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 kg N ha^{-1} y^{-1}, which was ca. 60% of the estimated N input rate from wet deposition. The seagulls have added, on average, 47 kg N ha^{-1} 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 (17-27 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

54   productive species to arrive (Grime, 1977). A positive reciprocal relationship can be expected

55   between SOC (and its source, biomass production) and nutrient accumulation (Li and Han, 2008).

56   On the one hand, SOC facilitates the retention of nutrients, while on the other hand improved

57   nutrient supply has a positive effect on plant biomass in all terrestrial systems (Gruner et al.,

58   2008), which leads to increased SOC accumulation. Therefore, we expected the amount of

59   nutrient input to be an important determinant of biomass and C accumulation during primary

60   succession. Once the system has reached a sufficient level of fertility for, often more productive,

61   secondary colonizers to establish, they will enhance SOC production and a positive feedback

62   loop between biomass production (SOC) and nutrient accumulation will initiate. Subsequently,

63   the rate of primary succession has been shown to increase following such fertility change (Olff et

64   al., 1993; Vitousek et al., 1993; Sigurdsson and Magnússon, 2010).

65

66   Of all nutrients, nitrogen (N) is most frequently the limiting nutrient for plant growth in high

67   latitude terrestrial ecosystems due to the adverse effect of cold temperatures on biogeochemical

68   processes (Aerts and Chapin, 2000; Reich and Oleksyn, 2004; Storm and Suess, 2008), and this is

69   even more pronounced on young substrates (Vitousek et al., 1993; Vitousek and Farrington,

70   1997; Elser et al., 2007). Therefore, N is expected to be strongly linked with SOC accumulation

71   during primary succession of young volcanic islands at high latitudes.

72　Surtsey is a volcanic island which surfaced during a submarine eruption between 1963 and 1967,

73　and has from the very beginning been strictly protected for research (Baldurson and Ingadóttir,

74　2007). This makes it an exceptionally suitable location to study the natural course of successional

75　processes. As Surtsey is still a young volcanic island, its vegetation is expected to be N limited

76　(Vitousek et al., 1993; Vitousek and Farrington, 1997; Elser et al., 2007). Nitrogen has indeed

77　been identified as a strong limiting factor for plant growth and succession at Surtsey

78　(Hendriksson, 1976; Magnússon and Magnússon, 2000), and the N:P ratio of five dominant plant

79　species on Surtsey generally indicates a strong N limitation (N:P<14; Aerts and Chapin, 2000)

80　(Thuys et al., 2014).

81　The importance of nutrients became very visible after the establishment of a seabird colony in

82　1986 (mainly lesser black backed gull, *Larus fuscus*) on the SW side of the island (Magnússon

83　and Magnússon, 2000) (Fig. 1). Seabirds are known to transfer nutrients, primarily ammonium

84　and nitrate, from sea to land (Polis and Hurd, 1996; Anderson and Polis, 1999; Ellis et al., 2006;

85　Nie et al., 2014). The effect of enhanced nutrient inputs has been studied by comparing surfaces

86　that were unaffected by seabirds with the seabird-colonized area (Magnússon and Magnússon,

87　2000; Magnússon et al., 2009; Sigurdsson and Magnússon, 2010). In the seabird colony, the rapid

88　increase in soil N elicited subsequent increases in plant cover and species richness. These earlier

89　studies did, however, not attempt to quantify the rate of N accumulation or study the development

90　of the whole ecosystem biomass, C or nutrient stocks.

91 Within the seabird colony at Surtsey, the earlier studies have revealed diverging successional

92 trajectories of vascular plant communities between areas with deep tephra sand or with surfacing

93 lava rocks (Magnússon and Magnússon, 2000). This has become even more pronounced during

94 the past decade (Del Moral and Magnússon, 2014), showing faster development of species

95 richness and plant cover in seabird colony plots on deep tephra sand.

96 The main goal of this study was to quantify the rate of N accumulation in different permanent

97 study plots on Surtsey and investigate how this compared to changes in the whole ecosystem

98 biomass and C stocks. Despite the fact that earlier studies have revealed drastic effects of the

99 seabird-derived N input on the ecosystem structure and functions on Surtsey (Magnússon and

100 Magnússon, 2000; Kristinsson and Heidmarsson, 2009; Magnússon et al., 2009; Petersen, 2009;

101 Sigurdsson and Magnússon, 2010; Del Moral and Magnússon, 2014; Thuys et al., 2014) no data

102 exist on the annual N input coming from seabirds, except from a coarse estimate of (Magnússon

103 et al., 2009), who combined excretion and food models for the lesser black-backed gull (*Larus*

104 *fuscus*) and the herring gull (*Larus argentatus*) derived from Hahn et al. (2007), and nest counts

105 on Surtsey. We therefore attempted to obtain a more precise approximation of the seabird derived

106 N input by measuring total N stocks and correcting for the total colonization time. Our null

107 hypothesis was that the annual net N accumulation rate inside the seabird colony amounts to ca.

108 30 kg N ha^{-1} as was estimated by Magnússon et al. (2009).

109   Further, we tested four hypotheses in detail:

110   (i) Atmospheric N deposition is the main N source outside the seabird colony. As we do not

111   expect that this sparsely vegetated area is very efficient in N retention, large amounts of N can be

112   lost due to leaching during large rain events. Field observations in different ecosystems with low

113   N input rates, as is the case outside the colony, revealed an average N retention of 75% (Thomas

114   et al., 2013). Therefore, we hypothesized that total N stocks outside the seabird colony would

115   approximate 75% of the total estimated accumulated atmospheric N deposition during the past 50

116   years.

117   (ii) Among similar vegetation types, those with deeper root systems were shown to be more

118   effective in avoiding N leaching losses than their shallower rooting equivalents (Bowman et al.,

119   1998). On Surtsey, most N that leaches through the upper substrate layer is removed from the

120   system by seeping into cracks and fissures in the lava bedrock. Therefore, we hypothesized that

121   plots on deep tephra sand show higher N retention compared to plots on shallow tephra sand.

122   (iii) Nutrient rich systems are known to invest relatively more in aboveground plant growth than

123   nutrient poor systems (e.g. Warembourg and Estelrich, 2001; Wang et al., 2008; Gao et al., 2011;

124   Zhou et al., 2014). Therefore we expected to find a shift from belowground to aboveground

125   biomass, C and N stocks inside the seagull colony, compared to outside the colony.

126   (iv) An important factor in the process of soil development, the process in which bedrock

127   material is transformed into a soil with defined horizons by a combination of climate, biota,

128   topography, parent material and time, is the accumulation of SOC (Kögel-Knabner et al., 2013).

129   As SOC is a product of biomass degradation, we hypothesized that the increased productivity

130   within the seagull colony enhances the rate of soil development.

131

132 **2. Material & Methods**

133 *2.1. Site description*

134 Samples were collected on Surtsey (63°18´11"N 20°36´17"W) in mid July 2012 and mid July

135 2013. The island surfaced during an eruption between 1963 and 1967 and was 1.41 km^2 in 2004.

136 Surtsey is the youngest island of the Vestmannaeyjar archipelago, which is located on the insular

137 shelf 32 km off the south coast of Iceland. The archipelago constitutes a separate volcanic

138 system, which initiated activity around 100.000 years BP (Jakobsson, 1979). Climate conditions

139 on the archipelago are humid sub-arctic. Winter and summer average temperatures between 1971

140 and 2000 were 1.5-2 °C and 10 °C, respectively (Icelandic Meteorological Office). Total annual

141 precipitation during the same period was on average 1600 mm and fell mainly between October

142 and March. The prevailing wind direction is East, and wind speed exceeds hurricane force (>32.7

143 m s^{-1}) on average 15 days per year (Icelandic Meteorological Office). The bedrock of the higher

144 parts of Surtsey consists of basalt tuff, whereas in its lower parts it is made out of basaltic lava

145 (Jakobsson, 1968). The island is still too young to have well developed soils. The lava is partly

146 filled with tephra sand and silt, which originates from the eruption, from erosion of the bedrock

147 material and by aeolian transport from the mainland. The vegetation on these sandy areas is

148 dominated by *Honkenya peploides* and *Leymus arenaria* (Magnússon et al., 2014; Stefansdottir et

149 al., 2014). In 1986, a seabird colony of lesser black backed gulls (*Larus fuscus*) was established

150 in a confined area on the SW edge of the island (Petersen, 2009), and has been expanding in size

151   ever since. The dominant plant species inside the seagull colony are *Poa pratensis, P. annua* and

152   *Festuca richardsonii* (Magnússon et al., 2009).

153   *2.2. Sample sites*

154   Between 1990 and 1995, permanent 10x10 m plots were established on Surtsey to survey

155   ecosystem changes in and outside the seabird colony (Fig. 1). Out of these plots, we selected 18

156   representative plots inside and outside the seabird colony, partly on deep ($\geq$ 30 cm deep) and

157   partly on shallow tephra sand (< 30 cm deep). Ten plots were situated outside the colony (of

158   which six were sampled in 2012 and four in 2013) and eight plots were situated inside the colony

159   (of which four were sampled in 2012 and four in 2013). In every case, half of the plots were

160   located on shallow and the other half on deep tephra sand. We placed three subplots (20x50 cm)

161   for destructive sampling 0.5 m outside the southern edge of each permanent plot ($n_{outside\ colony}$ =

162   30; $n_{inside\ colony}$ = 24).

163   *2.3. Vegetation & soil sampling*

164   During the two expeditions to Surtsey, all vascular plants were cut in each subplot (20x50 cm)

165   and subsequently separated into species in the field. Next, the litter layer was collected from the

166   same plots, except in the more vegetated seabird colony, where it was collected from a 20x20 cm

167   subplot within the harvest plot. Soil was then sampled from where the litter had been removed

168   using a hand-driven soil corer (8.67 cm diameter). Consecutive soil samples of 5 cm depth were

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

170   further analyses.

171   *2.4. Sample preparation and chemical analysis*

172   Fine roots (all roots were of diameter < 2 mm) were picked manually from soil samples in the

173   laboratory, for maximum 60 minutes per sample. In case where litter was found during the

174   sorting process, it was added to the litter sample. The root-free soil was sieved through a 2 mm

175   sieve in order to separate the coarse soil fraction (> 2 mm) from the sand, silt and clay particles

176   (< 2 mm). All fractions (1) roots, (2) soil particles < 2 mm and (3) soil particles > 2 mm) were

177   dried for 48 h at 40 °C. The coarse fraction was assumed to contain only a marginal amount of

178   organic C or N. In few cases where the sample weight was too small for analysis (< 1 g dry

179   weight), samples from the same layer were merged by neighboring subplots within the same plot.

180   The basaltic tephra sand in Surtsey does not contain any carbonates (mineral C), and inorganic N

181   was assumed to be negligible compared to the total SON (soil organic nitrogen) stock

182   (Ponnameruma et al., 1967), and was therefore not measured.

183   After drying all biomass samples for 48 h at 40 °C, dry mass of (1) all aboveground vascular

184   plants (separated in monocotyledons, eudicotyledons and ferns and horsetails), (2) moss, (3) litter

185   and (4) fine roots (in 0-5, 5-10, 10-20 and 20-30 cm depth layers) was weighed.

186   For each sample, 1 g dry mass (DM) was milled using a ball mill (Retsch MM301 Mixer Mill,

187   Haan, Germany) and then total C and N concentrations were analysed by dry combustion on

188   Macro Elementary Analyzer (Model Vario MAX CN, Hanau, Germany). C and N concentration

189   was determined for (1) all aboveground vascular plant parts together, (2) litter, (3) moss, (4) roots

190   and (5) soil particles (< 2 mm) per aforementioned soil layers. Soil samples were then dried at

191   105 °C for 48 hours and weighed again to get the correct DM.

192   *2.6. C and N stocks and accumulation rates*

193   Carbon- and N stocks in (1) aboveground vascular plant biomass, (2) litter and (3) moss were

194   estimated by multiplying total DM with the respective concentrations and were expressed per unit

195   area. Carbon- and N stocks in (1) roots and (2) soil particles (< 2 mm) per unit area were

196   calculated per soil layer by multiplying total DM < 2mm of the soil layer with the respective

197   concentrations.

198   For the plots outside the seabird colony, N accumulation rate was calculated by dividing the total

199   N stock by the number of years since the start of accumulation (from 1963, the year of the

200   surfacing of the island), assuming a constant N accumulation rate. For the plots inside the seabird

201   colony, a separate estimate was made for the N accumulation rate of seabird derived N. Therefore

202   the total N stock of plots inside the colony was first subtracted by the amount of total N stock

203   outside the colony, assuming that this equals the non-bird N input over the whole island.

204 Subsequently, the remaining N stock was divided by the years since seagulls started to breed

205 within 1000 m^2 of each plot; information that was available from (Magnússon and Magnússon,

206 2000; Magnússon et al., 2009).

207 *2.7. Data analyses*

208 Differences in ecosystem N stocks, biomass and C stocks were tested with two-way ANOVA's

209 in the R software (R Development Core Team, 2012), with seabird colony (yes − no) and tephra

210 depth (deep-shallow) as fixed variables. Differences in N accumulation rate and in proportional

211 distribution of SON and root N per soil depth layer were tested in the same way. The correlations

212 between (1) biomass stocks, (2) ecosystem C stocks and (3) root/shoot ratios (R/S ratios) and

213 ecosystem N stocks were tested separately for plots within and outside the seagull colony.

214 Therefore, we used a correlation test, applying the "Spearman" method, whenever the

215 assumptions of homoscedasticity (tested with residual plot) or linearity (tested with the runs test

216 (Turlach, 2011; Trapletti et al., 2012; Zeileis et al., 2012)) were not met. Null hypotheses were

217 rejected when $p < 0.05$.

218

219 **3. Results**

220 *3.1. Ecosystem N stock and distribution*

221 The total N stock outside and inside the seabird colony after 50 years of island development and

222 ca. 26-27 years after the first lesser black backed gull colonization differed significantly, by a

223 factor of approximately 30 (Fig. 2, Table 1). Soil depth had no significant effect on total

224 accumulated N stock (in biomass and soil), neither outside nor inside the seabird colony. Also,

225 the N stock of the living compartment (shoots, roots and moss together) and of shoots, roots and

226 moss separately did not differ between deep and shallow tephra sand. However, inside the seagull

227 colony, the N stock of the dead OM (organic material) compartment (litter and SON combined),

228 and of the litter and SON separately, was significantly higher in deep tephra sand than in shallow

229 tephra sand on lava (Fig. 2, Table 1).

230 Of the total N stock outside the colony, approximately 96% of the N was stored belowground in

231 roots and SON, while within the colony this was reduced to about 78 and 88% in deep and

232 shallow tephra sand, respectively (Fig. 2).

233 The amount of N stored as SON was 24 (on deep tephra sand) and 11 (on shallow tephra sand)

234 times higher inside than outside the colony (Fig. 2, Table 1). Despite this drastic effect on

235 absolute SON stocks, the seagull colony did not change the relative distribution of SON trough

236 the upper 30 cm of the soil profile. Irrespective of the bird influence, about 35% of the total SON

237   in deep tephra sands was located in the upper 5 cm, and decreased gradually to about 5% at 25-30

238   cm depth (Fig. 3, Table 2).

239   *3.2. Nitrogen accumulation rate*

240   The average rate of total N accumulation (in both living and dead compartments) over the 50

241   years of island succession was 0.7 kg ha^{-1} y^{-1} outside the seagull colony and the effect of tephra

242   depth was not significant (Fig. 4, Table 1). In sharp contrast, the seabirds accelerated the N

243   accumulation rate, with a factor of almost 50 - 100, to 36 - 58 kg ha^{-1} y^{-1} (Fig. 4). Within the

244   seabird colony, there was no difference in N accumulation rate between tephra depths (Table 2).

245   *3.3 Ecosystem biomass and C stocks and SOC concentrations*

246   The area inside the colony contained 50 times more biomass than the plots outside of the bird

247   colony, irrespective from tephra depth. For C, the area inside the colony contained 29 times more

248   C than the area not affected by the seabirds on deep tephra sand, and 16 times more C on shallow

249   tephra sand (Fig. 5, Table 1).

250   The seabird colony increased all individual stocks of biomass and C, both belowground as

251   aboveground (Fig. 5, Table 1). The living biomass stock was over 50 times larger (0.7 vs 36 kg

252   ha^{-1} outside and inside the colony, respectively), and the living biomass C stock was almost 70

253   times higher (0.19 vs 13 kg ha^{-1} outside and inside the colony, respectively) (Fig. 5). The

254   proportion of C stored in living biomass compared to SOC also shifted drastically; from a 24:76

255   distribution outside the colony, to a 68:32 distribution inside the colony.

256   Tephra depth, however, had only an effect inside the colony. There, the plots on deep tephra sand

257   stored more litter, litter C and SOC than those on shallow sand layers (Fig. 5, Table 1). The SOC

258   stock in deep tephra sand (10 kg C ha^{-1}) was more than twice as large than on shallow tephra sand

259   (4 kg C ha^{-1}) (Fig. 5).

260   On deep tephra sand, the seabird colony had a pronounced effect on the relative distribution of

261   the roots (Fig. 3). Outside the colony, the roots were evenly distributed throughout the upper 10

262   cm of the soil. Inside the colony, however, the roots were concentrated in the top 5 cm (57% of

263   the total root weight within 30 cm depth), and declined to a fraction of only 4% between 20 and

264   30 cm depth.

265   The SOC concentration in the upper 5 cm of the tephra sand outside the colony was 0.12 ± 0.02

266   % (error is SE; data not shown). Inside the colony, there was a significant depth effect on SOC

267   concentration in the upper 5 cm of the tephra sand. On deep tephra sand, the SOC concentration

268   was 0.9 ± 0.3 %, whereas it was as high as 4.6 ± 0.4 % on shallow tephra sand (errors are SE's;

269   data not shown).

270   *3.4. Impacts of ecosystem N stock on biomass and C stocks*

271   There was a highly significant positive linear relationship within the seagull colony between total

272   ecosystem biomass and C stock on the one hand and total ecosystem N stock on the other hand

273   (Fig. 6), while almost half of the N and C was located in the soil (50 and 40% on deep and

274   shallow soils respectively), and was therefore not directly related to the biomass. An increase of

275   one g of N could support extra 32 g biomass and 20 g of ecosystem C. Outside the colony, neither

276   biomass nor C showed a significant correlation with total N stock (here approximately 80% of N

277   and C was located in the soil), but for one g N, a median of 17 and 12 g of biomass or C stock

278   were found (Fig. 6). There was no significant correlation between R/S ratio and ecosystem N

279   stock, outside, neither inside the colony (Fig. 7). The variation in the measured R/S ratio was

280   large. The values ranged from 0.1 to 194 outside the colony and from 1.8 to 96 inside (Fig. 7).

281   The median R/S ratios were 18 and 5, outside and inside the seabird colony, respectively.

282

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 kg ha^{-1} 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 kg N ha^{-1} 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% ±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

300   retention on Surtsey has increased and is now close to the 75-80% reported for ecosystems with

301   low N inputs (Thomas et al. 2013).

302   We assume atmospheric deposition to be the main source of N outside the seabird colony.

303   Additional mechanisms of N input could be: (1) N inputs from volcanic processes, (2) chemical

304   weathering of N-containing bedrock, (3) N input from overflying birds, (4) symbiotic N_2 fixation

305   (5) free living N_2 fixation and (6) N fixation by lichens and biological soil crusts (BSC).

306   Mechanisms (1) and (2) can be largely rejected, since Ponnameruma et al. (1967) showed that the

307   tephra sands of Surtsey did not contain any organic N and very little inorganic NH_4 and NO_3; the

308   latter probably mostly originating from rainfall during the first 4 years since the eruption started.

309   This study did report some inorganic N in recently deposited tephra, which could indicate

310   volcanic N sources (cf. Huebert et al., 1999). However, the concentrations were lower in the

311   older tephra layers, probably indicating leaching due to initial lack of biological activity to retain

312   the NO_3. Further, we argue that N deposited by overflying birds (3) was of minor importance,

313   because, as was stated above, total plant cover did not increase between 1994 and 2012 in any of

314   the permanent plots outside the seabird colony (Magnússon, unpublished data). A steady increase

315   of vegetation cover after 1986 (the establishment of the colony) would be expected if overflying

316   birds added a substantial amount of N. Also N input mechanisms (4) and (5) were probably of

317   lesser importance as well, since to date no plant species known to have N_2-fixing symbionts have

318   colonized Surtsey (Magnússon et al., 2014), and because the low water retention of the tephra

319   sand and the low soil temperatures would not support large populations of free-living N_2 fixing

320   microbes (Zielke et al., 2005; Sorensen et al., 2006). The mean annual soil temperature and

321   volumetric water content were 7.5 °C and only 8.4%, respectively, at 5 cm depth during 2010-

322   2012 (unpublished data). Mechanism (6), N-fixation by lychens or biological soil crusts, must be

323   occurring on Surtsey, because Kristinsson and Heidmarsson (2009) found known N_2-fixing

324   species on the island. However, these species had a very limited distribution on the island, and

325   their N input to the ecosystem is therefore assumed to be negligible for the island as a whole.

326

327   *4.2. Nitrogen accumulation inside the seabird colony*

328   The SON values from Surtsey ranged from 0.03 to 0.65 ton ha^{-1}, and span the whole range that

329   Lin et al. (2000) modeled for Iceland (0.0 - 0.5 ton ha^{-1}). This shows well the large effect the

330   seabirds have had on the N stock on Surtsey in only 27 years. The apparent lack of other major N

331   inputs on Surtsey, which typically complicate the quantitative estimation of seabird-driven N

332   input rates, enabled us to calculate a reliable estimate of N input rates by seabirds from the

333   measured N stocks and seabird colonization duration.

334   The seabirds increased the ecosystem N-stock 30-fold during 26-27 years, compared to the area

335   outside the seagull colony, equivalent to an input rate of on average 47 kg ha^{-1} y^{-1}. This value was

336   much higher than we originally hypothesized, but it corresponded almost exactly with the

21

337 estimate of Bancroft et al. (2005) (50.9 kg ha^{-1} y^{-1}) for a Wedge-tailed Shearwaters (*Puffinus*

338 *pacificus*) colony on Rottnest Island (West-Australia), who used guano traps to estimate seabird-

339 derived N deposition. We are not aware of other studies that attempted to estimate seabird N

340 input rates, but our own calculations, based on a study of Breuning-Madsen et al. (2010), who

341 measured the N stocks in a 24-years old Cormorant colony in the Horsens Fjord (Denmark),

342 resulted in even higher N input rates (an average of 292 kg ha^{-1} y^{-1}).

343 The SON concentration in the upper 10 cm of soil inside the bird colony at Surtsey (2.5 mg g^{-1}

344 DM) was higher than what was found by Ligeza and Smal (2003) in perennial colonies of

345 piscivorous birds in northern and eastern Poland (~0.6 mg g^{-1} DM), but was very similar to that

346 reported by Anderson and Polis (1999) for seabird colonies on hyperarid, naturally nutrient-poor

347 islands in the Gulf of California (~2 mg g^{-1} DM). It must be noted that both these studies

348 investigated longer-lived bird colonies. Given the high organic-matter retention capacity of the

349 andosols at Surtsey, it might be that SON concentrations increase even further, but this remains

350 speculation.

351

352 *4.3. Effect of tephra-layer depth on N retention*

353 Even if SON and litter N accumulation were significantly higher at the deeper tephra sands

354 within the seagull colony, we did not find a significant effect of tephra-layer depth on total N

355 stock, when biomass-N was included. This suggests a high N retention potential in the upper

356 centimeters of the tephra sand. This finding contradicts with our second hypothesis, that deeper

357 substrates would positively affect N retention, as was shown by Selmants et al. (2014). Faster

358 succession rates on the deeper tephra sands in Surtsey (Magnússon and Magnússon, 2000; Del

359 Moral and Magnússon, 2014) can therefore not be explained solely by increased N accumulation

360 rates.

361

362 *4.4. Shifts from belowground to aboveground plant biomass*

363 Despite the fact that the median R/S ratio outside the colony (18) was almost three times higher

364 than the upper extreme for cool temperate deserts reported by (Mokany et al., 2006), it

365 corresponded closely with the mean ratio of 19 reported by (Stefansdottir et al., 2014) for the

366 *Leymus* area outside the seabird colony. For the grassland inside the colony, the median R/S of 5

367 did not differ much from the median reported by Mokany et al. (2006) for cool temperate

368 grasslands without bird colonies. Given the more severe nutrient limitation expected for cool

369 temperate grasslands compared to grasslands in a seabird colony, this similar R/S was

370 unexpected. We therefore assume that the low water retention capacity of the sands on Surtsey

371 caused frequent droughts and that the positive impact of drought on R:S offset the negative effect

372 of seabird-driven nutrient inputs (see discussion below).

373 Changes in nutrient availability can often be detected by looking at R/S ratios (Levang-Brilz and

374 Biondini, 2003; Chu et al., 2006), as increased nutrient availability promotes investment in

375 aboveground plant parts. Therefore, we hypothesized (hypothesis iii) a decrease in R/S ratio with

376 increasing ecosystem N stock. Despite the fact that previous research has shown negative

377 correlations between R/S ratio and nutrient availability in grassland ecosystems (Levang-Brilz

378 and Biondini, 2003; Chu et al., 2006), no such relationship was found on Surtsey, neither inside,

379 nor outside the colony. Outside the seabird colony, such a potential relationship might be

380 concealed by the patchiness of the aboveground vegetation, the homogeneous root distribution

381 (Stefansdottir et al., 2014) and the relatively small size of the measurement frames. The

382 combination of these three factors probably explains why we measured several unrealistically

383 high R/S ratio's, ranging up to 194. Inside the seabird colony, the lack of relationship between

384 R/S and N stock is possibly due to other factors, such as limiting water availability, overruling

385 the effect of N availability on the R/S ratio. Drought has been reported to be an important

386 determinant of R/S ratios (Donkor et al., 2002; Gianoli et al., 2009; Dreesen et al., 2012) and

387 water infiltration in Andosols is rapid compared to most other soils (Basile et al., 2003),

388 especially when the carbon content is below 12% as is the case on Surtsey (Arnalds, 2008).

389 Therefore, we attribute the absence of a clear nutrient influence on R/S to an overruling effect of

390 drought in all occurring nutrient situations.

391

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

392

393   The clear shift in both N and C from belowground to aboveground stocks inside the colony

394   agrees with our hypothesis iii that the increase in nutrient availability inside the colony would

395   stimulate the system to invest more in aboveground growth. This relationship between nutrient

396   availability and growth investment confirms many earlier studies (e.g. Warembourg and

397   Estelrich, 2001; Wang et al., 2008; Gao et al., 2011; Zhou et al., 2014). This shift from below- to

398   aboveground was accompanied by a doubling of the N use efficiency; the grassland inside the

399   colony supported ~ 2 times more biomass and biomass-C per g N, compared to the almost

400   unvegetated area outside the colony. This large increase in the 'N use efficiency' indicated a

401   positive feedback between N stock and the storage of both biomass and C. This increase was

402   caused by the drastic shift in C distribution: from a 76:24 towards a 32:68 proportion in SOC and

403   biomass, respectively. The C/N ratio of SOC was smaller than that of biomass (10.4 ± 0.6 vs.

404   39.1 ± 2.3 (mean $\pm$ SE)), in line with the C/N ratios for undisturbed soils reported by Chapin et

405   al. (2011) (~14) and for leaves reported by Sterner and Elser (2002) (~36). Hence, the overall

406   C/N ratio of ecosystems with most C stored in SOC (such as the non-colonized area) is typically

407   smaller than the overall C/N ratio of ecosystems with a high fraction of C stored in living

408   biomass (such as in the seabird colony).

409   The reason why higher N-stocks can support more biomass and C per unit N remains to be better

410   explored. Several studies on immature volcanic soils in New Zealand, Chile and Japan have

411   found a positive relationship between total N stock and net N-mineralization rates (and

412   consequently plant available N) (Parfitt et al., 2005; Hirzel et al., 2010; Yamasaki et al., 2011). In

413   the last study, the increased N-mineralization following N-addition was proved to be correlated

414   with the inhibition of microbial N-immobilization (and consequently decreased competition

415   between plant and microbial N-uptake). This inhibition of N uptake by microbes was proposed to

416   result from (1) nitrification-induced acidification, (2) increased soil osmotic potential to toxic

417   values and (3) an inhibition of ligninolytic enzyme production. The significant acidification

418   inside the seabird colony on Surtsey (Sigurdsson and Magnússon, 2010) supports this hypothesis,

419   however, further study is needed to investigate the role of microbial N-immobilization in N-

420   availability for plants on Surtsey.

421

422   *4.6. Seabird effect on biomass and C stocks*

423   Aboveground biomass outside the colony (0.13 ± 0.08 ton ha^{-1}) was very small and has almost

424   not changed since the first measurements of aboveground biomass in the permanent plots in 1999

425   (0.1 ton ha^{-1}) (Magnússon et al., 2009). This invariable aboveground biomass probably also

426   indicates relatively little changes in belowground biomass. As biomass degradation is an

427   important source of SOC (Kögel-Knabner et al., 2013), the low biomass production rates outside

428   the seagull colony explain largely the quasi constant SOC concentration and the lack of soil

429   formation. Since 1986, the seabird influence caused an over 50-fold increase of total biomass,

430   from 0.7 to 36 ton ha^{-1}, which corresponds to a shift from values typical for deserts (0-20 ton DM

431   ha^{-1}) to values typical for grassland ecosystems (20 to 50 ton DM ha^{-1}) (Larcher, 2003). This

432   large increase in only 25 years can largely be attributed to seabird N input, as there was a strong

433   positive relationship between total ecosystem biomass stock and N stock (as proxy for available

434   N) inside the seabird colony.

435   The aboveground biomass has been increasing nearly linearly from 1.4 ton ha^{-1} in 1999 to 4.1 ton

436   ha^{-1} in 2007 (Magnússon et al., 2009) to 5.9 ± 0.9 ton ha^{-1} (error = SE) in 2012-2013 . This

437   steady increase indicates that aboveground limitations on growth, such as competition for light

438   and space, were minor compared to the belowground limitations for water and nutrients. This

439   could be expected in a natural grassland ecosystem with relatively low nutrient levels (Kiaer et

440   al., 2013). This was also supported as well by the strong link between biomass and N stock.

441   The C stock in living biomass showed a clear shift as well, from a typical desert C stock outside

442   the colony (0.19 ton ha^{-1}; desert ecosystems: 0-10 ton ha^{-1}; Larcher, 2003) to a stock typical for

443   grassland ecosystems inside the colony (13 ton ha^{-1}; grassland ecosystems: 10-25 ton ha^{-1};

444   Larcher, 2003). However, despite the fact that biomass and living C-stock both have been

445 developing from desert to grassland, the SOC accumulation was lagging behind, and remained

446 far below the average for temperate grassland soils according to (Schlesinger, 1997) (see also

447 4.7).

448

449 *4.7. Did the N accumulation accelerate soil development?*

450 Outside the colony, the soil development has been proceeding very slowly, as the SOC

451 concentration, which is a reliable indicator of soil development (Kögel-Knabner et al., 2013), had

452 only increased slightly since 1986 in the upper 5 cm of the tephra sand (0.12 ± 0.02% SOC vs.

453 0.10 ± 0.02% SOC; errors are SE's) (Arnalds, unpublished data). When Surtsey had just

454 emerged, the SOC concentration was 0.012 ± 0.009% (error is SE) (Ponnameruma et al., 1967).

455 Inside the colony, the SOC concentration has been increasing with a factor of 10 to 60 since the

456 establishment of the colony, from 0.08% (taking the 1986 value as baseline SOC concentration as

457 this was the first year of permanent seabird colonization) to 0.9 ± 0.3 % on deep tephra sand an

458 4.6 ± 0.4 % on shallow tephra sand (errors are SE's). This large increase agrees with (Stockmann

459 et al., 2013) who hypothesized that priming effects, such as N addition, might stimulate SOC

460 accumulation in grasslands with a high R/S. However, Stockmann et al. (2013) reported that

461 grassland soils typically contain more than 1 - 3% SOC. Yang et al. (2014), for instance,

462 measured a SOC concentration of 28 up to 58% in an arid grassland in North China. So despite

463   the rapid buildup, the area inside the bird colony has not yet been lifted to a SOC concentrations

464   that are typical for grassland ecosystems. Also the current stock of SOC of about 4 (shallow) to

465   10 (deep) ton ha^{-1} is still marginal compared to the average SOC stock in temperate grassland

466   soils of 192 ton ha^{-1} according to Schlesinger (1997). This indicates that the soil development at

467   Surtsey is still in its first phase. Therefore, we expect that the SOC content will continue to

468   accumulate for many centuries before it reaches an equilibrium with the aboveground

469   productivity.

470

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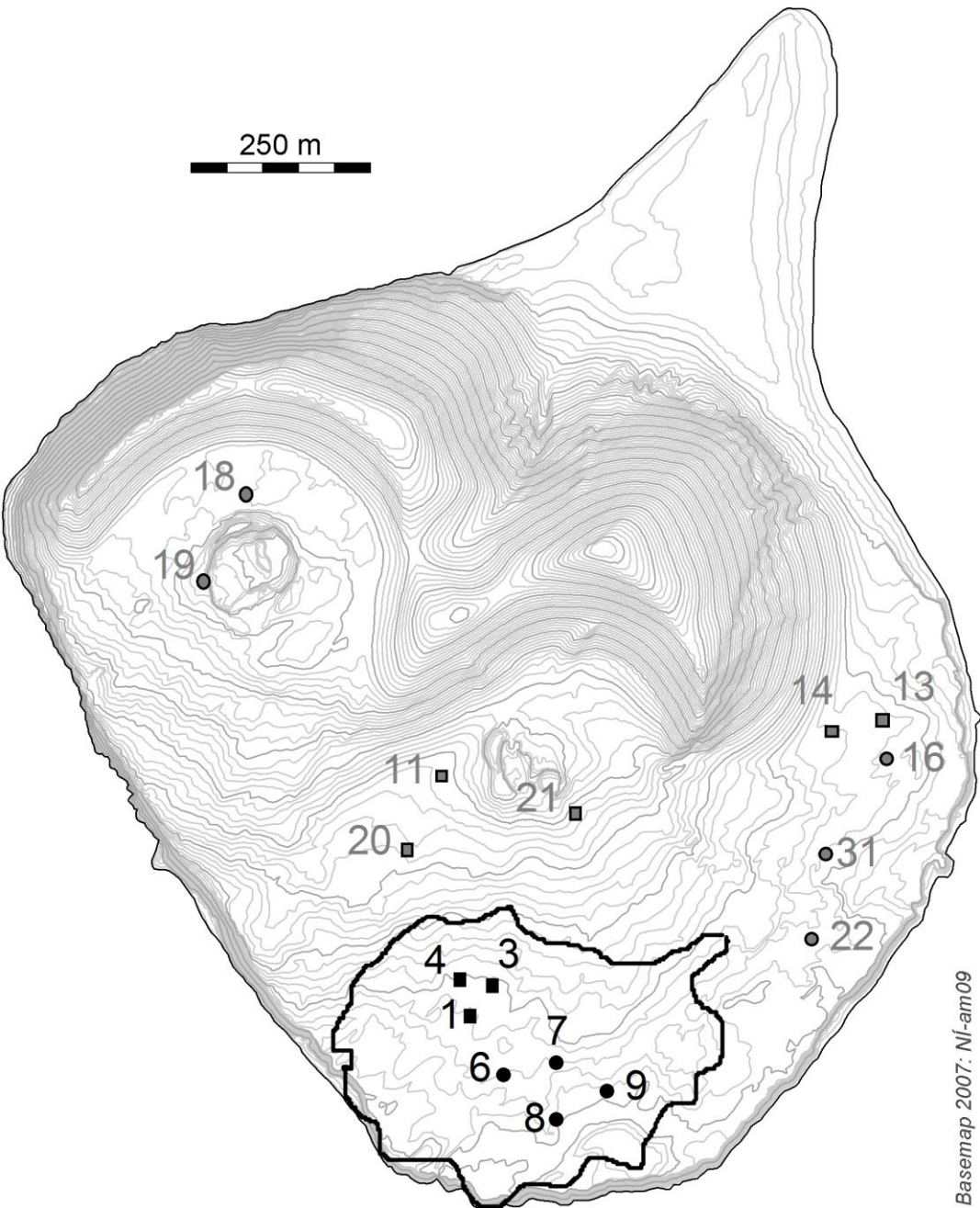
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**Fig. 1.** Location of the permanent study plots on Surtsey that were used in this study, shown on a topographical map from 2007. Contour intervals are 2m, the highest point on the island is 152m a.s.l.. The Eastern crater is located close to plots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

36

693   within the seabird colony in 2012 is marked with a black line (Approximation from aerial and

694   sattelite images, by Anette Th. Meier; Magnússon et al., 2014). Grey = Outside seabird colony;

695   Black = Inside colony; Squares = Deep tephra sand; Circles = Shallow tephra sand.

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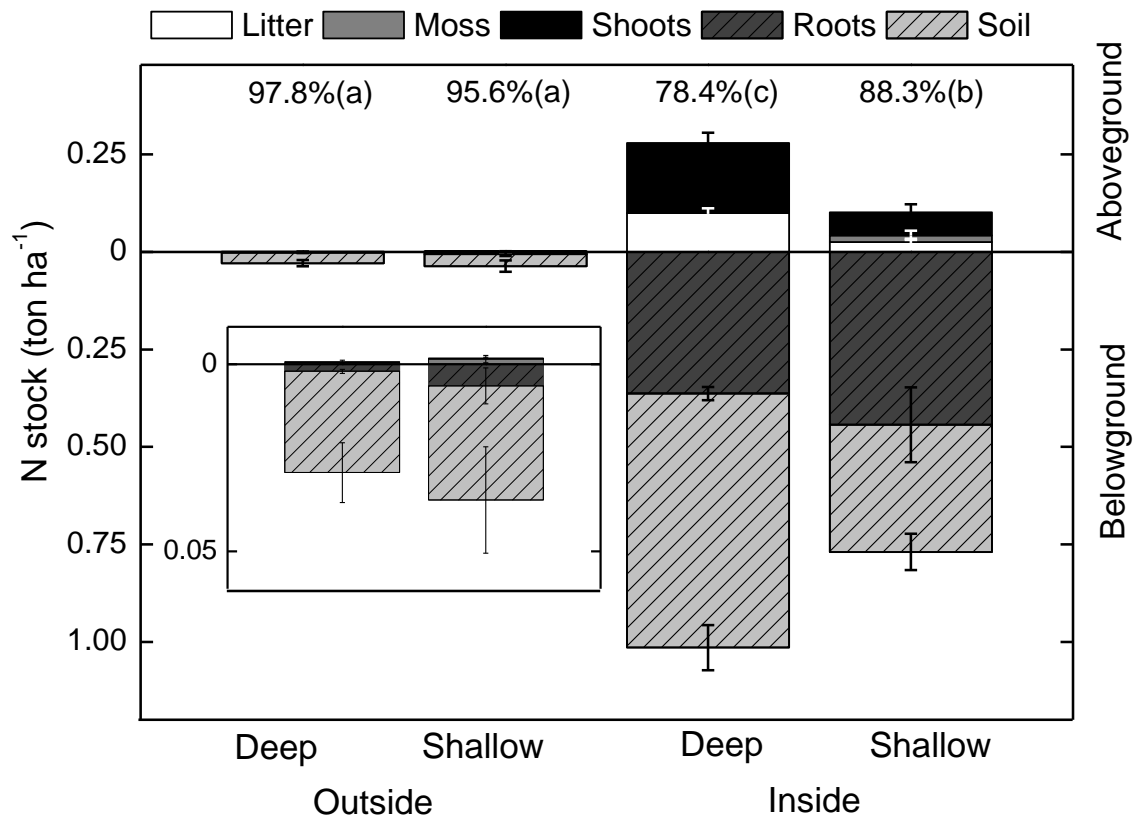
698   **Fig. 2.** Mean (±SE) values of the nitrogen (N) stocks in litter, shoots, roots (to 30 cm depth) and

699   soil organic nitrogen (SON) (to 30 cm depth) in four ecosystem types on Surtsey. The inserted

700   graph gives the small N stock outside the colony in more detail. 'Shoots' include all aboveground

701   living plant parts. Statistical results for are given in Table 1. Percentages above the graph indicate

702   the % of total N that is located belowground. Letters show statistical differences.

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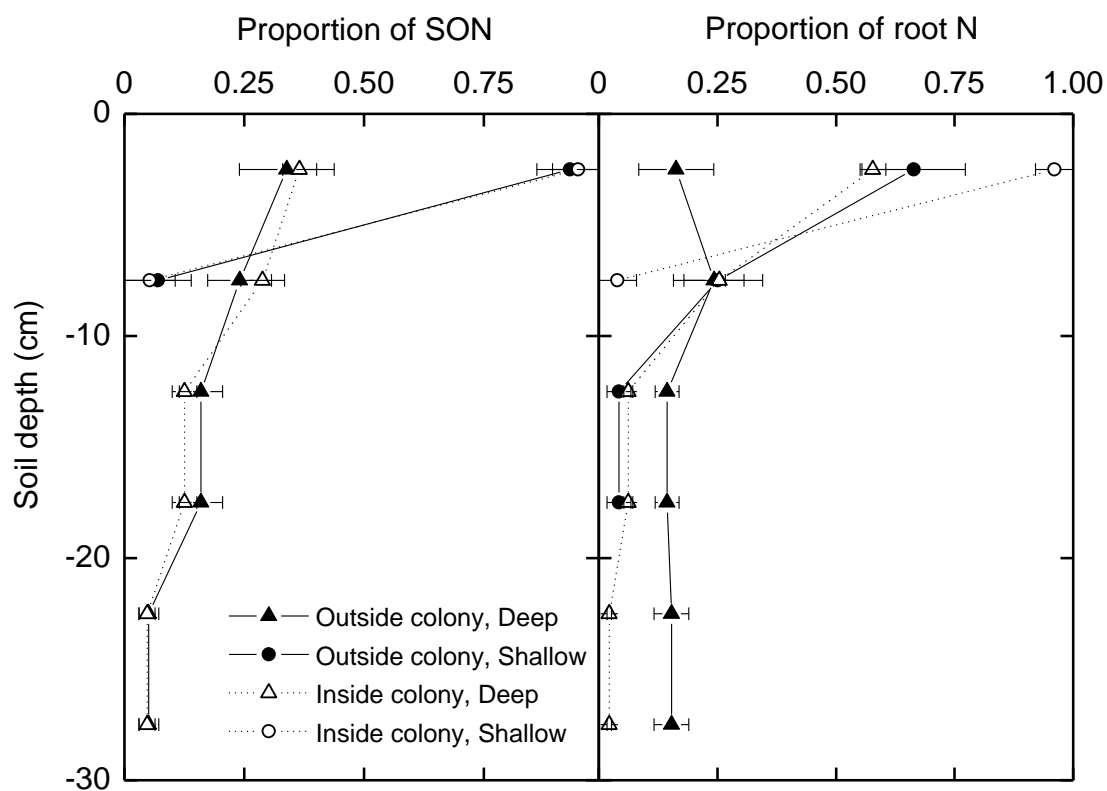
Fig. 3. Depth distribution of soil organic nitrogen (SON) and root N in four ecosystem types on Surtsey. Mean (±SE) proportions at each depth layer were calculated relative to the total SON or root N content in the top 30 cm. Statistical results can be found in Table 2.

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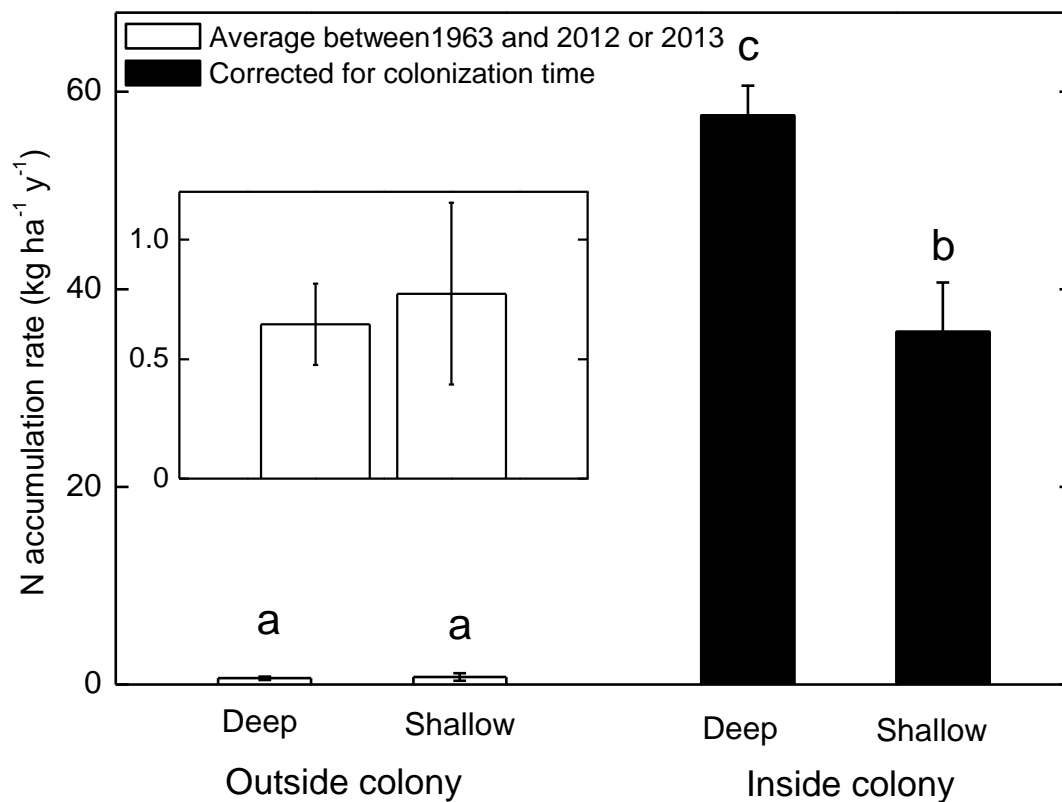
Fig. 4. Mean (±SE) values of the nitrogen (N) accumulation rate in four ecosystem types on

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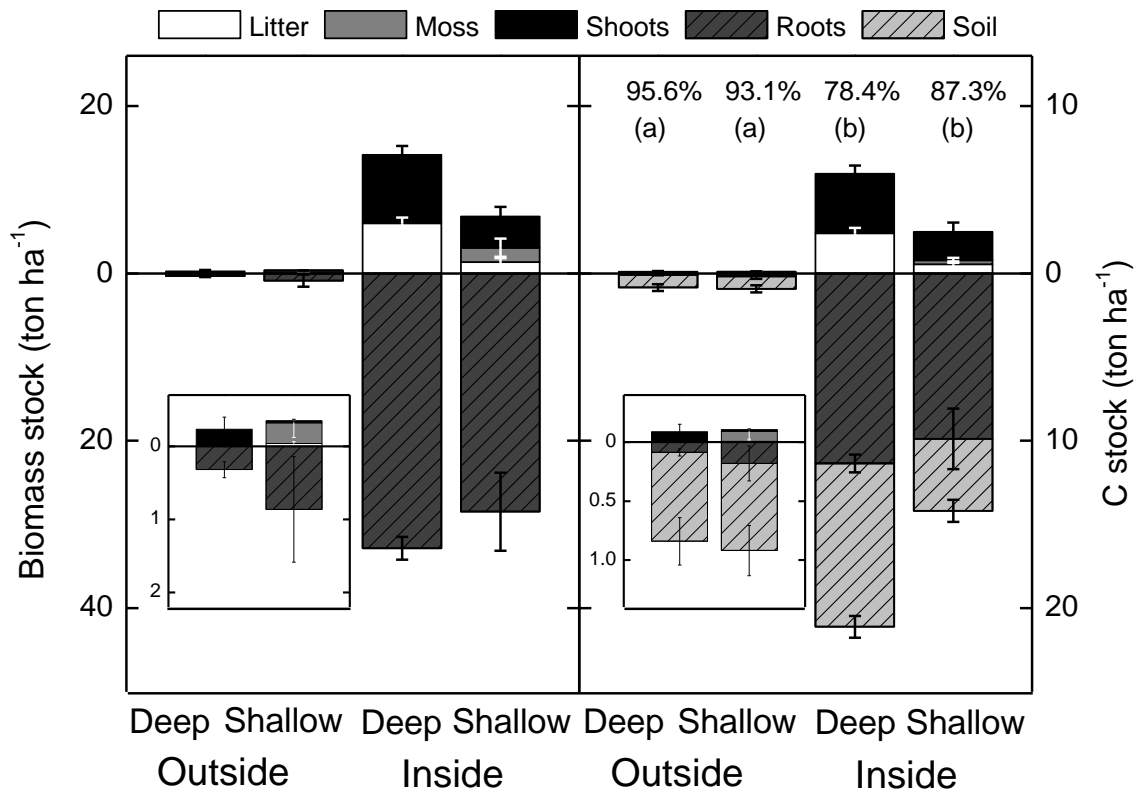
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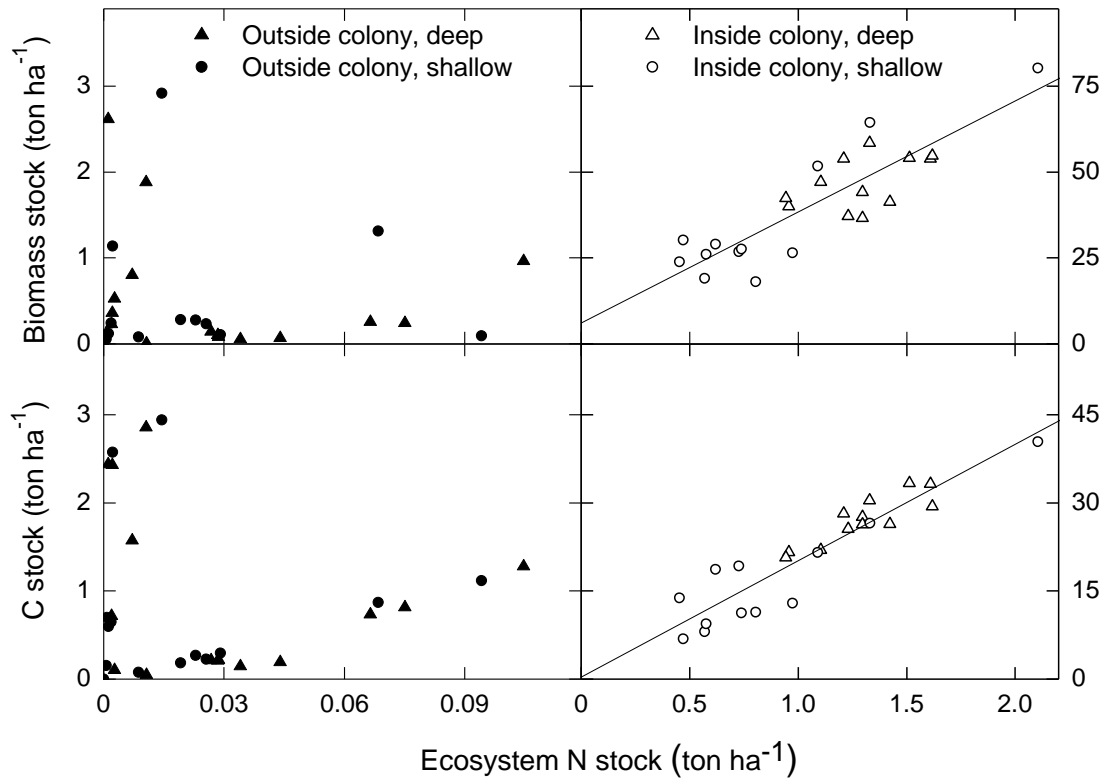
Fig. 6. Relationships between ecosystem biomass stocks (upper graphs) and ecosystem carbon stocks (bottom graphs) and ecosystem N stocks. Left graphs show the relationship outside the seagull colony, right graphs show the relationship and inside the seagull colony. Note the difference in scale of the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

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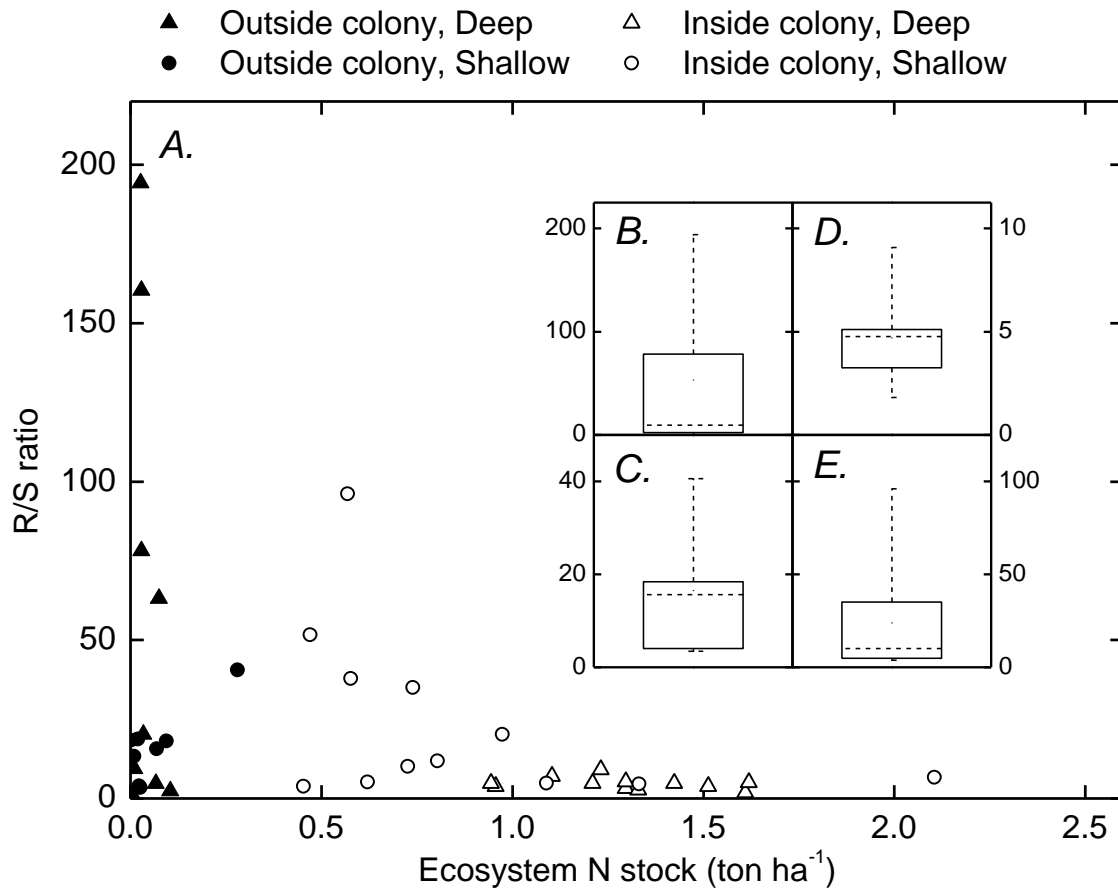
Fig. 7. Relationship between R/S ratio (Root/Shoot ratio) and N stock (A). Central figure shows boxplots of the R/S ratio on deep tephra sand outside the colony (B), shallow tephra sand outside the colony (C), deep tephra sand inside the colony (D) and shallow tephra sand inside the colony (C). Boxes 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																	
Df Numerator	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Df Denominator	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15
F-value	5.82	0.24	1.62	0.03	13.63	7.20	9.56	3.29	1.83	0.10	1.29	0.21	8.02	0.50	2.78	0.24	0.6
p-value	*	ns	ns	ns	**	*	**	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Colony																	
Df Numerator	-	1	1	1	-	-	-	1	1	1	1	1	-	1	1	1	1
Df Denominator	-	17	17	17	-	-	-	17	17	17	17	17	-	17	17	17	17
F-value	-	0.00	1.15	40.40	-	-	-	83.14	10.95	23.30	0.89	23.86	-	25.03	22.06	32.70	0.4
p-value	-	***	ns	***	-	-	-	***	**	***	ns	***	-	***	***	***	ns
Depth																	
Df Numerator	-	1	1	1	-	-	-	1	1	1	1	1	-	1	1	1	1
Df Denominator	-	16	16	16	-	-	-	16	16	16	16	16	-	16	16	16	16
F-value	-	0.28	1.87	0.01	-	-	-	2.32	1.91	0.04	2.29	0.12	-	0.34	2.66	0.28	2.7
p-value	-	ns	ns	ns	-	-	-	ns	ns	ns	ns	ns	-	ns	ns	ns	0.1
Colony effect on deep tephra sand																	
Df Numerator	1	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-
Df Denominator	8	-	-	-	8	8	8	-	-	-	-	-	8	-	-	-	-
F-value	0.00	-	-	-	11.97	0.00	0.00	-	-	-	-	-	17.35	-	-	-	-
p-value	***	-	-	-	*	***	***	-	-	-	-	-	**	-	-	-	-

Colony effect on shallow tephra sand

Df Numerator	1	-	-	-	1	1	1	1	-	-	-	-	1	-	-	-	-
Df Denominator	7	-	-	-	7	7	7	7	-	-	-	-	7	-	-	-	-
F-value	3.21	-	-	-	5.02	0.00	0.00	3.21	-	-	-	-	1.20	-	-	-	-
p-value	ns	-	-	-	ns	***	***	ns	-	-	-	-	ns	-	-	-	-

Depth effect outside colony

Df Numerator	1	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-
Df Denominator	8	-	-	-	8	8	8	-	-	-	-	-	8	-	-	-	-
F-value	0.53	-	-	-	1.83	0.02	0.02	-	-	-	-	-	0.00	-	-	-	-
p-value	ns	-	-	-	ns	ns	ns	-	-	-	-	-	ns	-	-	-	-

Depth effect inside colony

Df Numerator	1	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-	-
Df Denominator	7	-	-	-	7	7	7	-	-	-	-	-	7	-	-	-	-
F-value	5.16	-	-	-	11.97	6.57	8.68	-	-	-	-	-	8.95	-	-	-	-
p-value	ns	-	-	-	*	*	*	-	-	-	-	-	*	-	-	-	-

(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				Root N			
	Soil depth (cm)							
	0-5	5-10	10-20	20-30	0-5	5-10	10-20	20-30
Colony x depth								
Df Numerator	1	1	n/a	n/a	1	1	1	n/a
Df Denominator	11	11	n/a	n/a	15	15	15	n/a
F-value	0.01	0.63	n/a	n/a	0.28	2.06	0.20	n/a
p-value	ns	ns	n/a	n/a	ns	ns	ns	n/a
Colony								
Df Numerator	1	1	1	1	1	1	1	1
Df Denominator	12	12	6	6	16	16	16	17
F-value	0.25	0.15	0.49	0.13	16.18	1.15	6.83	4.59
p-value	ns	ns	ns	ns	***	ns	*	*
Depth								
Df Numerator	1	1	n/a	n/a	1	1	1	n/a
Df Denominator	13	13	n/a	n/a	17	17	17	n/a
F-value	55.15	10.45	n/a	n/a	10.76	1.49	4.54	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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