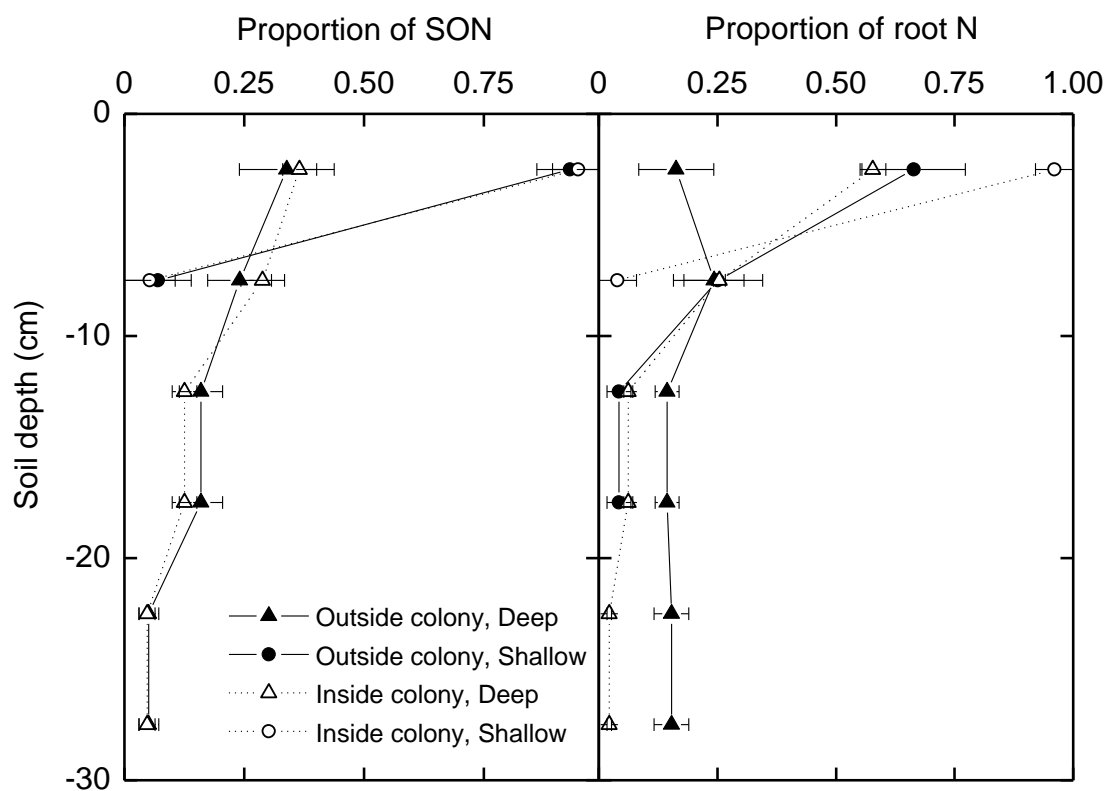


Fig. 3. Depth distribution of soil organic nitrogen (SON) and root N in four ecosystem types on Surtsey. Mean (\pm SE) proportions at each depth layer were calculated relative to the total SON or root N content in the top 30 cm. Statistical results can be found in Table 2.

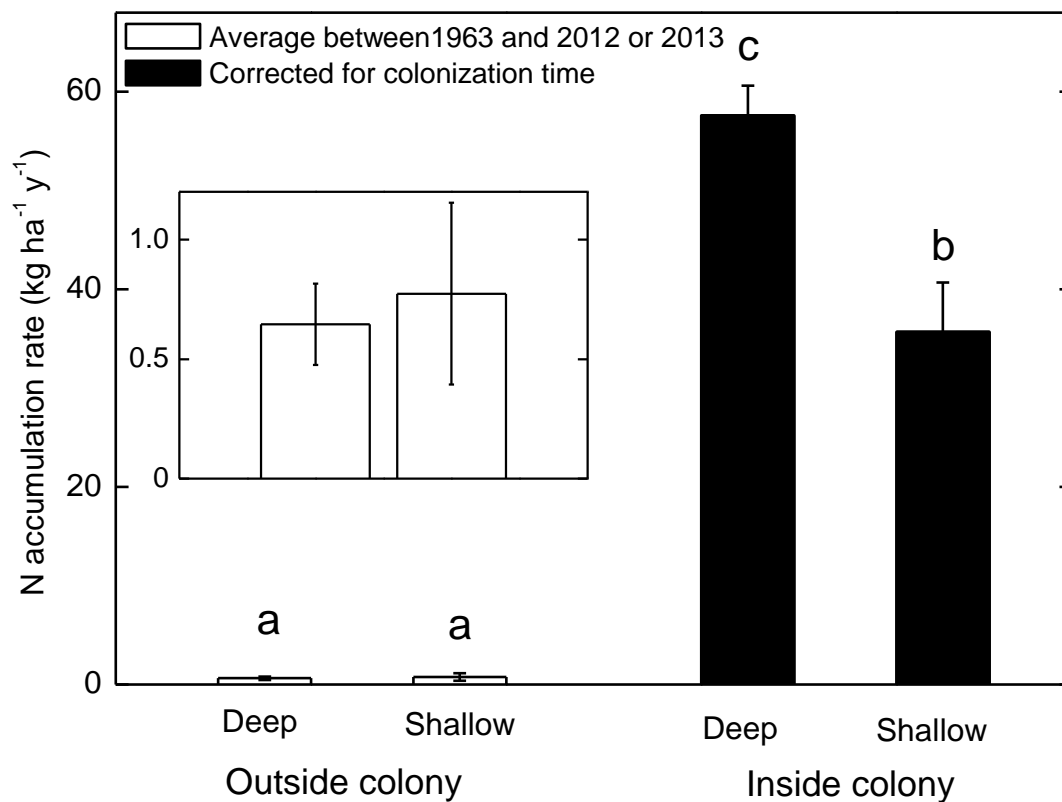


Fig. 4. Mean (\pm SE) values of the nitrogen (N) accumulation rate in four ecosystem types on Surtsey. The inserted graph gives values outside the colony in more detail. White bars show the average N accumulation values between 1963 and the sampling year (2012 or 2013). Black bars show the N accumulation after the start of seagull colonization. Statistical results are shown in Table 1.

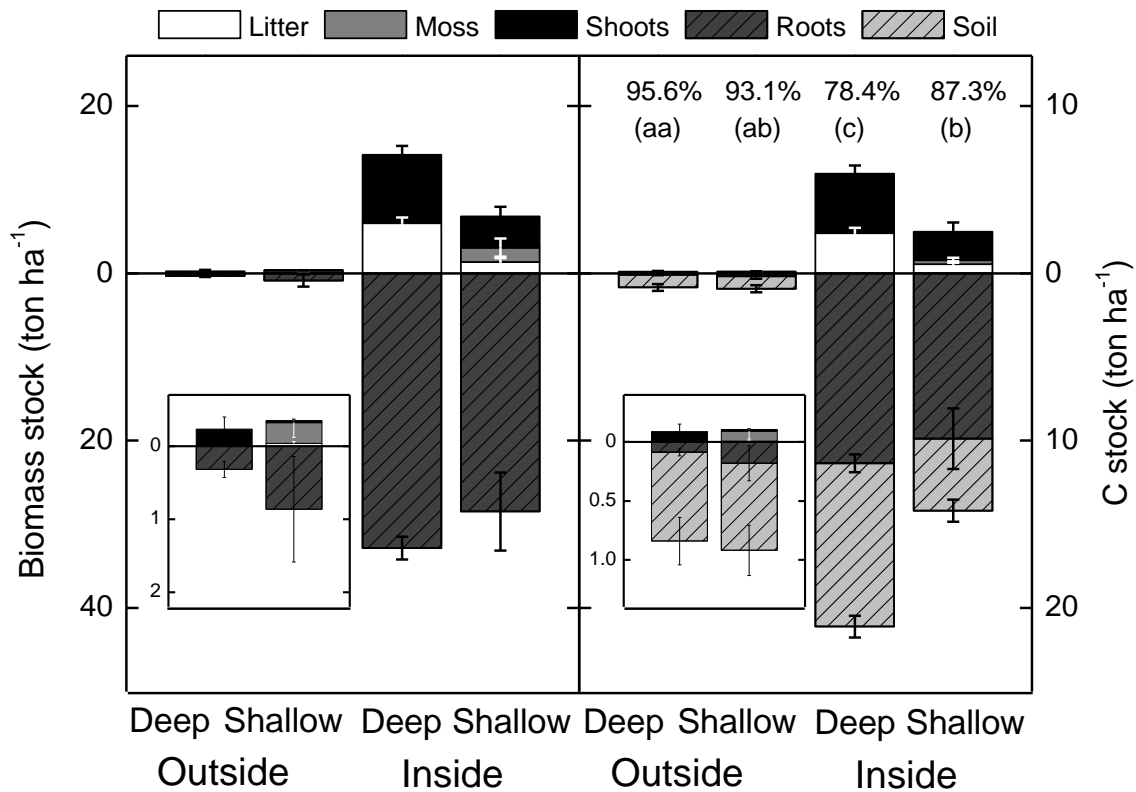


Fig. 5. Mean (\pm SE) values of the biomass stock and carbon stock of litter, shoots, roots (to 30 cm depth) and soil organic carbon (SOC) (to 30 cm depth) in four ecosystem types on Surtsey. The inserted graphs give the values outside the seabird colony in more detail.. ‘Shoots’ include aboveground living vascular plant parts. Statistical results are shown in Table 1. Percentages above the graph indicate the % of total C that is located belowground. Letters show statistical differences.

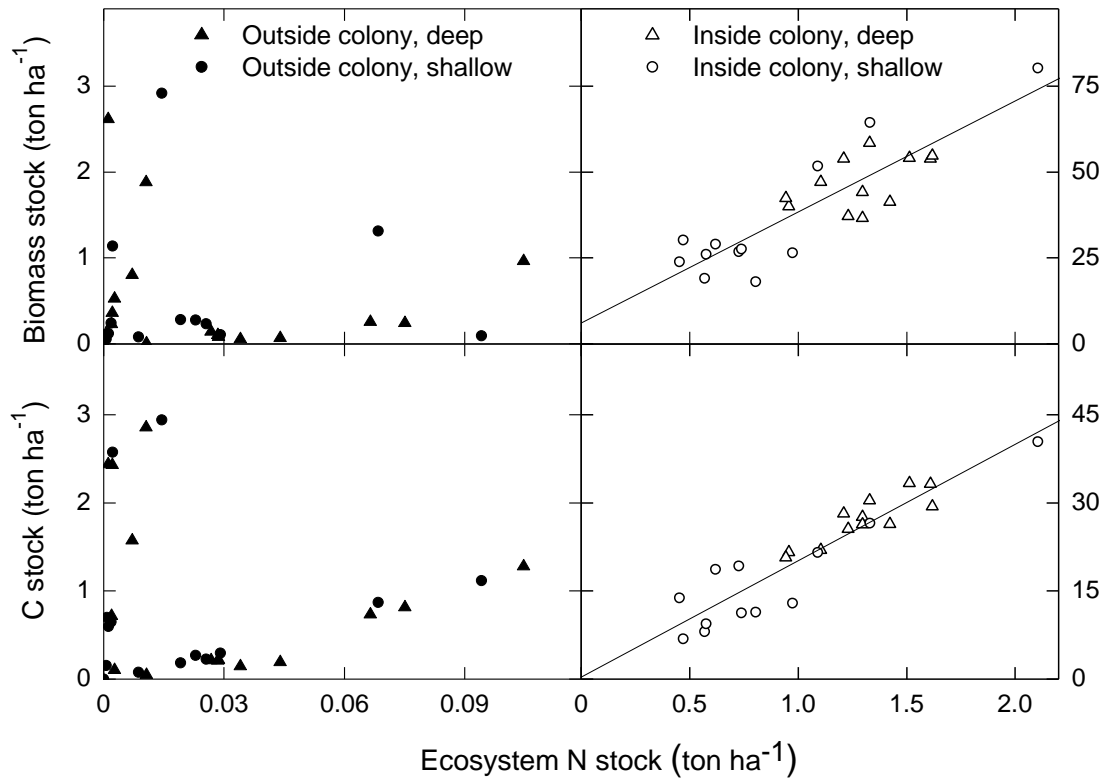


Fig. 6. Relationships between ecosystem biomass stocks (upper graphs) and ecosystem carbon stocks (bottom graphs) and ecosystem N stocks. Left graphs show the relationship outside the seagull colony, right graphs show the relationship and inside the seagull colony. Note the difference in scale of the y-axis between the left and the right panel. Correlation function for biomass inside the colony: $\text{Biomass} = 6 (\pm 4) + 32 (\pm 4) * \text{ecosystem N stock}$ ($r = 0.86$; $t = 8.01$; $Df = 22$; $p < 0.001$). Correlation function for C inside the colony: $C = 0.4 (\pm 1.9) + 19.8 (\pm 1.7) * \text{ecosystem N stock}$ ($r = 0.93$; $t = 11.75$, $Df = 22$, $p < 0.001$). Errors = SE's.

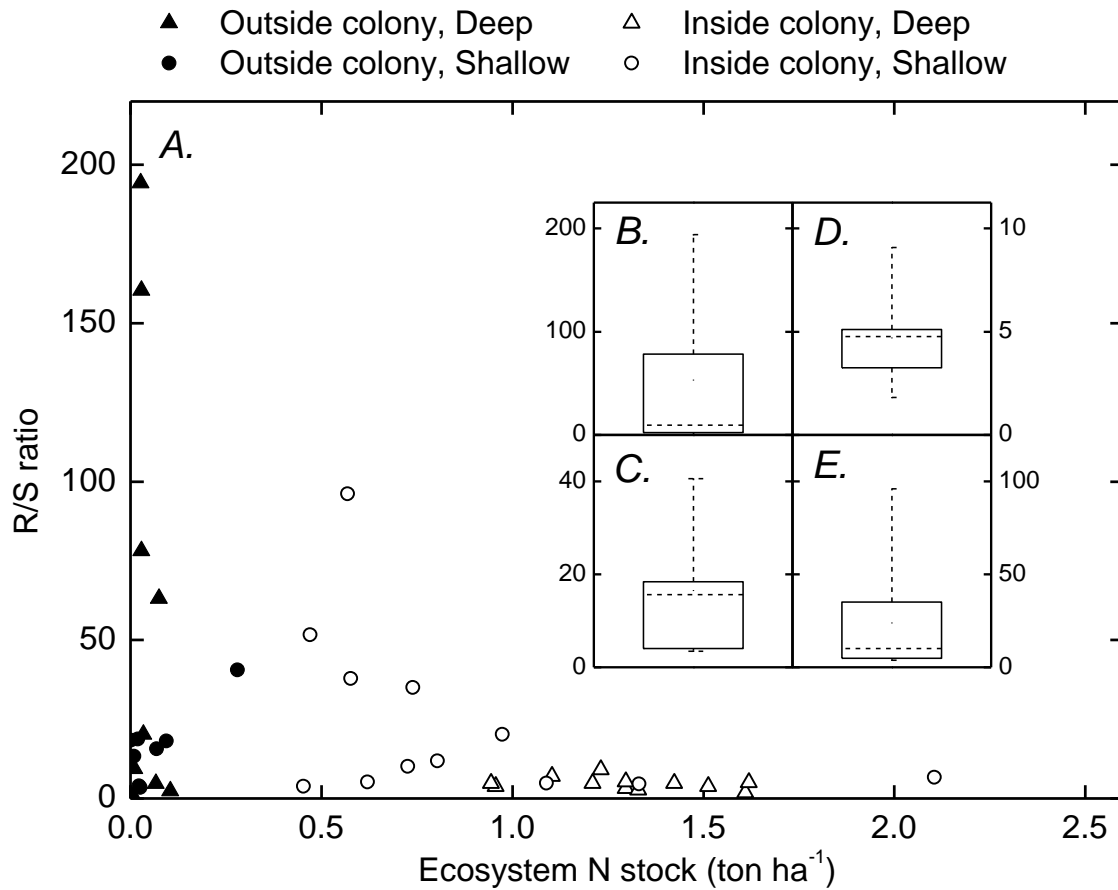


Fig. 7. Relationship between R/S ratio (Root/Shoot ratio) and N stock (A). Central figure shows boxplots of the R/S ratio on deep tephra sand outside the colony (B), shallow tephra sand outside the colony (C), deep tephra sand inside the colony (D) and shallow tephra sand inside the colony (E). Boxes show 25, 50 and 75 percentile, whiskers show 5 and 95 percentile. Note the differences in scale of the y-axes. Samples lacking roots or shoots were excluded from the graphs.

Table 1. Results of a generalized linear model for N stock, biomass stock, C stock and N accumulating rate, using colony and tephra depth as fixed variables and plots, and sampling year as random variable. ‘Shoots’ include all aboveground living plant parts, ‘Living’ includes ‘Shoots’ and ‘Roots’ and ‘Dead’ includes ‘Litter’ and soil organic nitrogen (SON) or soil organic carbon (SOC). Significant source variables ($p < 0.05$) with respect to ecosystem parts are indicated with asterisks: ns = $p > 0.05$, * $p = 0.05-0.01$, ** $p = 0.01-0.001$, *** $p < 0.001$.

	N stock (ton ha ⁻²)								Biomass stock (ton ha ⁻²)								
Source	Shoots	Roots	Moss	Living	Litter	SON	Dead	Total	Shoots	Roots	Moss	Living	Litter	Total	Shoots	Roots	Mo
Colony x depth																	
Sum of squares	3.76	0.17	0.97	0.01	37.34	23.07	31.36	2.3	2.09	0.37	0.83	0.56	44.94	1.28	1.66	0.19	0.1
Degrees of freedom	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
p-value	ns	ns	ns	ns	***	***	***	ns	ns	ns	ns	ns	***	ns	ns	ns	ns
Colony																	
Sum of squares	6.6	9.71	1.08	10.62	-	-	-	15.34	7.64	14.70	0.94	14.79	-	14.84	7.39	13.45	0.1
Degrees of freedom	1	1	1	1	-	-	-	1	1	1	1	1	-	1	1	1	1
p-value	*	**	ns	**	-	-	-	***	***	**	ns	***	-	***	**	***	ns
Depth																	
Sum of squares	0.10	0.06	0.31	0.04	-	-	-	0.04	0.41	0.08	0.77	0.07	-	0.03	0.29	0.01	14.3
Degrees of freedom	1	1	1	1	-	-	-	1	1	1	1	1	-	1	1	1	1
p-value	ns	ns	ns	ns	-	-	-	Ns	ns	ns	ns	ns	-	ns	ns	ns	***
Colony effect on deep tephra sand																	
Sum of squares	-	-	-	-	40.44	51.38	56.66	-	-	-	-	-	43.37	-	-	-	-
Degrees of freedom	-	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-
p-value	-	-	-	-	***	***	***	-	-	-	-	-	***	-	-	-	-
Colony effect on shallow tephra sand																	
Sum of squares	-	-	-	-	28.5 (a)	44.71	45.49	-	-	-	-	-	11.29	-	-	-	-
Degrees of freedom	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-	-

p-value	-	-	-	-	**	***	***	-	-	-	-	-	**	-	-	-	-
Depth effect outside colony																	
Sum of squares	-	-	-	-	2.21	0.06	0.07	-	-	-	-	-	1.86	-	-	-	-
Degrees of freedom	-	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-
p-value	-	-	-	-	ns	ns	Ns	-	-	-	-	-	Ns	-	-	-	-
Depth effect inside colony																	
Sum of squares	-	-	-	-	25.47	19.27	26.09	-	-	-	-	-	33.11	-	-	-	-
Degrees of freedom	-	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-
p-value	-	-	-	-	***	***	***	-	-	-	-	-	***	-	-	-	-

(a) W-value of non parametrical Wilcoxon signed rank test

751

752

Table 2. Results of generalized linear models of depth distribution of SON (soil organic nitrogen) and Root N (root nitrogen) per soil depth, using colony and tephra depth as fixed variables and plot and sampling year as a random variable. Significant source variables ($p < 0.05$) with respect to soil depth are indicated with asterisks: ns = $p > 0.05$, * $p = 0.05-0.01$, ** $p = 0.01-0.001$, *** $p < 0.001$.

	SON				Root N			
	Soil depth (cm)							
Source	0-5	5-10	10-20	20-30	0-5	5-10	10-20	20-30
Colony x depth								
Sum of squares	0.01	0.31	n/a	n/a	0.57	3.11	0.95	n/a
Degrees of freedom	1	1	n/a	n/a	1	1	1	n/a
p-value	ns	ns	n/a	n/a	ns	ns	Ns	n/a
Colony								
Sum of squares	0.38	0.03	0.49	0.02	23.52	2.36	10.02	10.09
Degrees of freedom	1	1	1	1	1	1	1	1
p-value	ns	ns	ns	ns	***	ns	**	**
Depth								
Sum of squares	90.21	13.85	n/a	n/a	25.56	2.08	15.07	n/a
Degrees of freedom	1	1	n/a	n/a	1	1	1	n/a
p-value	***	***	n/a	n/a	***	ns	***	n/a

n/a: Not applicable: No SON or Root N in shallow tephra sand