

Effects of seabird nitrogen input on biomass and carbon accumulation

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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, 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 $0.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, which was ca. 60 % of the estimated N input rate from wet deposition. The seagulls have added, on average, $47 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, 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 reached normal values for grasslands, while the soil organic carbon stocks (SOC; $4\text{--}10 \text{ kg C ha}^{-1}$) were only a fraction of normal grassland values. Thus, it will take a long time until the SOC stock reaches equilibrium with the current primary production; during which conditions for new colonists may change.

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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

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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 Magnusson, 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).

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). 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 Magnusson, 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 Magnusson, 2014; this issue), 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.

In detail, we tested five hypotheses:

1. Atmospheric N deposition is the main N source outside the seabird colony. As we do not expect that this sparsely vegetated area is very efficient in N retention, considerable amounts of N can be lost due to leaching during large rain events. Therefore we hypothesize that total N stocks outside the seabird colony are less than the estimated accumulated atmospheric N deposition during the past 50 years.
2. Inside the seabird colony, an additional N source is the seabird derived N input. We hypothesize that the annual net N accumulation rate inside the seabird colony amounts to ca. 30 kg N ha^{-1} , as has been coarsely estimated by Magnússon et al. (2009).
3. Deeper root systems are more effective in keeping the N from being lost by leaching. Therefore we hypothesize that plots on deep tephra sand show improved N retention compared to plots on shallow tephra sand.
4. Nutrient rich systems are known to invest relatively more in aboveground plant growth than nutrient poor systems (e.g. Warembourg and Estelrich, 2001; Wang et al., 2008; Gao et al., 2011; Zhou et al., 2014). Therefore we expect to find

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a shift from belowground to aboveground biomass, C and N stocks inside the seagull colony, compared to outside the colony.

5. An important factor in the process of soil development is the accumulation of SOC (Kögel-Knabner et al., 2013). As SOC is a product of biomass degradation, we hypothesize that the increased productivity within the seagull colony enhances the rate of soil development.

2 Material and 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 ms⁻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* (Magnusson et al., 2014; Stefansdottir et al., 2014). In 1986, a seabird colony of lesser black backed gulls (*Larus fuscus*) was

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established in a confined area on the SW edge of the island (Petersen, 2009), and has been expanding in size ever since (Magnusson et al., 2014). 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 10 m × 10 m plots were established on Surtsey to survey ecosystem changes in and outside the seabird colony. 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 (20 × 50 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 (20 cm × 50 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 20 cm × 20 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.

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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 min 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, dicotyledons 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.

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

2.5 C and N stocks and accumulation rates

Carbon- and N stocks per area in (1) aboveground vascular plants, (2) litter and (3) moss were found by multiplying total DM with the respective concentration, and by

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taking the sample surface into account. For the (1) roots and (2) soil particles (< 2 mm), C and N stocks per area were calculated per soil layer by multiplying total DM < 2 mm of the soil layer with the respective concentration, and by taking the surface of the soil corer into account.

For the plots outside the seabird colony, N accumulation rate was calculated by dividing the total N stock by the number of years since the start of accumulation (from 1963, the year of the surfacing of the island), assuming a constant N accumulation rate. For the plots inside the seabird colony, a separate estimate was made for the N accumulation rate of seabird derived N. Therefore the total N stock of plots inside the colony was first subtracted by the amount of total N stock 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).

2.6 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 $p < 0.05$.

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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. 1, 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. 1, 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.

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. 1, 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. 2, 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 $0.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ outside the seagull colony and the effect of tephra depth was not significant (Fig. 3, Table 1). In sharp contrast, the seabirds accelerated the N accumulation rate, with a factor of almost 50–100, to 36

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and $58 \text{ kg ha}^{-1} \text{ yr}^{-1}$ on shallow and deep tephra sands, respectively (Fig. 3). 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. 4, Table 1).

The seabird colony increased all individual stocks of biomass and C, both belowground as aboveground (Fig. 4, Table 1). The living biomass stock was over 50 times larger (0.7 vs. 36 kg ha^{-1} outside and inside the colony, respectively), and the living biomass C stock was almost 70 times higher (0.19 vs. 13 kg ha^{-1} outside and inside the colony, respectively) (Fig. 4). 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. 4, 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. 4).

The belowground biomass (roots) on shallow tephra sand was located in the upper 30 cm, as expected (Fig. 2). On deep tephra sand, the seabird colony had a pronounced effect on the relative distribution of the roots (Fig. 2). 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.

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The SOC concentration in the upper 5 cm of the tephra sand outside the colony was $0.12 \pm 0.02\%$ (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 $0.9 \pm 0.3\%$, whereas it was as high as $4.6 \pm 0.4\%$ 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 positive linear relationship between total ecosystem biomass and C stock and total ecosystem N stock within the seagull colony (Fig. 5). 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, but for one g N, a median of 17 and 12 g of biomass or C stock were found (Fig. 5). There was no significant correlation between R/S ratio and ecosystem N stock, outside, neither inside the colony (Fig. 6). 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. 6). 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 ($0.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Fig. 3), which is ca. 50–60 % of the expected annual atmospheric N deposition rate in Iceland corrected to 1600 mm annual precipitation ($1.3\text{--}1.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) (Gislason et al., 1996; Sigurdsson et al., 2005). This was not according to the initial hypothesis, because we did not expect that these sparsely vegetated areas would be very efficient in retaining the N. However, during sampling it became evident that the unvegetated tephra sand was fully colonized by roots. Another study, which took place on and around *Leymus* dunes of the same

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area outside the seagull colony, but not at the permanent study plots, found similar pattern of root distribution (Stefansdottir et al., 2014; this issue), and even showed that part of the “missing” N has been transported into the *Leymus* dunes. Further, high N retention in bare dune habitats is supported by a study in the Netherlands as well, where ten Harkel et al. (1998) found a > 80 % a retention of N.

We assume atmospheric deposition to be the main source of N outside the seabird colony, but other possible sources of N inputs could be: (1) N from volcanic processes, (2) chemical weathering of N containing bedrock sources, (3) symbiotic N₂ fixation and (4) free living N₂ fixation. The (1) and (2) can be largely rejected, since Ponnameruma et al. (1967) showed that the tephra sands of Surtsey did not contain any organic N and inorganic NH₄ and NO₃ concentrations were low in 1966 and probably mostly originating from rainfall during the first 4 years since the eruption started. They found, however, some inorganic N in recently deposited tephra, which could indicate volcanic N sources (cf. Huebert et al., 1999), but the concentrations were lower in the older tephra layers, probably indicating leaching due to initial lack of biological activity to retain the NO₃. The (3) and (4) are probably also most not important, since no plant species that are known to have N₂-fixation have yet colonized Surtsey (Magnússon et al., 2014) and low water retention of the tephra sand and 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).

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 tha⁻¹). This shows well the large effect the seabirds have had on the N input on the island in only 27 years. The apparent lack of other major N inputs on Surtsey, which typically complicate the quan-

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titative estimation of seabird-driven N input rates, makes it possible to use stock data to calculate a reliable rate of N inputs by seabirds there.

The seabirds had increased the ecosystem N-stock 30-fold during 26–27 years, compared to the area outside the seagull colony, or on average by $\sim 47 \text{ kg ha}^{-1} \text{ yr}^{-1}$ across both substrate types. This value was much higher than we hypothesized, but corresponded almost exactly with the estimate of Bancroft et al. (2005) ($50.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$) for a Wedge-tailed Shearwaters (*Puffinus pacificus*) colony on Rottneest 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 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 (Danmark) and found even higher N input rates (an average of $292 \text{ kg ha}^{-1} \text{ yr}^{-1}$), assuming that the total bird nitrogen input over 24 years approached the difference between control and colony.

Studies that have looked at SON in seabird colonies found, however, lower SON concentrations in the upper 10 cm of the soil compared to Surtsey, despite the fact that both those studies investigated colonies that had been subjected to bird influence for a longer timespan (Anderson and Polis, 1999: $\sim 2 \text{ mg g}^{-1} \text{ DM}$; Ligeza and Smal, 2003: $\sim 0.6 \text{ mg g}^{-1} \text{ DM}$, compared to $2.5 \text{ mg g}^{-1} \text{ DM}$ in Surtsey).

4.3 Effect of tephra-layer depth on N retention

Even if SON and litter N accumulation was 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 contradicts with our expectation that deeper substrates would positively affect N retention, as was shown by Selmants et al. (2014). Faster succession rates on the deeper tephra sands in Surtsey (Magnússon and Magnússon, 2000; del Moral and Magnusson, 2014; this issue), can therefore not be explained solely by increased N accumulation rates there. This further suggests a high N retention potential in the upper centimeters of the tephra sand, and probably indicates a strong N limitation of the system.

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4.4 Shifts from belowground to aboveground plant biomass

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 expected 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 and the relatively small sub-plots, which results in a large variability in the aboveground biomass sampling, while the amount of roots is rather stable throughout the soil. Inside the seabird colony, the lack of relationship with 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 assign the absence of nutrient influence on R/S to an overruling effect of drought in all occurring nutrient situations.

The R/S ratios in this study were above average, especially outside the seabird colony. The median ratio there was 18, which is almost three times higher than the upper extreme for cool temperate deserts reported by Mokany et al. (2006) and close to the mean R/S ratio of 19 reported for *Leymus* outside the seagull colony in Surtsey by Stefansdottir et al. (2014). For the grassland inside the colony, the median of 5 does not differ much from the median that Mokany et al. (2006) report for cool temperate grasslands (4.5).

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4.5 Shifts from belowground to aboveground N and C and “N use efficiency”

The clear shift in both N and C from belowground to aboveground stocks inside the colony, agrees with our hypothesis that the increase in nutrient availability inside the colony would stimulate the system to invest more in aboveground growth. This relationship between nutrient availability and growth investment was shown by many studies before (e.g. Warembourg and Estelrich, 2001; Wang et al., 2008; Gao et al., 2011; Zhou et al., 2014). This shift was accompanied by a doubling of the N use efficiency; the grassland inside the colony supported ~ 2 times more biomass and C per g N, compared to the almost unvegetated area outside the colony. This large increase in the “N use efficiency” indicated a positive feedback between N stock and the storage of both biomass and C. This increase was caused by the drastic shift in C distribution, from a 76 : 24 towards a 32 : 68 proportion in SOC and biomass respectively. As the C/N ratio of SOC was smaller than the one of biomass (10.4 ± 0.6 vs. 39.1 ± 2.3 (deviations = SE)), which is in line with the CN ratio for undisturbed soils reported by Chapin et al. (2011) (~ 14) and the CN ratio for leafs reported by Sterner and Elser (2002) (~ 36), the overall C/N ratio of ecosystems which primarily consist of SOC (such as the non-colonized area) will be smaller than the overall C/N ratio of ecosystems which primarily consist of living 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 volcanic immature soils in New Zealand, Chile and Japan have found a positive relationship between total N-stock and net N-mineralization (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), which was proposed to result from (1) nitrification-induced acidification, (2) increase of the soil osmotic potential to toxic values and (3) an inhibition of ligninolytic enzyme production. The significant acidification inside the seabird colony on Surtsey (Sigurds-

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son and Magnusson, 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

5 The aboveground biomass outside the colony ($0.13 \pm 0.08 \text{ t ha}^{-1}$; error = SE) was very small and had almost not changed since the first measurements of aboveground biomass in the permanent plots in 1999 (0.1 t ha^{-1}) (Magnússon et al., 2009), which probably also indicates relatively little changes in belowground biomass. As biomass degradation is an important source of SOC (Kögel-Knabner et al., 2013), this explains
10 largely the quasi constant SOC concentration and the lack of soil formation outside the seagull colony. 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 ($0\text{--}20 \text{ tDM ha}^{-1}$) to values typical for grassland ecosystems (20 to 50 tDM ha^{-1}) (Larcher, 2003). This large increase in only ca. 25 years can largely be
15 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 t ha^{-1} in 2007 (Magnússon et al., 2009) to $5.9 \pm 0.9 \text{ t ha}^{-1}$ (error = SE) in
20 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.

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

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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?

5 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).

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

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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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Table 1a. 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 , *** $p < 0.001$.

Source	N stock (t ha^{-1})								N stock (t ha^{-1})					
	Shoots	Roots	Moss	Living	Litter	SON	Dead	Total	Shoots	Roots	Moss	Living	Litter	Total
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
Degrees of freedom	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
Colony														
Sum of squares	6.6	9.71	1.08	10.62	–	–	–	15.34	7.64	14.70	0.94	14.79	–	14.84
Degrees of freedom	1	1	1	1	–	–	–	1	1	1	1	1	–	1
p value	*	**	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
Degrees of freedom	1	1	1	1	–	–	–	1	1	1	1	1	–	1
p value	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	–	–	–	–	***	***	***	–	–	–	–	–	***	–

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Table 1b. Continued.

Source	N stock (t ha ⁻¹)								N accumulation rate
	Shoots	Roots	Moss	Living	Litter	SON	Dead	Total	
Colony x depth									
Sum of squares	1.66	0.19	0.10	0.44	38.76	38.08	60.81	9.16	18.09
Degrees of freedom	1	1	1	1	1	1	1	1	1
<i>p</i> value	ns	ns	ns	ns	***	***	***	**	***
Colony									
Sum of squares	7.39	13.45	0.10	12.58	–	–	–	–	–
Degrees of freedom	1	1	1	1	–	–	–	–	–
<i>p</i> value	**	***	ns	***	–	–	–	–	–
Depth									
Sum of squares	0.29	0.01	14.83	0.01	–	–	–	–	–
Degrees of freedom	1	1	1	1	–	–	–	–	–
<i>p</i> value	ns	ns	***	ns	–	–	–	–	–
Colony effect on deep tephra sand									
Sum of squares	–	–	–	–	35.59	60.81	74.10	84.51	0 ^a
Degrees of freedom	–	–	–	–	1	1	1	1	–
<i>p</i> value	–	–	–	–	***	***	***	***	***
Colony effect on shallow tephra sand									
Sum of squares	–	–	–	–	11.31	31.70	32.18	39.95	0 ^a
Degrees of freedom	–	–	–	–	1	1	1	1	–
<i>p</i> value	–	–	–	–	**	***	***	***	***
Depth effect outside colony									
Sum of squares	–	–	–	–	2.40	0.00	0.00	0.06	135 ^a
Degrees of freedom	–	–	–	–	1	1	1	1	–
<i>p</i> value	–	–	–	–	ns	ns	ns	ns	ns
Depth effect inside colony									
Sum of squares	–	–	–	–	24.90	35.21	55.08	11.98	14.23
Degrees of freedom	–	–	–	–	1	1	1	1	1
<i>p</i> value	–	–	–	–	***	***	***	**	**

^a *W* value of non parametrical Wilcoxon signed rank test

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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 , *** $p < 0.001$.

Source	SON Soil depth (cm)				Root N			
	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

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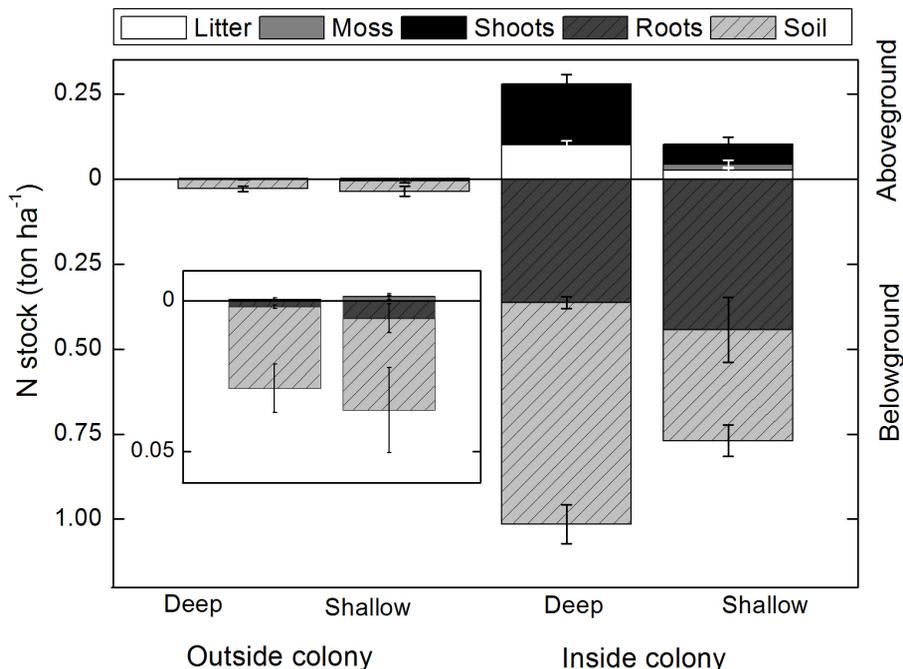


Fig. 1. Mean (\pm SE) values of the nitrogen (N) stocks in litter, shoots, roots (to 30 cm depth) and soil organic nitrogen (SON) (to 30 cm depth) in four ecosystem types on Surtsey. The inserted graph gives the small N stock outside the colony in more detail. “Shoots” include all aboveground living plant parts. Statistical results are shown in Table 1.

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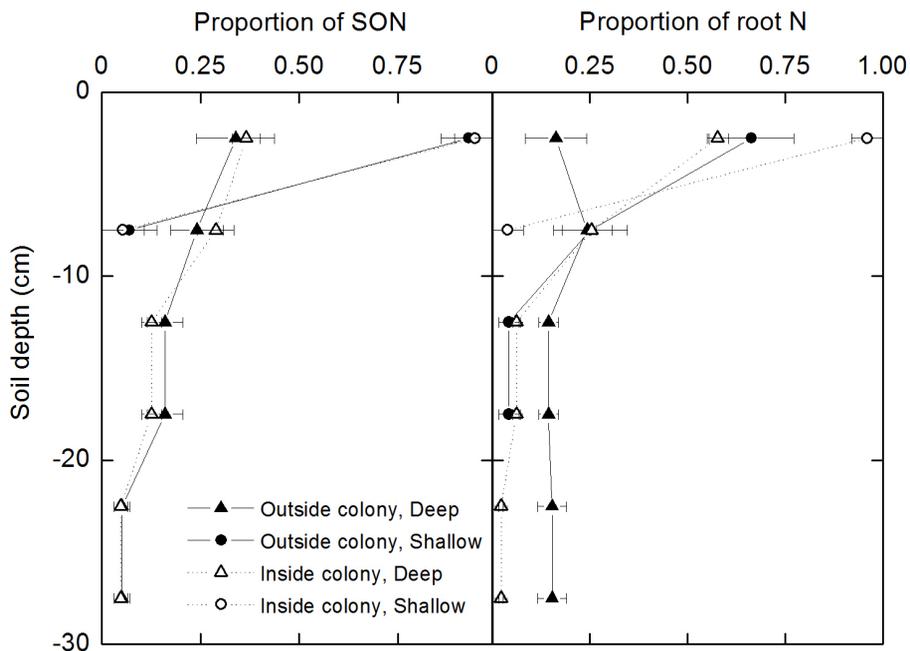


Fig. 2. Depth distribution of soil organic nitrogen (SON) and root N in four ecosystem types on Surtsey. Mean (\pm SE) proportions at each depth layer were calculated relative to the total SON or root N content in the top 30 cm. Statistical results can be found in Table 2.

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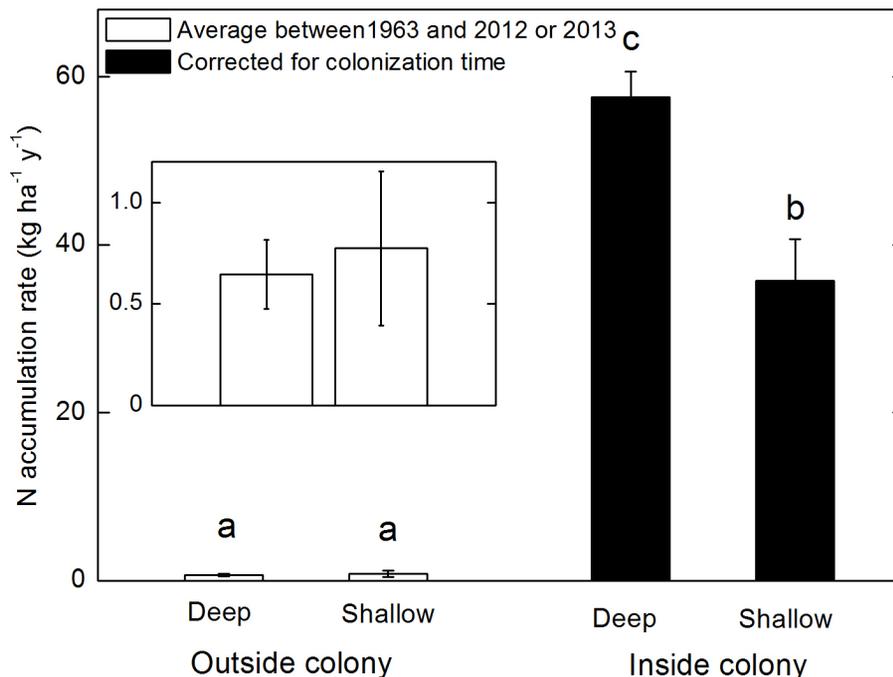


Fig. 3. Mean (\pm SE) values of the nitrogen (N) accumulation rate in four ecosystem types on Surtsey. The inserted graph gives values outside the colony in more detail. White bars show the average N accumulation values between 1963 and the sampling year (2012 or 2013). Black bars show the N accumulation after the start of seagull colonization. Statistical results are shown in Table 1.

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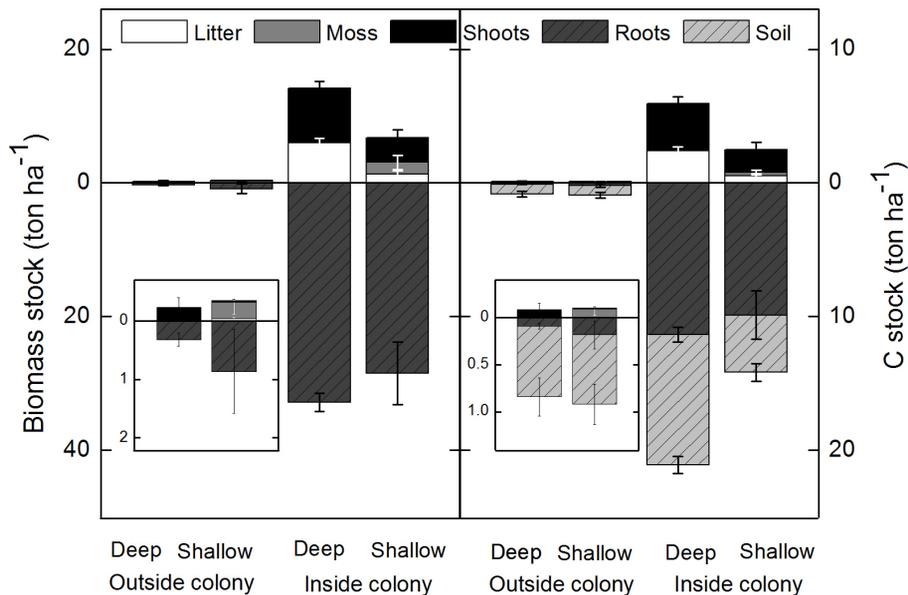


Fig. 4. Mean (\pm SE) values of the biomass stock and carbon stock of litter, shoots, roots (to 30 cm depth) and soil organic carbon (SOC) (to 30 cm depth) in four ecosystem types on Surtsey. The inserted graphs give the values outside the seabird colony in more detail. “Shoots” include aboveground living vascular plant parts. Statistical results are shown in Table 1.

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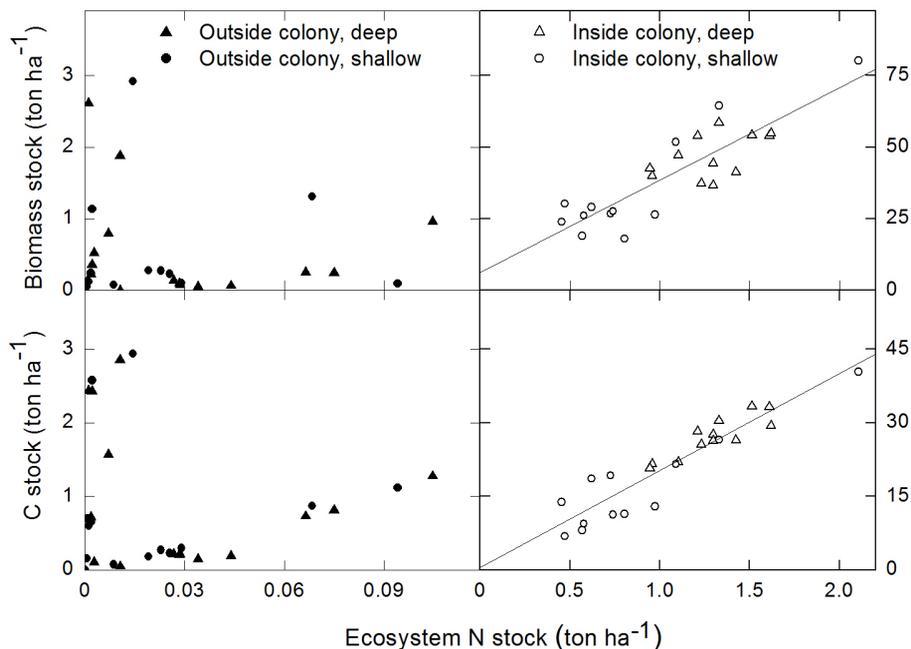


Fig. 5. Relationships between ecosystem biomass stocks (upper graphs) and ecosystem carbon stocks (bottom graphs) and ecosystem N stocks. Left graphs show the relationship outside the seagull colony, right graphs show the relationship and inside the seagull colony. Note the difference in scale of the y-axis between the left and the right panel. Correlation function for biomass inside the colony: $\text{biomass} = 6(\pm 4) + 32(\pm 4) \times \text{ecosystem N stock}$ ($r = 0.86$; $t = 8.01$; $Df = 22$; $p < 0.001$). Correlation function for C inside the colony: $C = 0.4(\pm 1.9) + 19.8(\pm 1.7) \times \text{ecosystem N stock}$ ($r = 0.93$; $t = 11.75$, $Df = 22$, $p < 0.001$). Errors = SE's.

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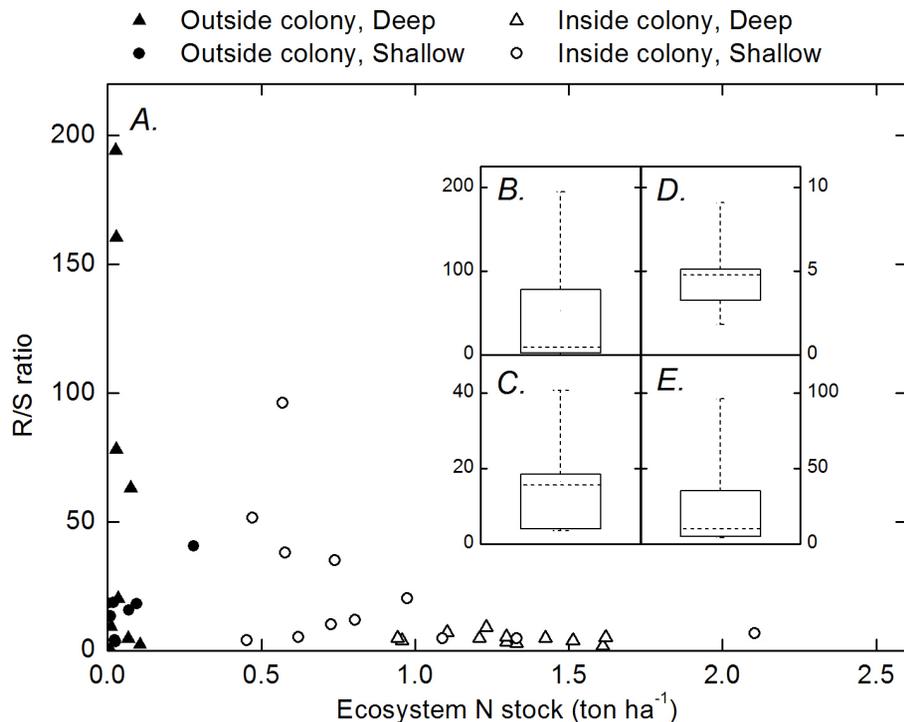


Fig. 6. Relationship between R/S ratio (Root/Shoot ratio) and N stock (**A**). Central figure shows boxplots of the R/S ratio on deep tephra sand outside the colony (**B**), shallow tephra sand outside the colony (**C**), deep tephra sand inside the colony (**D**) and shallow tephra sand inside the colony (**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.