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Transfer of ornithogenic influence through different trophic levels of the Arctic terrestrial ecosystem of Bjørnøya (Bear Island), Svalbard

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ABSTRACT

Despite widespread recognition of the crucial role seabirds play in the fertilization of nutrient-poor polar terrestrial ecosystems, no studies have attempted a concurrent analysis of the entire or large proportion of an ornithogenically-supported food web. The aim of the current study was to assess the significance of allochthonous nutrient enrichment of key elements of the Bjørnøya (Svalbard) terrestrial ecosystem by investigating how different seabird species influenced the characteristics of soil, vegetation, and soil invertebrates (direct ornithogenic effects), and also how those characteristics were interrelated (indirect ornithogenic effects). We sampled in the vicinity of a little auk (*Alle alle*) colony, and in areas occupied by great skua (*Stercorarius skua*) and glaucous gull (*Larus hyperboreus*) nests. Our data demonstrate clear, multi-trophic-level, ornithogenic impacts across the terrestrial ecosystem, with most of the measured parameters of soil, vegetation and invertebrates being altered by proximity to bird nesting areas, though to varying degrees. The ornithogenic effects tended to weaken with increasing complexity of interactions between the ecosystem components, with progression through successive trophic levels. The clearest responses were observed for soil (higher nitrogen stable isotope ratio δ^{15}N, nitrogen and water content) and vegetation characteristics (higher δ^{15}N, N content and total cover, lower diversity and species number, and modified community composition). The responses seen in the invertebrate communities were less clear (community composition change), and were only apparent when major invertebrate groups were considered together and for the assumed decomposers: springtails and oribatid mites, while not in the case of predators (mesostigmatid mites and one spider species). There were also suggestions in the data that different seabird species may have different impacts on the surrounding environment, probably due to their different diet and nesting area topography. However, generally, the species of bird was a weaker factor than the presence of a seabird colony or nest itself.

> ‘A frightening desolation, it was a weird combination of the wickedly repellent and unwillingly fascinating, an evil and dreadful and sinister place. (…) Bear Island was black. That was the shocking, the almost frightful thing about it. Bear Island was black, black as widow's weeds.’
>
> —Alistair MacLean, *Bear Island*, 1971

1. Introduction

That was the first impression of the movie-making crew embarked on the *Morning Rose* vessel when they were approaching ‘perhaps the most inhospitably bleak coastline in the world’ (MacLean, 1971), that of Bjørnøya (Bear Island), Svalbard. Indeed, the terrestrial ecosystem of this isolated and relatively small Arctic island is generally regarded as relatively simple, species-poor, and characterised by short trophic chains due to, among other reasons, nutrient deficiency, climate harshness, presence of permafrost, and short growing season. This ecosystem was first presented

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schematically by Summerhayes and Elton (1923) in the form of a 'nitrogen cycle' diagram indicating relationships amongst organisms on Bjørnøya, and this scheme has often been reproduced and/or slightly modified by other subsequent authors (e.g. Remmert, 1980). However, it is now widely recognized as being a considerable generalization, informative only when illustrating the major pathways of nutrient and energy fluxes between the terrestrial and aquatic ecosystems (Hodkinson and Coulson, 2004).

When considering Arctic terrestrial vertebrates, trophic chains do show great simplicity. On Bjørnøya they consist of very few elements, these being grazing geese (present only periodically), insectivorous birds, such as snow bunting (*Plectrophenax nivalis*) and purple sandpiper (*Calidris maritima*), and predatory Arctic foxes (*Vulpes lagopus*). The latter feed also on locally nesting seabirds, and this part of the food web is therefore also directly connected to the marine ecosystem. Intricate fine-scale food web relationships, with significantly longer and more complex trophic chains, and higher species richness within each level are represented by the far less conspicuous invertebrate fauna, and particularly the fraction inhabiting the soil and soil surface (Hodkinson, 2013; Coulson et al., 2014). Soil-dwelling organisms play a key role in the provision of a range of ecosystem services, including herbivory, predation and decomposition (Bardgett, 2005; Bardgett and Wardle, 2012). They ensure effective nutrient cycling in tundra ecosystems by altering the balance between microbial immobilization and mineralization, and consequently make the nutrients available for plants. In favourable habitats, such as those enriched by allochthonous resources originating, for instance, from neighbouring marine ecosystems, soil invertebrates may reach high abundances and diversity giving a considerable positive feedback effect for the vegetation, and further driving the local food webs (e.g. Coulson et al., 2014; Hodkinson, 2013; Kolb et al., 2010, 2012, 2015; Wright et al., 2010).

One of the very effective vectors of nutrients from sea to land are seabirds (Mulder et al., 2011). The crucial role of seabirds, especially those nesting in large colonies, for the otherwise low productivity, species-poor polar terrestrial environment is relatively well known (e.g. Lindeboom, 1984; Odasz, 1994; Stempniewicz et al., 2007; Zwolicki et al., 2016b). Thanks to the transfer of marine nutrients to the land, mainly in the form of guano, but also feathers, eggshells and carcasses, seabirds fertilize the soil, facilitating vegetation growth and abundance, and consequently subsidise higher trophic levels (Croll et al., 2005; Bokhorst et al., 2007; Jakubas et al., 2008; Zmudczyńska et al., 2008, 2012; Zmudczyńska-Skarbek et al., 2013b; Zwolicki et al., 2013; Zawierucha et al., 2016). Further, community composition of microorganisms, plants and invertebrates in the so-called ornithogenic tundra is also distinctly altered (Aislabie et al., 2009; Eurola and Hakala, 1977; Elvebakk, 1994; Kim et al., 2012; Zmudczyńska et al., 2009, 2012; Zmudczyńska-Skarbek et al., 2015b; Zawierucha et al., 2016; Zwolicki et al., 2016a). Apart from this simple, unidirectional way in which seabirds influence tundra ecosystems, there are various marginal factors and/or feedback effects that locally modify habitats on land and the relationships between organisms both above- and below-ground. These include, for instance, physical disturbance of the ground in the neighbouring environment through various nesting behaviours of the birds (e.g. burrowing and trampling), considerable alteration of the three-dimensional structure and associated microclimates within the habitats, direct foraging on bird carrion and lost food remnants by invertebrate scavengers and detritivores, altered moisture levels within and under different species of ornithocoprophilous vegetation that may affect the associated invertebrate communities, and top-down regulation of populations of some animals by their predators (Mulder et al., 2011; and references therein).

Although the impact of seabirds on Arctic terrestrial ecosystems has been documented in various studies, these have generally focused on single or limited components of the food webs, such as vegetation (Eurola and Hakala, 1977; Elvebakk, 1994; Zmudczyńska et al., 2009; Zwolicki et al., 2016a), one or only few invertebrate groups (Byzova et al., 1995; Uvarov and Byzova, 1995; Fjellberg, 1997; Sømme and Birkemoe, 1999; Zmudczyńska et al., 2012; Zmudczyńska-Skarbek et al., 2015b; Zawierucha et al., 2016), or large herbivores (Jakubas et al., 2008), and on selected measured parameters, such as soil physicochemistry (Zwolicki et al., 2013), isotopic composition of plants (Wainright et al., 1998; Zmudczyńska-Skarbek et al., 2015a; Zwolicki et al., 2016b), or individual traits of some species (Zmudczyńska et al., 2008; Zmudczyńska-Skarbek et al., 2013b; Zawierucha et al., 2015; Wojciechowska et al., 2015). To our knowledge, no studies have attempted a concurrent analysis of the entire or a large proportion of the ornithogenically-supported terrestrial Arctic food web, to quantify the significance of its different linkages in detail, or to determine the relative role of direct and indirect pathways of allochthonous organic matter transfer through the local trophic webs, as has been tested elsewhere, for instance by Kolb et al. (2010, 2012, 2015) on islands of the Stockholm archipelago, Sweden, Wright et al. (2010) on the Isle of May, Scotland, and Sánchez-Piñero and Polis (2000) in the Gulf of California, Mexico.

Bjørnøya constitutes an excellent model ecosystem for conducting thorough studies of seabird-mediated changes in terrestrial food webs (see also Mulder et al., 2011; Vitousek, 2002). It is a remote, relatively small, discrete unit of land with restricted flora and fauna, low migration rate, and thus high susceptibility to alterations caused by different environmental factors. This Arctic island is amongst the last examples of environments that remain intact or only slightly modified by human activity. Due to high productivity of the surrounding sea (Mehlum et al., 1998; Węsławski et al., 1999), the island hosts large populations of seabirds characterised by differences in topography of their nesting places, distance from the coast, nesting and foraging habits, their density and therefore likely the intensity (amount) of guano deposition. However, most studies conducted in recent years on the island and its surroundings have focused on the feeding ecology of seabirds (e.g. Vader et al., 1990; Mehlum et al., 1998; Węsławski et al., 1999; Cherel et al., 2001), while its terrestrial biodiversity has been poorly described in detail (Gwiazdowicz et al., 2009; Zmudczyńska-Skarbek et al., 2013a).

The best-known seabird colonies of Bjørnøya, which are also some of the largest bird colonies in the world, are those of common and Brünnich's guillemots (*Uria aalge*, 125,000 individuals, and *U. lomvia*, 185,000 ind; Strøm, 2007), and black-legged kittiwakes (*Rissa tridactyla*, 130,000 occupied nests; Strøm, 2007), situated on stunning cliffs around the island's southern tip. Nonetheless, the majority of guano-derived nutrients deposited in these locations is expected to drain back to the sea from the coastal cliffs (Young et al., 2011; Zmudczyńska-Skarbek et al., 2015a; Zmudczyńska-Skarbek and Balazy, 2017), limiting the potential for tundra fertilization in their vicinity, although wind transfer of nutrient-rich seabird waste from the cliff faces up onto the terrestrial landscape above has also been observed (Hargan et al., 2017; Wright et al., 2010). There are also ground- and inland slope-nesting bird species in the remaining land area, including great skuas (*Stercorarius skua*, 350 occupied territories; Strøm, 2007), glaucous gulls (*Larus hyperboreus*, 650 occupied nests; Strøm, 2007), and little auks (*Alle alle*, roughly estimated at 10,000–100,000 pairs; Isaksen and Gavrilo, 2000), whose excreta and lost food remains may accumulate on site. In this study we focused on these areas. Earlier studies, both from our own and other research groups, suggest that different seabird species may influence the environment around their colonies differently, via differences in their diets and thus faeces composition, as well as local topography (Bédard et al., 1980; Jakubas et al., 2008; Pietryka et al., 2016; Zwolicki et al., 2013, 2016a).

Our primary hypothesis was that, due to marine-derived nutrient enrichment, seabirds would modify all of the Arctic terrestrial ecosystem components, but each of them, and each of their individual parameters, to a different degree. Within this overarching hypothesis, we addressed two complementary component hypotheses:

(1) the ornithogenic effect would dissipate gradually with progression through the trophic levels, due to the increasing complexity of interactions at each specific level;
(2) owing to their different diets and nesting area topographies, different seabird species would influence their nest vicinities in different and specific fashions.

To assess the significance of allochthonous nutrient enrichment of the key elements of a complete ecosystem, we investigated direct ornithogenic effects, including specific seabird species (glaucous gulls, great skuas and little auks), on different characteristics of: (i) soil (nitrogen stable isotope ratio δ^{15}N, total nitrogen content, and water content); (ii) vegetation (δ^{15}N, total N content, abundance, species richness, diversity, and community composition); and (iii) invertebrates, additionally with a simplified division into decomposers and predators (abundance, species richness, diversity, and composition). δ^{15}N is the most commonly used proxy for estimating the influence of seabirds on the ecosystem (e.g. Kolb et al., 2010; Zmudczyńska-Skarbek and Balazy, 2017; Zwolicki et al., 2016b; and references therein). Higher measured δ^{15}N values close to a seabird colony result from the isotopic fractionation of N occurring, first, with progress through the food web (seabirds are the top predators), and second, when ammonia volatilizes from guano (Hobson and Welch, 1992; Kelly, 2000; Wainright et al., 1998).

Furthermore, we examined interrelationships between the abovementioned soil, vegetation, and invertebrate variables to identify which parameters of the potentially seabird-influenced habitats subsequently affected other components of the ecosystem. We considered these to be indirect ornithogenic effects, although also accept that many other factors and feedback loops operating simultaneously which may also mediate and/or modulate the transfer of the seabird subsidies and could not be considered here.

2. Materials and methods

2.1. Study area

Bjørnøya (74°N 19°E) is the southernmost island of the Svalbard archipelago. It is situated midway between the Norwegian mainland and Spitsbergen, and comprises an area of 178 km^2 (it is ca. 20 km long and 15 km wide). The island is surrounded to the east, south and west by the polar front (i.e. the area where cold water from the north and east is mixed with warm and stratified Atlantic water; Loeng, 1991), and is characterised by high occurrence of fog reducing the amount of direct sunlight available, as well as frequent and strong winds, especially in winter, which results in thinning and removal of snow cover, and exposure of soil/vegetation to low temperatures (Summerhayes and Elton, 1923; Engelskjøn, 1986). The climate is Arctic oceanic. During the period 1961–1990 the mean temperature for July and August (the warmest months) was 4.4 °C, and that of the coldest month (January) was −8.1 °C. Average annual temperature was −2.4 °C and annual precipitation was 371 mm water equivalent (eKlima, 2014). Most of the land area is flat, with some mountainous areas in the south (Miseryfjellet is highest at 535 m asl). Approximately 740 small lakes are scattered around the island (Norwegian Polar Institute, 2016). Bjørnøya has a steep, largely inaccessible coastline occupied by numerous seabird colonies, including common and Brünnich's guillemots, black-legged kittiwakes, northern fulmars (*Fulmarus glacialis*), black guillemots (*Cepphus grylle*), and Atlantic puffins (*Fratercula arctica*). Nests of great and Arctic skuas (*Stercorarius parasiticus*) and glaucous gulls are located on the plateau, the latter species close to cliff edges. Several colonies of little auks are situated on Alfredfjellet (421 m asl). Apart from historical hunting for marine mammals and birds, today's human activities are limited to a year-round operating meteorological station run with a crew of not more than 10 people, and a small number of researchers and tourists during the summer months.

2.2. Sampling protocol

The study was conducted in July and August 2008. Three areas in the vicinity of different seabird species nesting sites (SEABIRD; factor levels here and henceforth indicated in ‘small capitals’), together with their respective control areas (CONTROL), were sampled (Fig. 1):

AUK area (74°38′N 19°03′E): SEABIRD – close to a relatively large colony of planktivorous little auks, situated on a gentle slope of Alfredfjellet, exposed to the north and descending to Lake Ellasjøen. The upper part of the site consisted of vegetation-covered rock debris, while the lower part approaching the lake shore was flat and waterlogged. The cover of vegetation consisted of vascular plants interspersed with compact moss carpets and clumps, and was complete in both parts of the area. Samples were collected along line transects oriented downslope in parallel and below the seabird colony (Fig. 1B). The transect consisted of 5 plots (160 × 160 cm each) that were located from the transect starting point (plot 1) as follows: plot 2 (15 m), 3 (49 m), 4 (125 m), and 5 (296 m).

CONTROL – a transect with 5 plots parallel to SEABIRD but ca. 500 m distant from the colony, and separated from it by a seasonal stream. Vegetation cover was around one fifth of that growing within the SEABIRD transect (the measurement method is described in section 2.3).

GULL area (74°47′N 18°78′E) – located in the north-west, completely flat part of the island, close to the cliff edge and to a concentration of the predatory glaucous gull nests. SEABIRD – consisted of patches of dense vegetation surrounding each nest. Vascular plants were usually underlain by a dense moss layer. Two plots (100 × 100 cm each) were sampled in the vicinity of each nest: plot 1, with a nest situated in the centre, and plot 2 adjoining plot 1, still within the patch of dense vegetation surrounding the nest (in total, 5 vegetation patches surrounding a nest were examined; Fig. 1C).

CONTROL – situated beyond the dense vegetation patches surrounding individual nests. Total vegetation cover values, and especially those of vascular plant species, were lower than those of the respective SEABIRD sites. One plot beyond the boundary of the compact vegetation patches, 3 m on average from the relevant nest, was sampled.

SKUA area (74°47′N 18°76′E) – located inland from the glaucous gull area, in close proximity to predatory great skua nests. Vegetation was similar to that of the GULL area, with a generally more species rich herb/shrub flora, and more abundant mosses present. Two plots (100 × 100 cm) from the SEABIRD, and one plot from the CONTROL area were sampled according to the pattern described above (in total, 25 vegetation patches investigated; Fig. 1D).

The nests around which samples were obtained had been

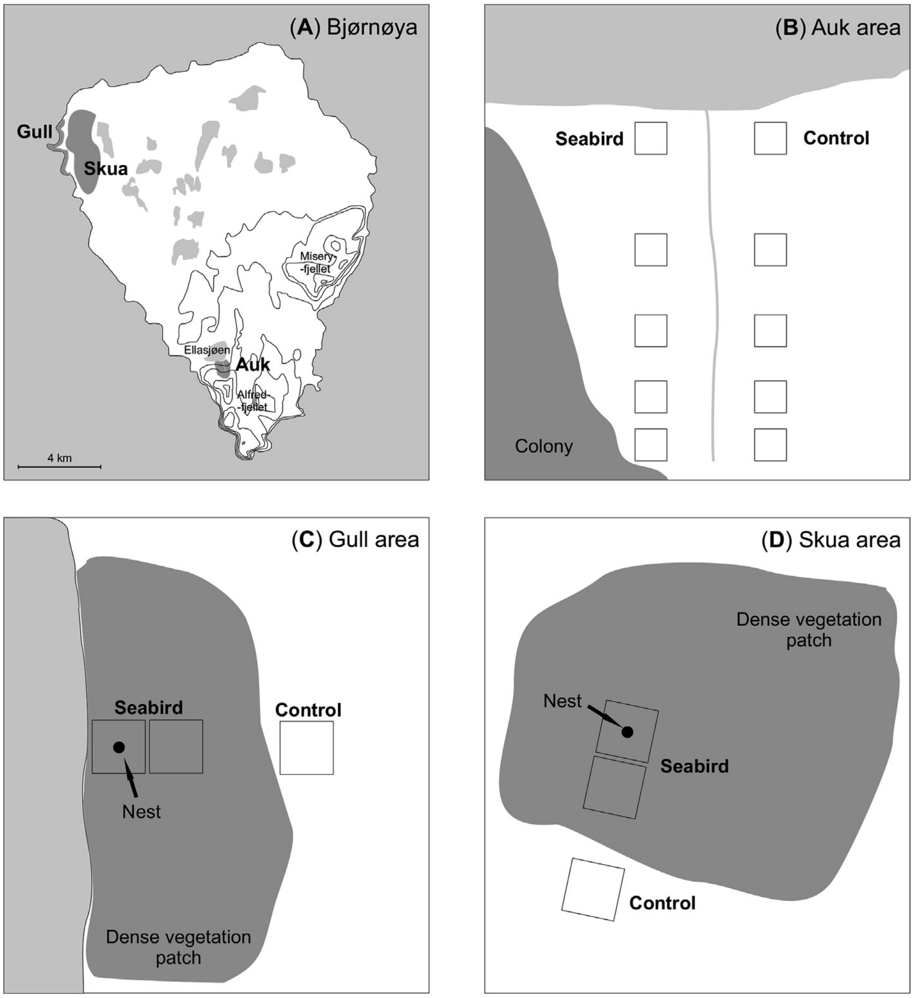


Fig. 1. Bjørnøya, with 100 m contour lines and larger lakes marked. The three study areas are indicated with dark grey (**A**). Schemes of sampling plot locations in relation to a seabird colony (SEABIRD and CONTROL transects in the AUK area; **B**), and examples of individual vegetation patches with nests, and SEABIRD and CONTROL plots in the GULL (**C**) and SKUA (**D**) areas.

recently occupied as evidenced by presence of down and other nest material, and food remnants. Nests containing eggs or chicks during the fieldwork were not sampled.

Sampling protocols differed between the AUK versus GULL and SKUA areas since the former was also a part of another study in which longer transects and larger plots were always sampled (and with respect to at least vegetation, a little auk colony vicinity is evidently more heterogeneous than the area in the immediate vicinity of individual great skua and glaucous gull nests).

2.3. *Vegetation abundance and species composition*

Within all sampling plots of the three study areas (AUK: $N = 10$, GULL: $N = 15$, SKUA: $N = 75$; in total $N = 100$) we identified vascular plant species, and visually (using a plot-sized quadrat frame subdivided into 20 × 20 cm units) estimated total cover of vegetation and individual vascular plant species percentage contributions to the overall vegetation cover. We identified and assessed the cover of moss species from the vegetation covering the soil cores that remained after invertebrate extraction (cf. below). We rescaled the abundance of both vascular plant and moss species into a six-level scale which roughly reflected logarithmic transformation of the mean percent cover in each level (modified van der Maarel scale; van der Maarel, 1979): level 1 (cover less than 5%), 2 (5–12.4%), 3 (12.5–24.9%), 4 (25–49.9%), 5 (50–74.9%), and 6 (75–100%). Shannon's diversity index was used to describe vegetation community diversity ($H' = \Sigma_i(n_i N^{-1}) \ln(n_i N^{-1})$, where n_i was the cover of species i, and N was the total vegetation cover; Shannon and Weaver, 1949), with the help of DIVer 10.o1 (AZB analysis and software, 2010).

2.4. *Invertebrate abundance and species composition*

Around the little auk colony we collected three soil cores (together with vegetation cover) from three sites along one diagonal of each sampling plot (from the centre and the two corners of each square). In the cases of glaucous gull and great skua nesting sites we sampled one soil core from the centre of each plot, except in plot 1 where the sample was taken immediately adjacent to the nest. Samples (in total $N = 100$) were taken with a cylindrical probe (diameter 6 cm) from the soil surface (mainly organic) layer, and included the vegetation covering the area and the underlying soil to a depth of ca. 5 cm. Each sample was sealed in a plastic container and, within few hours, returned to the laboratory where it was subsequently placed for 48 h in a modified Tullgren apparatus illuminated with 60 W bulbs (Barton, 1995). Extracted invertebrates were preserved in 70–96% ethanol and identified to species level following Bayartogtokf et al. (2011), Colloff (1993), Fjellberg (1998, 2007), Giljarov and Krivolutsky (1975), Gwiazdowicz and Rakowski (2009), Gwiazdowicz et al. (2011), Teodorowicz et al. (2014), Trägårdh (1910) and Weigmann (2006). We calculated total densities of all the invertebrates, densities of presumed decomposers (including herbivorous, fungivorous, bacteriovorous, and detritivorous Collembola and Oribatida together) and predators (Mesostigmata and Aranae), and densities of the species (number of individuals m^{-2}). For cores obtained from the 160 × 160 cm plots (different size of the plots resulted from the AUK area also being a part of another study), total invertebrate species counts for each plot (i.e. the sum of the three samples obtained) were analysed. Shannon's diversity index was used to describe invertebrate species diversity similarly to that of vegetation (Shannon and Weaver, 1949; AZB analysis and software, 2010).

2.5. Soil and vegetation isotopic analyses

We took samples of soil adjacent to the same collection sites as used for invertebrate sampling ($N = 67$; some samples were lost during analyses). Each sample, containing ca. 500 cm^3 of soil, was taken with a shovel from the soil surface layer (to a depth of ca. 5 cm). At sampling locations with very compact vegetation, we removed and discarded the upper layer of live and dead, poorly decomposed, plant material. Immediately after returning from the field an 80 cm^3 sub-sample of each sample was weighed with electronic scales (precision 0.1 g), dried at 40–60 °C to constant mass, and weighed again to calculate water content per unit dry mass (%) according to the formula: $W = (m_w\, m_s^{-1})$ 100%, where m_w was the mass of water, and m_s – the dry mass of soil.

After drying, soil sub-samples were dry-sieved through a 0.25 mm mesh to remove stones and large plant debris, and ground with a vibrating mill (LMW-S, Testchem) to a grain size of less than 0.03 mm diameter. A small amount of each soil sub-sample (1–2 mg, weighed with a microbalance, precision 0.001 mg) was packed into a tin capsule. Nitrogen isotope ratio was determined by a continuous flow mass spectrometer (Thermo Fisher, Delta V Advantage) coupled to an elemental analyser (Thermo Fisher, Flash EA 1112) at the University of La Rochelle, France. Results were expressed in the conventional $\delta^{15}N$ (‰) notation, according to the equation: $\delta^{15}N = (R_{sample}\, R_{standard}^{-1} - 1)$ 1000, where R_{sample} was the stable isotope ratio $^{15}N/^{14}N$ in the analysed sample, and $R_{standard}$ was the stable isotope ratio $^{15}N/^{14}N$ in the reference material i.e. atmospheric N_2 (Kelly, 2000). At the same time the analysis enabled assessment of the percent of total nitrogen content (total N) in the soil (%).

For the assessment of $\delta^{15}N$ and total N in vegetation, within each sampling plot we collected three samples of the aboveground parts of: mosses (regardless of the species), graminoids (*Festuca* cf. *rubra* ssp. *richardsonii*), forbs (*Oxyria digyna*), and dwarf shrubs (*Salix* spp.), as the representatives occurred with sufficient abundance (in total $N = 613$). On return from the field the vegetation was dried at 40–60 °C to constant mass, ground with a vibrating mill and further processed in the same way as soil samples. For the purpose of this study, all the vegetation taxa were analysed together.

2.6. Statistical analyses

Numerical ordination methods were used to describe total (qualitative and quantitative) variability of vegetation and invertebrate communities (the two communities analysed separately): (1) detrended correspondence analysis, DCA – independently of any environmental influence, to describe the general pattern of variability in the studied community; and (2) canonical correspondence analysis, CCA – in relation to environmental factors: the *Seabird* factor, determining the presence (SEABIRD) or absence (CONTROL) of a seabird nest/colony in the vicinity of sampling sites, and the *BirdSpe* factor, representing the species of seabirds nesting, i.e. glaucous gull (GULL), great skua (SKUA), and little auk (AUK). The values of the first two axes of the two DCA ordinations (the main theoretical gradients) were used as separate variables in subsequent SEM analyses (see below). Invertebrate species data were log-transformed to normalize their distributions. After each CCA, a Monte Carlo permutation test was performed (with 499 permutations) to identify which of the factors significantly influenced the model. To calculate the factors' unique and shared contributions to explaining variability in the species composition we used a variation partitioning test (ter Braak and Šmilauer, 2012). To provide more accurate estimation of variation explained with CCA, we adjusted the variation value using the number of degrees of freedom as suggested by Peres-Neto et al. (2006). Each time the results of constrained ordination were compared with those of unconstrained ordination (% variability explained by an environmental factor was divided by % variability explained by one (in the case of *Seabird*) or two (*BirdSpe*) axes of the unconstrained analysis). Thus we estimated the efficiency of the environmental factor(s) (%) in explaining the total variability present in the data (ter Braak and Šmilauer, 2012).

We analysed all individual response variables (soil $\delta^{15}N$, total N and water content; vegetation $\delta^{15}N$, total N, cover, diversity, number of species, and DCA axes 1 and 2; and invertebrate density, diversity, number of species, and DCA axes 1 and 2) first by using linear mixed models that included: (i) the fixed effects of the presence of seabirds – the *Seabird* factor, (ii) the fixed effect of the bird species – the *BirdSpe* factor (both of the factors identical to those used in CCA), and (iii) their interaction. Study plots defined within each seabird species were included as a categorical random effect. Models were fitted using the identity link function (i.e. as general linear mixed models) in the *lme4* package using the *lmer* function, and the *lmerTest* package to aid in fixed effects testing. Some response variables were log-transformed prior to model fitting after the inspection of residuals from initial model fits, to ensure normality and homogeneity of variance of residuals (transformed variables: soil water and total N content, vegetation cover, vegetation diversity, invertebrate density, invertebrate diversity). The numbers of vegetation and invertebrate species were treated as non-normal and analysed using generalized linear mixed models, fitted in using *glmer* and the Poisson error distribution (with log link function). In all models non-significant interactions ($P > 0.05$) were removed. Significance of fixed effects was tested using the *t* statistics (*lmerTest* function; with the number of degrees of freedom approximated using the Satterthwaite method) or *Z* statistic (*glmer* function).

In the second step, we performed a structural equation modelling (SEM) analysis to identify possible causal links and interrelationships between the variables. SEM was executed in the *lavaan* package, and visualized using the *semPlot* library (plots were later edited for clarity). The analysis was performed starting with the most complex model (including all the variables) which was then simplified following the minimization of the Akaike Information Criterion (AIC). SEM was performed in two rounds. The first round included soil water content and all the vegetation and invertebrate parameters beside the nitrogen variables, and all the samples, while the second round additionally included $\delta^{15}N$ and total N content in soil and plants (which were available for a smaller subset of the data, $N = 67$). In order to use the SEM method, the categorical variables of seabird presence and seabird species where coded as binary variables (binary contrasts). Hence, the *Seabird* factor was coded as 0 (no seabirds, CONTROL area) and 1 (seabirds present, SEABIRD area). The *BirdSpe* factor was coded as two binary variables: *Bspec1*, i.e. AUK vs. GULL (1 = AUK), and *Bspec2*, i.e. SKUA vs. GULL (1 = SKUA). We used default variance and covariance constraints from the *lavaan* package.

The numerical ordination analyses were performed in CANOCO 5.0 software (ter Braak and Šmilauer, 2012). All regression and SEM analyses were performed in the R computing environment version 3.1.2 (R Development Core Team, 2015).

3. Results

3.1. Species composition of vegetation and invertebrate communities around the seabird nesting sites

The unconstrained DCA ordination describing variability in plant species composition (44 species in total, Suppl. Table 1) demonstrated good separation of plots along the two main axes showing hypothetical environmental gradients (Fig. 2A). The split along axis 1 rather clearly distinguished plots of the SEABIRD (right side of the diagram) from those of the CONTROL areas (left side). Axis 2 presents the separation of plots related to the *BirdSpe* factor, with the AUK plots situated in the upper part, and the GULL plots in the lower part of the ordination space, whereas plots from the SKUA area spread along the whole axis length. This was confirmed by CCA (constrained ordination) and the permutation test, which revealed that the *Seabird* factor was responsible for 53.8% ($F = 7.2$, $P = 0.002$), while the *BirdSpe* factor accounted for 19.2% ($F = 2.7$, $P = 0.002$) of the total explained vegetation variability, and that the two variables shared less than 0.5%. Plant species most abundant and frequently occurring in the SEABIRD areas included *Festuca* cf. *rubra* ssp. *richardsonii* and *Sanionia uncinata*, while the composition of the CONTROL areas was more diverse (Fig. 2A and B, Suppl. Table 1). *Festuca* cf. *rubra* ssp. *richardsonii* and *Salix* spp. predominated close to the great skua nests, and the former species was the most abundant also around the glaucous gull nests, and the latter close to the little auk colony (Fig. 2C, Suppl. Table 1).

The first two axes of the DCA ordination of plots, based on the total invertebrate species composition (43 species in total, Suppl. Table 2), showed similarities to some degree in the patterns apparent in their community variability to that described for vegetation (Fig. 3A). Axis 1 roughly split all the plots into those originating from the SEABIRD and CONTROL areas. Axis 2 showed a less clear gradient than in the case of vegetation, and both the GULL and AUK plots occupied the upper part of the ordination space. Of the total invertebrate species composition variability defined by the CCA model, 29.8% was explained by the *Seabird* factor ($F = 3.0$, $P = 0.002$), and 27.8% by the *BirdSpe* factor ($F = 2.8$, $P = 0.002$). The effects of the two variables were independent from each other. *Hermannia reticulata*, *Folsomia quadrioculata*, and *Oligaphorura ursi* were among the invertebrate species predominating within the SEABIRD areas (the latter found only in the SKUA area; Fig. 3B, Suppl. Table 2). CONTROL areas, as with the vegetation, exhibited greater variability, with no distinct dominant species. Among the invertebrate species best fitted to the ordination space created by the *BirdSpe* factor were those more frequently occurring in the GULL area, such as *Willemia scandinavica* and *Protaphorura macfadyeni* (never and only once, respectively, recorded from the AUK area), and a few others which were exclusively or more frequently found in the AUK sites, e.g. *Desoria tchernovi* and *Liochthonius lapponicus* (Fig. 3C, Suppl. Table 2).

Analyses performed separately for decomposers and predators gave similar results to those described above in the case of decomposers (*Seabird*: 31.5%, $F = 3.6$, $P = 0.002$; *BirdSpe*: 27.7%, $F = 2.9$, $P = 0.002$), and identified no significant effects of the *Seabird* or *BirdSpe* factors on the predator community ($P > 0.05$; data not shown).

3.2. Individual environmental variable responses to the influence of different seabird species

All the studied soil parameters, i.e. δ^{15}N, total N and water content, were significantly influenced by the presence of birds (*Seabird* factor), being higher in the SEABIRD than in the CONTROL areas (Fig. 4, Table 1; full results of the linear mixed models presented in Suppl. Table 3). In the case of δ^{15}N there were also significant interactions between the *Seabird* and both *BirdSpe* AUK and *BirdSpe* SKUA factors. This was due to the soil δ^{15}N being much higher within the GULL SEABIRD area as compared with both the AUK and SKUA SEABIRD areas, while there were no clear differences in total soil N and water content between the bird species.

The *Seabird* factor significantly influenced vegetation δ^{15}N, total N, diversity (Shannon's diversity index), and number of species (Table 1). Vegetation δ^{15}N and total N were significantly higher while species diversity was lower in areas where the birds nested (Fig. 4). The number of plant species was also lower in the SEABIRD as compared with the CONTROL areas in the cases of gulls and skuas, but it was greater in the case of auks. The cover of vegetation was significantly influenced by *BirdSpe* AUK and *BirdSpe* SKUA factors, and by the interactions between both and the *Seabird* factors. Nevertheless, differences in the cover of plants among different seabird species were observed mostly in the CONTROL areas (the lowest cover in the SKUA area, and the highest in the GULL sites), while all the SEABIRD areas reached the maximum vegetation coverage. The AUK areas were clearly distinguished from the remaining sites with the lowest vegetation δ^{15}N, and the highest diversity index and number of plant species. The highest nitrogen isotope ratio was found in the GULL SEABIRD area but without the interaction with the *SEABIRD* effect, suggesting habitat differences.

There were no effects of seabird presence on invertebrate (both all the taxa together, as well as decomposers and predators considered separately) measures, i.e. density, diversity, and number of species (Table 1, Fig. 4). The *BirdSpe* AUK factor (but without the interaction with the *Seabird* effect) appeared to significantly impact the total number of invertebrate species, decomposer diversity, and predator density. Within the AUK area we observed an overall higher number of invertebrate species and density of predators, and lower decomposer diversity, though at the limit of statistical significance in the latter case.

3.3. Direct and indirect effects of seabirds on the terrestrial ecosystem

To find the best working model of the causal network connecting direct and indirect effects of seabird presence and species on the terrestrial ecosystem, we analysed several SEM variants substituting individual response variables, and modifying relationships among them. The models included: vegetation, decomposer and predator number of species, also considering interrelationships with vegetation cover and soil water content (models 1–3, Fig. 5A), vegetation and invertebrate diversity, through soil water content (models 4–5, and 12; replacing diversity with abundance worsened the results, with AIC being 2–4 times higher, data not shown), and vegetation and invertebrate diversity and species composition (expressed with DCA gradients; models 6–13). The optimal model, 12, selected by the lowest AIC = 108.15, applied for diversity indices. It indicated a slightly negative direct effect of the presence of birds (*Seabird* factor) and positive effect of both the contrasts between seabird species (the factors *BSpec1*, i.e. AUK vs. GULL, and *Bspec2*, i.e. SKUA vs. GULL) on vegetation diversity, and emphasised the strong positive influence of *Bspec1* (in line with the above-mentioned linear models). The direct effect of

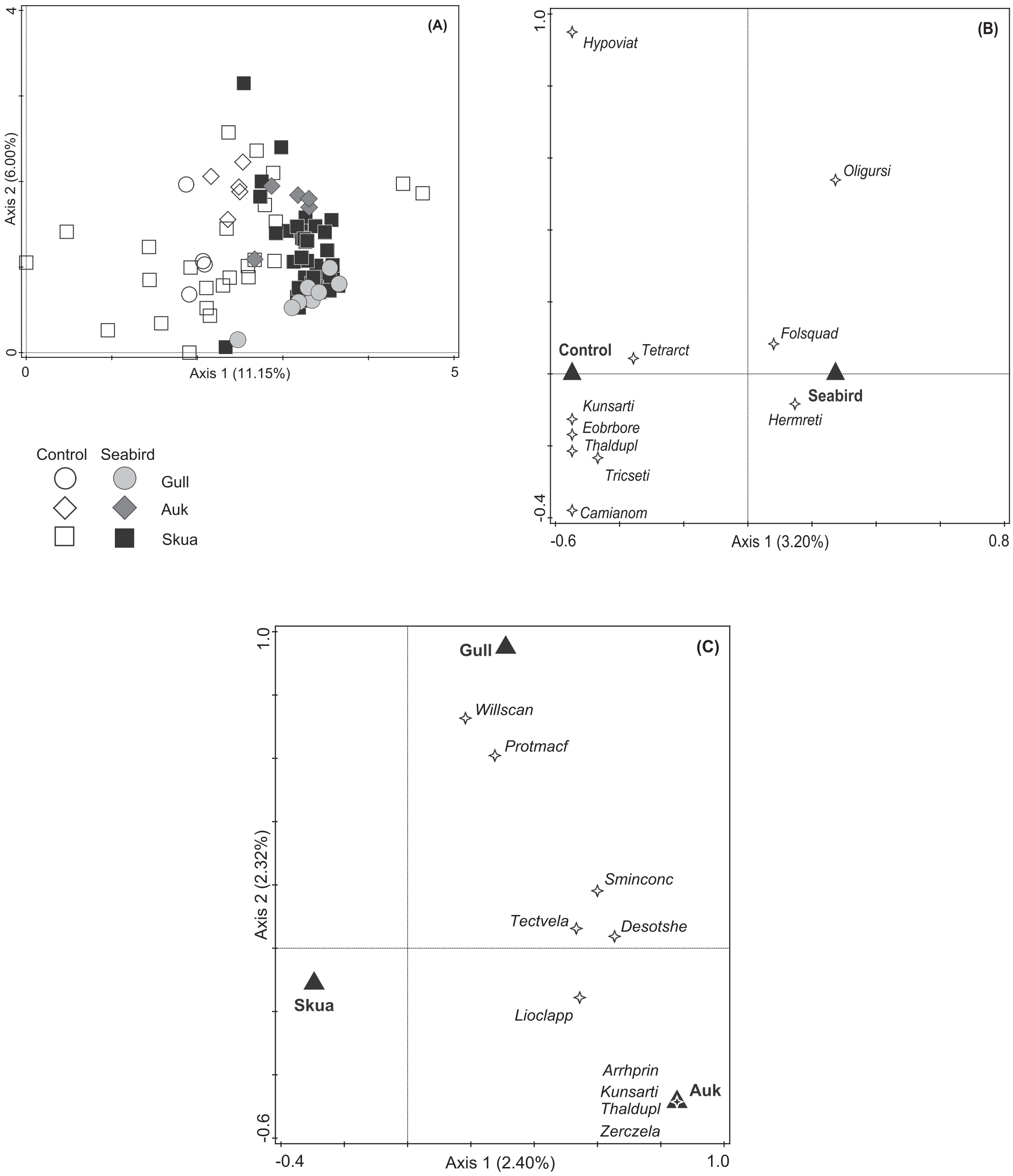


Fig. 2. Detrended correspondence analysis (DCA) ordination of plots classified with respect to vegetation community composition of different study areas (**A**). Canonical correspondence analysis (CCA) ordination of the 10 best-fitted vegetation species with respect to the *Seabird* (axis 1; **B**) and *BirdSpe* (**C**) factors (axes 1 and 2) in each area. Scaling of scores focused on distances among species. Species labels stand for: Bracturg – *Brachythecium turgidum*, Campoly – *Campylium polygamum*, Climdend – *Climacium dendroides*, Cochgroe – Cochlearia groenlandica, Dicrvari – *Dicranella varia*, Disticapi – *Distichium capillacaeum*, Drabsp. – *Draba* sp., Festrubr – *Festuca* cf. *rubra* ssp. *richardsonii*, Hypnbamb – *Hypnum bambergeri*, Polysaxa – *Polytrichum saxangulare*, Ranusulf – *Ranunculus sulfureus*, Saginiva – *Sagina nivalis*, Salispp. – *Salix* spp., Saniunci – *Sanionia uncinata*, Saxihirc – *Saxifraga hirculus*, Saxicaes – *S. caespitosa*, Saxioppo – *S. oppositifolia*, Timnnorv – *Timnia norvegica*.

seabird species on invertebrate diversity was more complex, and the AUK-GULL contrast affected it positively while the SKUA-GULL was negative. The diversity of plants clearly had a positive influence on invertebrate diversity, and this may be considered as an indirect seabird impact. Another low AIC value (113.22) characterized model 4, which was similar to model 12 but included the direct effect of seabird presence on invertebrate diversity while disregarding the bird species impact on this variable. All the remaining models had much higher AIC values (in the range 300.74–907.94), thus were regarded as describing all the interrelationships considerably less well.

Similar results were obtained for smaller data set considering also nitrogen variables (models 14–18, Fig. 5B). The most supported casual network (model 15 with AIC = 76.54; AIC values for the remaining models ranged from 274.54 to 734.04) accounted for direct effects of the seabird presence and seabird species on both the vegetation and invertebrate diversity, as well as indirect seabird impact on invertebrates via vegetation. The model excluded the importance of δ^{15}N and total N of soil and vegetation, as well as soil moisture, for the entire web of relationships.

4. Discussion

Our results show clear, multi-level, ornithogenic impact across the terrestrial ecosystem, with most of the measured parameters of soil, vegetation and invertebrates being altered through proximity

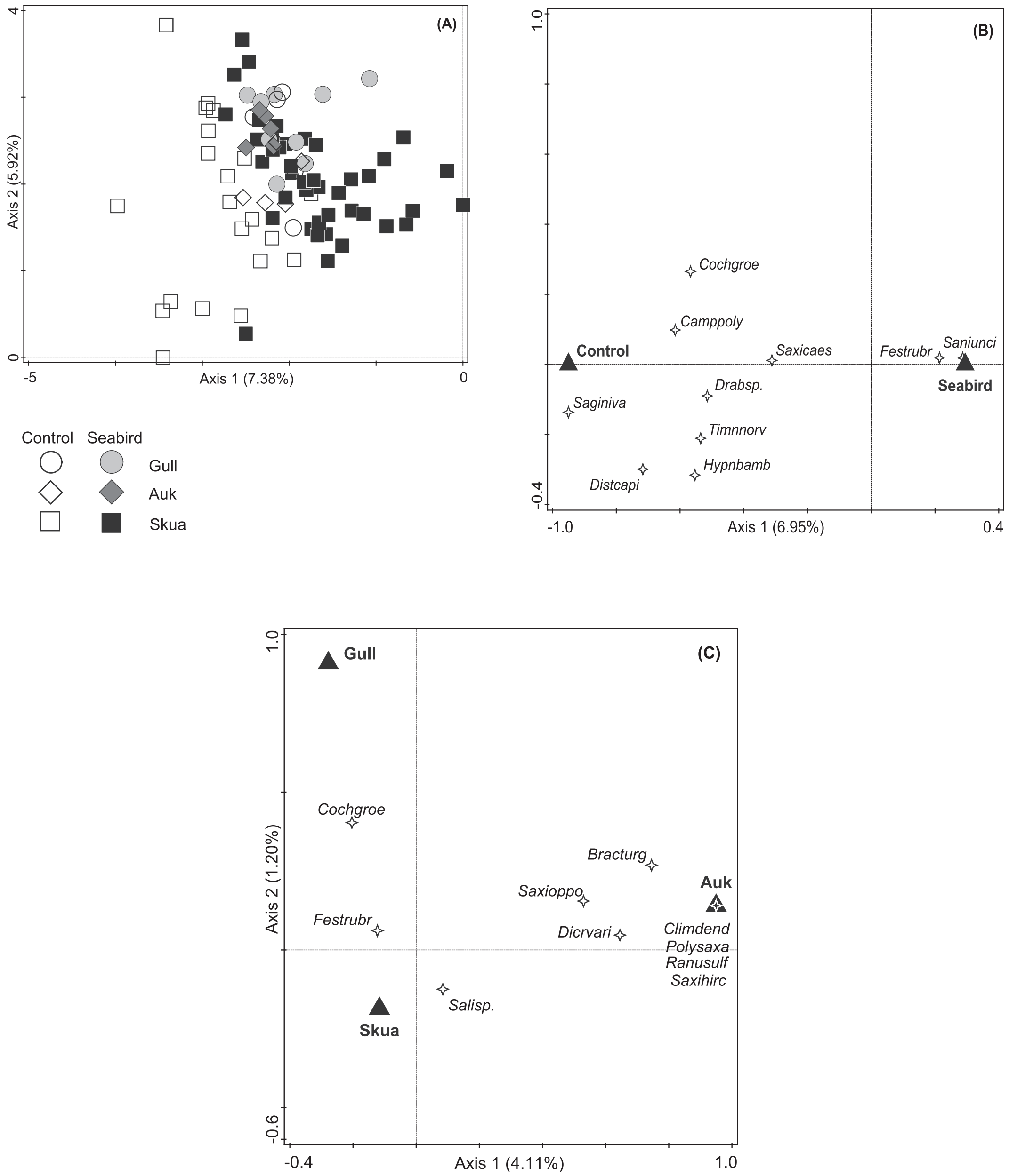


Fig. 3. Detrended correspondence analysis (DCA) ordination of plots classified with respect to invertebrate community composition of different study areas (**A**). Canonical correspondence analysis (CCA) ordination of 10 best-fitted invertebrate species with respect to the *Seabird* (**B**) and *BirdSpe* (**C**) factors in each area. Scaling of scores focused on distances among species. Species labels stand for: Arrhprin – *Arrhopalites principalis*, Camianom – *Camisia anomia*, Desotshe – *Desoria tshernovi*, Eobrbore – *Eobrachychthonius borealis*, Folsquad – *Folsomia quadrioculata*, Hermreti – *Hermannia reticulata*, Hypoviat – *Hypogastrura viatica*, Kunsarct – *Kunstidamaeus arcticus*, Lioclapp – *Liochthonius lapponicus*, Oligursi – *Oligaphorura ursi*, Protmacf – *Protaphorura macfadyeni*, Sminconc – *Sminthurinus concolor*, Tectvela – *Tectocepheus velatus velatus*, Tetrarct – *Tetracanthella arctica*, Thaldupl – *Thalassaphorura duplopunctata*, Tricseti – *Trichoribates setiger*, Willscan – *Willemia scandinavica*, Zerczela – *Zercon zelawaiensis*.

to seabird nests, though to a varying degree in each case. The ornithogenic effect dissipated with progression through the ecological hierarchy of trophic levels, in line with our expectation that it should weaken with the increasing complexity of interactions between the ecosystem components, and also due to the inherent partial loss of energy at each trophic level. The clearest responses were observed for soil and vegetation properties, whereas the reactions demonstrated by invertebrate communities were less explicit. Among the invertebrates, the decomposer community was affected by seabirds to the same degree as when all the taxa were taken into account, while the predators alone showed no significant response to the vicinity of seabird nesting sites. To our knowledge, this is the first broad view of the relationships functioning within such ornithogenically-subsidized polar terrestrial ecosystems.

The considerable ornithogenic nutrient enrichment is evidenced by significantly elevated δ^{15}N in soil and vegetation close to both the larger bird colonies and the solitary nests examined (e.g. Anderson and Polis, 1999; Kolb et al., 2010; Wait et al., 2005; Zwolicki et al., 2016b). However, the possibility of additional influx of marine-derived substances through sea spray and precipitation should also not be overlooked (Bokhorst et al., 2007). Consistent with such an input source, the nitrogen isotopic signal in soil and vegetation near to glaucous gull nests was higher in

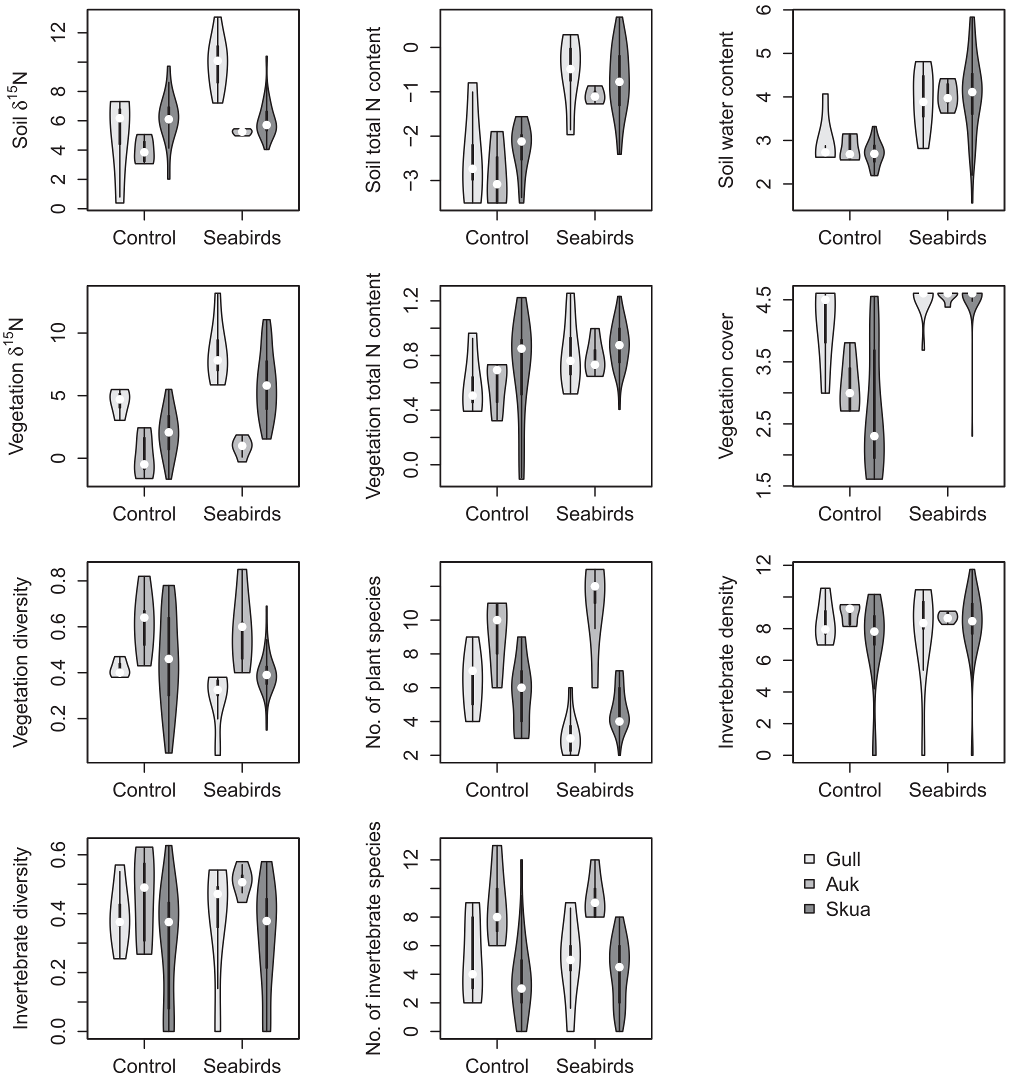


Fig. 4. Distribution of soil, and vegetation and invertebrate community parameters across different SEABIRD and CONTROL areas. White dots represent medians, thick black lines – interquartile ranges, and whiskers – maximum and minimum values, excluding outliers. The density of data is depicted by a symmetrical vertical Kernel density estimator. Soil total nitrogen and water contents, vegetation cover and diversity, and invertebrate density and diversity values were log-transformed.

comparison with areas occupied by great skuas (of similar diet, and therefore expectation of similar δ^{15}N in the guano, but nesting farther from the coast). A similar difference was observed in plants isotopic signals at the GULL and SKUA CONTROL sites.

4.1. Seabird influence on soil

The prime effect of the presence of seabirds was a considerable increase of soil fertility, as measured by nitrogen content, and soil moisture. It is well known that seabirds enrich the ground in fertilizing elements, such as phosphorus, potassium, magnesium, and many others (Wait et al., 2005; Zwolicki et al., 2013). It is apparent that in such barren polar areas as Bjørnøya, lacking human settlements and aggregations of other large vertebrates, seabirds are the most significant vectors and suppliers of nutrients originating in the sea (Bokhorst et al., 2007; Skrzypek et al., 2015; Zwolicki et al., 2016b). The higher soil water content was an indirect consequence of seabird presence through vegetation development (e.g. by forming dense carpets preventing loss of water) and an increase of soil organic matter amount (Wait et al., 2005; Zwolicki et al., 2016a).

Surprisingly, the most optimal SEM model of the causal network functioning in the studied ecosystem, indicating the seabird impact on plant and invertebrate diversity, disregarded the birds' effect on both soil nitrogen and water contents. Those variables were also not important for the other elements of the best model, even though vegetation did react to the seabird presence both with total N, abundance, species diversity, and community composition analysed individually in linear mixed models and CCA. The explanation may be that seabirds indirectly affected the vegetation parameters not just through increasing the soil nitrogen and water contents but due to more complex chemical and physical changes in the soil, such as changes in concentrations of other ions, pH, salinity, organic matter content or respiration rate, and only the multivariate combination of all these variables could be fully indicative of the seabirds' impact on the local environment (Wait et al., 2005; Zwolicki et al., 2013, 2016a, b). The excreted nitrogen compounds are also highly unstable, and a large proportion volatilizes in the form of ammonia, the process being intensified in wet and windy environments (Lindeboom, 1984; Staunton Smith and

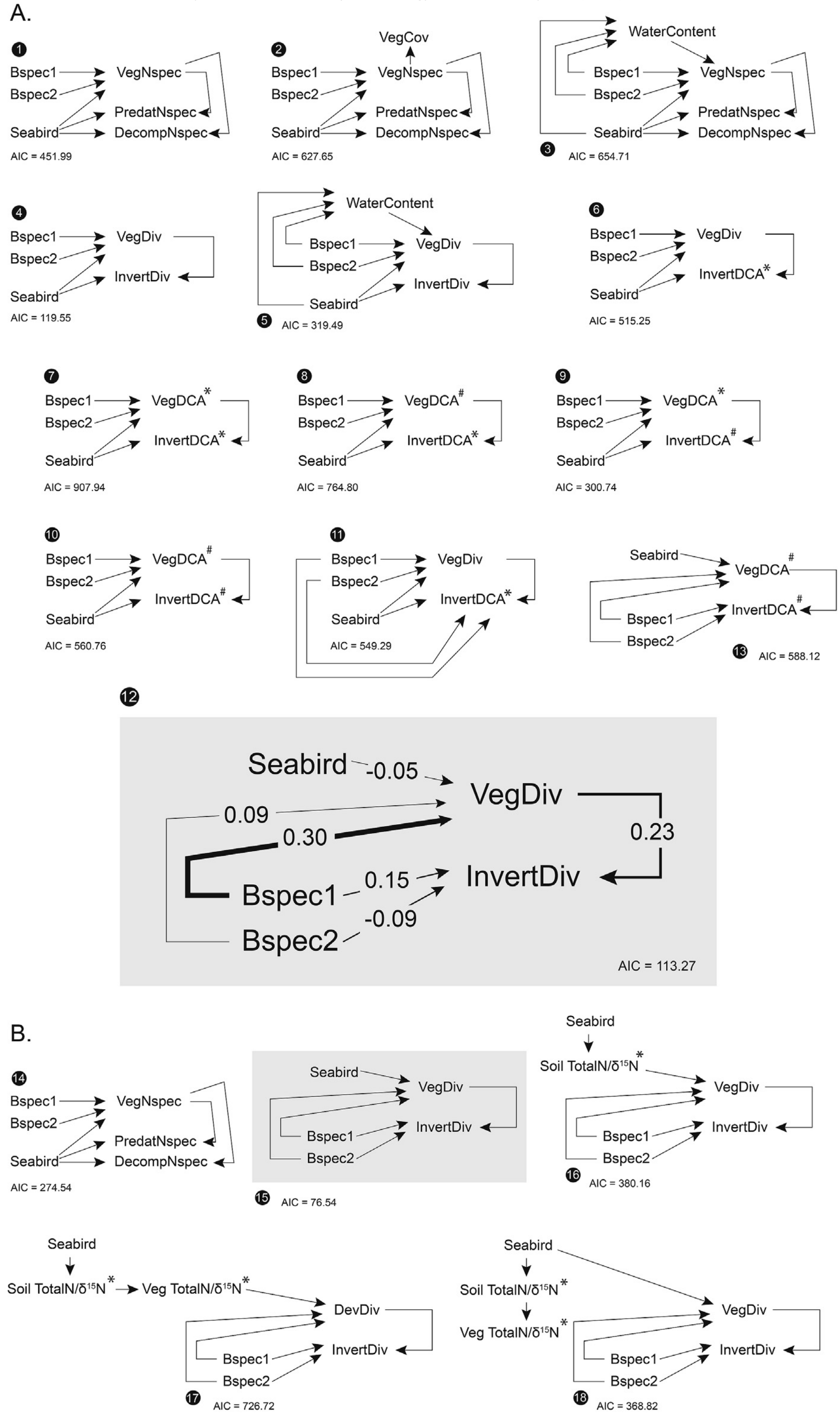
Table 1
Results of linear mixed models fitted to all individual response variables (only significant results shown, $P < 0.05$). See full results in Suppl. Table 3.

Environmental variable		Intercept	*Seabird*SEABIRD	*BirdSpe*AUK	*BirdSpe*SKUA	*BirdSpe*AUK:*Seabird*SEABIRD	*BirdSpe*SKUA:*Seabird*SEABIRD
Soil δ^{15}N	Estimate	4.979	4.957			−3.691	−5.147
	P	<0.001	<0.001			0.014	<0.001
Soil total N content (log)	Estimate	−2.251	1.614				
	P	<0.001	<0.001				
Soil water content (log)	Estimate	2.737	1.299				
	P	<0.001	<0.001				
Vegetation δ^{15}N	Estimate	4.931	3.646	−6.200	−2.735		
	P	<0.001	<0.001	<0.001	0.004		
Vegetation total N content	Estimate	0.621	0.180				
	P	<0.001	<0.001				
Vegetation cover (log)	Estimate	4.092		−0.968	−1.388	1.030	1.422
	P	<0.001		0.012	<0.001	0.038	<0.001
Vegetation diversity (log)	Estimate	0.371	−0.063	0.261			
	P	<0.001	0.030	<0.001			
Vegetation number of species	Estimate	1.856	−0.693	−0.736		0.854	0.542
	P	<0.001	0.006	0.001		0.008	0.046
Invertebrate density (log)	Estimate	7.537					
	P	<0.001					
Invertebrate diversity (log)	Estimate	0.364					
	P	<0.001					
Invertebrate number of species	Estimate	1.526		0.602			
	P	<0.001		0.005			
Decomposer density (log)	Estimate	7.525					
	P	<0.000					
Decomposer diversity (log)	Estimate	0.496		−0.203			
	P	<0.001		0.050			
Decomposer number of species	Estimate	1.466					
	P	<0.001					
Predator density (log)	Estimate			3.086			
	P			0.011			
Predator diversity (log)	Estimate	0.198					
	P	0.022					
Predator number of species	Estimate	−1.596					
	P	0.013					

Johnson, 1995), such as typify Bjørnøya. Furthermore, some species, including the locally abundant moss *S. uncinata* acquire nitrogen directly from the air and/or tundra surface, disregarding the soil N-pool (Skrzypek et al., 2015). Soil water content also showed relatively high variability between the SEABIRD plots, especially those around the skua nests, which were numerically dominant in our study compared to the remaining two seabird species. The part of the island where their nests are concentrated includes both dry and wet areas due to the presence of numerous small lakes and brooks crossing the area. It is hard to determine whether skuas show any preference in nest site choice with respect to soil moisture, but this is also an inherent habitat property partly independent of any seabird fertilization.

4.2. Seabird influence on vegetation

Vegetation reflected further well-defined consequences of the ornithogenic fertilization of soil. Plants abundance (cover) and their potential quality for consumers (as measured by N content; Anderson and Polis, 1999; Mosbacher et al., 2016; Wilson and Jefferies, 1996) significantly increased, while community composition was shifted towards lower local species number and lower diversity nearby the seabird nests. This is consistent with observations from many other localities around the world, other than locations with excessive guano deposition causing over-fertilization and devastation of the flora (Mulder et al., 2011; references therein; Klimaszyk and Rzymski, 2016; Zwolicki et al., 2015). A small number of species markedly predominated in sites subject to ornithogenic inputs while being very rare or even absent from the CONTROL areas. These included the graminoid *F.* cf. *rubra* ssp. *richardsonii* forming dense carpets around great skua and glaucous gull nests, and also recorded close to the little auk colony, underlain with a compact layer of the moss *S. uncinata* which occurred abundantly in all the SEABIRD sites. Both species are widespread across the entire Svalbard archipelago, including Bjørnøya, commonly occurring in a wide range of habitats, on different substrates and together with many other plant species (Ueno et al., 2001; The flora of Svalbard, 2016). Therefore, it is reasonable to assume that their extreme rarity within the CONTROL areas here resulted from the poorness of these local habitats receiving no ornithogenic subsidies. On the other hand, species recognized as typical for the bird-cliff vegetation, such as *Cochlearia groenlandica*, *Cerastium arcticum*, and *Oxyria digyna*, and predominating around seabird colonies in other regions of Svalbard (Eurola and Hakala, 1977; Elvebakk, 1994; Odasz, 1994; Zmudczyńska-Skarbek et al., 2015a, b; Zwolicki et al., 2016a, b), occurred only sporadically in our study areas, and even then rarely (and only in the case of *O. digyna*) exceeding a 5% contribution to the total vegetation cover. Most probably, those species require exceptionally (in the context of the polar regions) nutrient-rich substrate formed in the immediate vicinities of large seabird colonies and in places where guano accumulates, while neither solitary nesting great skuas and glaucous gulls, nor the inland medium-sized colony of little auks could provide them with such conditions in Bjørnøya. Locally, the only large and abundant individuals of these plant species were seen growing directly on the ledges of sea-descending cliffs inhabited by seabirds (Summerhayes and Elton, 1923; authors' pers. obs), suggesting there may be further important influences controlling their different distributions on the High Arctic mainland of Svalbard and the more isolated and oceanic-setting Bjørnøya.



Regression coefficients are not shown for the best model in the B set – this model is identical to the best model in the A set, but is based on a smaller data set (see text for details). Results of these two models are qualitatively identical.

Bspec1 – binary variable for seabird species: Auk (1) vs. Gull (0); **Bspec2** – binary variable for seabird species: Skua (1) vs. Gull (0);
Seabird: presence/absence of seabirds; **Soil TotalN/δ_{15}N**: soil nitrogen content/isotopic ratio; **WaterContent**: soil water content; **Veg TotalN/δ_{15}N**: vegetation nitrogen content/isotopic ratio; **VegCov**: total vegetation cover; **VegDiv**: vegetation diversity; **VegNspec**: vegetation no. of species; **VegDCA**: DCA axes values for vegetation; **PredatNspec**: no. of predators species of predators; **DecomNspec**: no. of species of decomposers ; **InvertDens**: invertebrates density; **InvertDiv**: invertebrates diversity; **InvertDCA**: DCA axes values for invertebrates (see text).

* In all cases **InvertDCA** and **Veg/Soil TotalN/δ15N** are represented by single boxes, but in all models they were included as two independent variables (values of the 2 separate DCA axes for invertebrates; the total N and δ15N measurements).
# Only the first DCA axis values included.

Fig. 5. Overview of the fitted structural equation models (SEM) together with their Akaike Information Criterion (AIC) values for the effects of seabird presence and species on soil, vegetation and invertebrate community parameters. Arrows indicate causal relationships defined as regression models (response variables at the arrowheads). (**A**) Models based on the full dataset (δ^{15}N and total N content in soil and plants excluded). (**B**) Models based on the reduced dataset (the nitrogen variables included). Numbers on arrows indicate regression coefficients from SEM regressions of the best model. The optimal models (the lowest AIC) for each dataset are indicated in grey.

4.3. Seabird influence on invertebrates

Among the plausible effects of the seabird-induced higher vegetation abundance and quality, and its modified species composition, are increased densities and/or changes in the community structure of herbivores, and subsequently of the higher-level consumers (Byzova et al., 1995; Croll et al., 2005; Jakubas et al., 2008; Sánchez-Piñero and Polis, 2000; Zmudczyńska et al., 2012; Zawierucha et al., 2016; Zmudczyńska-Skarbek et al., 2015b). However, we found no significant changes in the studied invertebrate community density, diversity, and species number near the seabird nesting sites as compared with the control areas. This might result from highly complex and inconsistent reactions of particular invertebrate groups (e.g. of similar feeding strategies) within the studied assemblages. Similarly, Kolb et al. (2012) observed greatly varying reactions among different arthropod groups subject to strong cormorant manuring on Swedish islands, including generally negative response of herbivorous coleopterans, positive responses of the coleopteran fungivores and scavengers, and no responses of heteropterans, cursorial spiders, and chironomids. Also Basset et al. (2014) underlined taxa-specific responses of invertebrates to seabird impact, based on data from the New Zealand sub-Antarctic Adams Island.

Density, diversity and number of species were comparable in the SEABIRD and CONTROL sites when the assumed decomposer and predator groups were analysed separately. In the case of decomposers, i.e. collembolans and oribatid mites (34 species and almost 3500 individuals), clearly the diversity includes representatives of different feeding strategies and preferences (herbivores, fungivores, bacteriovores, and general detritivores). It is also possible that the food resources preferred by each of these subgroups may change in different ways in response to seabird fertilization. For instance, soil microbial biomass increased while the fungal biomass decreased in the vicinity of a seabird colony studied by Wright et al. (2010). Zawierucha et al. (2016) found higher abundance of tardigrades within and around a little auk colony as compared with a more distant area, and related the observation to the locally-facilitated development of mosses, preferred by tardigrades, over lichens near the colony. Further, many species considered to be decomposers in these ecosystems actually have multi-trophic feeding specializations, while the precise knowledge of their diets and autecology is lacking (Hogg et al., 2006; Hodkinson, 2013). Nonetheless, earlier studies on springtail communities in Hornsund, south-west Spitsbergen did show a marked response to seabird impact as measured by considerable density increase and community diversity decrease near seabird colonies (Byzova et al., 1995; Uvarov and Byzova, 1995; Zmudczyńska et al., 2012). This was most likely associated with the exceptionally large sizes of the seabird colonies studied in Hornsund, one of little auks, and another of Brunnich's guillemots and kittiwakes, and thus intensive manuring having profound effects on the adjacent tundra (Zwolicki et al., 2013, 2016a, b). In contrast with the decomposer group, the predators are rather uniform in feeding mode (though some mesostigmatid mite species may be fungivorous in some conditions; Gwiazdowicz, 2007), including only 8 mesostigmatid mite and 1 spider species (55 individuals in total), and hence might be insufficiently numerous to allow detection of any seabird impact.

Another possible explanation of similar invertebrate densities across the SEABIRD and CONTROL areas may be the replacement of some species, including those resistant to the poorest habitat conditions recognized in the CONTROL areas, with others which grow in numbers under the conditions of ornithogenic nutrient enrichment. CCA ordination indicated that invertebrate species composition significantly differed between these two areas, being apparently more variable more distant from the seabird nesting sites. As with the trend observed for vegetation, few invertebrate species predominated around seabird nests, while other species occurred more evenly in density in the CONTROL areas. The three species best-fitted to the gradient represented by the *Seabird* factor, and most abundant in the SEABIRD areas, the two collembolans, *F. quadrioculata* and *O. ursi* (the latter present only in the SKUA area), and the oribatid mite *H. reticulata*, all regarded as herbivores and primary decomposers (i.e. feeding on litter/detritus with adhering fungi and bacteria; Chahartaghi et al., 2005; Seniczak et al., 2016), are quite common across different habitats within the Arctic, with no clear habitat preferences (Fjellberg, 1998, 2007; Seniczak et al., 2016). Therefore, and again similar to the vegetation pattern described above, they are generally regarded as indicating exceptionally inhospitable living conditions prevailing in locations not under direct seabird impact. Previous studies from the Arctic and Antarctic have underlined large- and small-scale differences in springtail community compositions, resulting from geographical location (with specific climates, and historical dispersal and colonization processes), microtopography, and natural tendency to patchy distribution (Caruso and Bargagli, 2007; Babenko, 2009; Usher and Booth, 1984, 1986; Zmudczyńska-Skarbek et al., 2015b, and references therein). For instance, *F. quadrioculata* has been often recorded in extremely high abundance below bird cliffs (Fjellberg, 1997; Sømme and Birkemoe, 1999; Zmudczyńska et al., 2012; Zmudczyńska-Skarbek et al., 2015b) but has also been recognized as having negative correlation with seabird (little auk) influence in north-west Spitsbergen (Zmudczyńska-Skarbek et al., 2015b).

Beside roughly similar patterns in community composition variability observed for plants and invertebrates, as revealed with CCA (though a lower proportion of the variability was explained by the *Seabird* factor in the case of invertebrates), the indirect effect seabirds exerted on the soil fauna through vegetation was demonstrated by the most optimal SEM model. Here, the total invertebrate diversity was positively linked to vegetation diversity, being also slightly negatively influenced by the *Seabird* factor. Such connection between seabirds and invertebrates through vegetation is not surprising, since many physical and trophic habitat properties, including local temperature, moisture, organic matter content, as well as the composition and abundance of algae, fungi, and many other microorganisms constituting food sources for invertebrates alter in association with vegetation change, and this is true both at the scale of the plant community and even of single species cushions or tufts (Coulson et al., 2003; Eskelinen et al., 2009).

4.4. The effect of a seabird species

One of the unique features of Bjørnøya for studying seabird impact on the terrestrial ecosystem is the location of several colonies of different seabird species in one relatively small area, allowing rejection of geographical factor impact which, at a larger scale, may have great influence on tundra community composition (Bokhorst et al., 2008; Ávila-Jiménez and Coulson, 2011; Ávila-Jiménez et al., 2011; Zmudczyńska-Skarbek et al., 2015b; Zwolicki et al., 2016b). Nonetheless, the local colonies differ in the detailed topography of their nesting area, distance from the coast, nest density, diet, and thus probably the quantity and quality of the faeces produced and deposited on land. A small number of earlier studies, as well as our own observations from several regions of Svalbard, suggest that variability in such characteristics between different seabird species contributes to the observed variance in soil physical and chemical parameters, cyanobacterial, algal, lichen, moss and vascular plant abundance and community composition, and tundra use by large herbivores (Bédard et al., 1980; Jakubas et al., 2008; Pietryka et al., 2016; Zwolicki et al., 2013, 2016a). For instance, Zwolicki et al. (2013, 2016a) underlined the role of higher phosphate content in piscivorous bird species diet and guano, as well as the colony topography (relatively short talus slope beneath the cliff), as compared with planktivorous species nesting within more spacious, mild-slope rock debris, in modifying soil and vegetation in the Hornsund area.

The results obtained in our study confirm that different seabird species may act differently on the surrounding environment, though the species usually appeared to be a weaker factor than the presence of a seabird colony or nest itself. Furthermore, it is often hard to separate single features of the species responsible for the observed changes due to high complexity and multidimensionality of their influence, as discussed above. Another difficulty is isolating the specific effects the seabirds themselves exert on the vicinities of their nesting sites, for instance through their diet and excrement composition, from the inherent properties of the site where a particular nest or a colony is situated, such as topography or distance from the coast (e.g. see the differences in total vegetation cover between the three CONTROL areas; Fig. 4). Hence, higher nitrogen isotopic ratios of soil and vegetation sampled in the GULL and SKUA areas as compared with the AUK area likely resulted from differences in the trophic level classification of their prey, i.e. higher δ^{15}N of birds and fish consumed by the gulls and skuas as compared to zooplankton being the primary food source for little auks (Bakken and Tertitski, 2000; Knutsen, 2010; Stempniewicz, 1981). However, at the same time, marine aerosols reaching the land appeared to contribute substantially to nitrogen enrichment of the coastal zone, as similar tendencies in δ^{15}N variability between the three species were observed not only for the SEABIRD but also for the CONTROL areas (see also Bokhorst et al., 2007; Hargan et al., 2017). Furthermore, the highest nitrogen isotopic signal characterised the GULL area located closest to the seashore, at the edge of a relatively low cliff (and other seabirds, such as fulmars and Atlantic puffins nested beneath), while locally the glaucous gull diet is very similar to that of the great skua (Bakken and Tertitski, 2000; Knutsen, 2010).

Significant effects of seabird species was also found in vegetation and invertebrate diversity, number of species, and community composition. In many cases those differences were mostly driven by the AUK area's distinctness (see Fig. 4, Table 1). A similar but weaker trend was also observed between the CONTROL sites. Thus we could not exclude the importance of factors other than the seabird presence underlying this variability, such as varying topography (Caruso and Bargagli, 2007; Hodkinson, 2013; Ims and Ehrich, 2013). Consistent with this, the most distinct AUK area was the only one located on a slope, while both the remaining areas examined were flat.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.soilbio.2017.09.008.

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