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ORIGINAL ARTICLE

Above-Cliff Tundra Reveals Hidden Seabird Footprint: Evidence from Bjørnøya (Svalbard)

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Abstract

Bjørnøya (Bear Island) hosts one of the largest seabird colonies in the Barents Sea, with high breeding densities on steep cliffs. While most guano-derived nutrients return to the ocean, a fraction is transported inland by wind, fertilizing tundra above the colonies. We investigated how these seabird nutrient subsidies influence tundra by analysing soil properties, $\delta^{15}N$ in soil and plant tissues, vegetation composition, and plant cover along six transects spanning SEABIRD (above-colony) and REFERENCE tundra. PERMANOVA confirmed strong effects of seabird presence on soil chemistry, vegetation composition, and $\delta^{15}N$. SEABIRD soils were more acidic and had elevated NH_4^+, NO_3^-, PO_4^{3-}, K^+, total nitrogen (TN), phosphorus (P), organic carbon (TOC), Na, and moisture. Soil $\delta^{15}N$ was markedly elevated in SEABIRD plots and closely tracked vegetation change. LINKTREE identified a NO_3^- threshold of 354 mg kg^{-1}, showing that higher NO_3^- in SEABIRD plots sharply separated them from REFERENCE plots and defined the main differences in plant composition between the two groups. A distance-based linear model identified TN, P, and Na as strongest predictors of vegetation composition. SEABIRD plots had significantly higher median plant cover (87.5%) than REFERENCE plots (15%), characterized by vegetation dominated by mosses, lichens, and nutrient-responsive vascular species. A structural equation model revealed an indirect nutrient cascade: seabird-derived nitrogen, indicated by $\delta^{15}N$, increased soil fertility (TN and P), which in turn enhanced vegetation composition and cover. These findings show that seabird nutrients shape inland tundra above the colonies, revealing a redistribution mechanism with limited attention in Arctic research.

Key words: seabirds; nutrient cycling; vegetation dynamics; Arctic ecosystems; Bear Island; ecosystem engineering; ornithogenic tundra.

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HIGHLIGHTS

- Above-cliff tundra reflects seabird nutrient input beyond direct guano deposition
- Non-classical ornithogenic tundra supports cryptogam-rich
- complex plant communities
- Nutrient cascade links seabird nitrogen to increased soil fertility and plant cover

INTRODUCTION

During the Oxford University Expedition to Spitsbergen in 1921, Charles Elton and Victor Summerhayes described nitrogen cycling on Bjørnøya as a key ecological process linking marine and terrestrial systems. Although Summerhayes and Elton (1923) did not use the term 'subsidy', their conceptualisation of seabirds as conduits of marine-derived nutrients to land provides an early example of what was later defined as a 'subsidized ecosystem' (Summerhayes and Elton 1923; Polis and Strong 1996). This represents a typical example of an autotrophic ecosystem that is constantly (or periodically on an annual scale) enriched with the matter produced in another ecosystem (Odum and Barrett 1971). Subsidies between different ecosystems are now recognized as a major process shaping ecosystem structure and functioning and energy flux across landscape and seascape (Ostfeld and Keesing 2000; Yang and others 2008; Lepoint and Hyndes 2022).

Seabirds act as critical vectors of nutrient transfer between marine and terrestrial ecosystems, particularly in high-latitude environments. Through the deposition of guano, feathers, eggshells, and carcasses, seabirds introduce substantial quantities of marine-derived nitrogen, phosphorus, and organic matter into otherwise nutrient-poor polar soils (Croll and others 2005; Mulder and others 2011; Zwolicki and others 2013). These marine subsidies strongly influence polar terrestrial ecosystems by enhancing primary productivity, modifying vegetation composition, stimulating microbial activity, and altering nutrient cycling (Blais and others 2005; Ellis and others 2006). Consequently, seabird colonies create localized biodiversity hotspots and drive key ecological processes across Arctic landscapes.

Several biological traits make seabirds exceptionally effective vectors of marine-derived matter to land. Seabirds are bi-environmental organisms, foraging at sea while breeding on land (Mulder and others 2011). Their breeding aggregations are often enormous, reaching hundreds of thousands or even millions of individuals (Kharitonov and Siegel-Causey 1988; Ainley and others 1995; Furness 2012). Furthermore, seabirds are long-lived species with strong site fidelity, ensuring a stable and recurrent nutrient transfer over long timescales (Tatur and others 1997; Furness 2012; Keslinka and others 2019). These characteristics underpin the profound and consistent fertilization of barren, nutrient-poor polar ecosystems, fostering the development of characteristic nitrophilous plant communities (Croll and others 2005; Ellis and others 2006; Stempniewicz and others 2007; Mulder and others 2011; Zwolicki and others 2013; Zmudczyńska-Skarbek and others 2017). Even a single nest, such as those of skuas, can alter surrounding vegetation and invertebrate communities, demonstrating that ornithogenic influence extends to very small spatial scales (Zmudczyńska-Skarbek and others 2017). Bjørnøya provides an exceptional example of such a seabird-driven ecosystem in the High Arctic, as first recognized by Summerhayes and Elton (1923).

Bjørnøya (Bear Island), the most isolated island of the Svalbard archipelago, is located at the junction of the Barents and Norwegian Seas. Its remote location, relatively small size, harsh Arctic climate, low current anthropogenic pressure, and the presence of a huge seabird population make it a valuable site for ecological studies, particularly on the functioning of subsidized natural ecosystems, including the dynamic interplay between seabirds and terrestrial vegetation (Mulder and others 2011; Vitousek 2002; Summerhayes and Elton 1923).

The ecological uniqueness of Bjørnøya is closely tied to the tremendous productivity of the Polar Front (Mehlum and others 1998; Węsławski and others 1999), which underpins the development of one of the largest and most ecologically influential seabird colonies in the Arctic region (Norderhaug and others 1977). Among the most abundant breeding seabird species are Brünnich's guillemots (*U. lomvia*, ca. 100,000 pairs common guillemot (*U. aalge*, ca. 72,000 pairs), black-legged kittiwake (*Rissa tridactyla*, ca. 10,000 pairs), and glaucous gull (*Larus hyperboreus*, ca. 2000 pairs) (Fauchald and others 2015). Their largest concentrations are located on towering coastal cliffs, 200–400 m high, extending continuously for approximately 9 kms along the southern tip of the island. These colonies not only constitute a major Arctic seabird aggregation but also play a pivotal role in shaping the surrounding terrestrial ecosystems.

Because the cliffs on Bjørnøya descend steeply and directly into the sea, the majority of guano-derived nutrients are lost to the marine environment, with only small amounts accumulating on inaccessible cliff ledges where few plant species can survive (Sømme and Birkemoe 1999; Zmudczyńska-Skarbek and others 2015; Zmudczyńska-Skarbek and Balazy 2017). In typical Arctic settings, lush ornithogenic tundra often develops at the foot of seabird cliffs, where nutrient runoff can accumulate on coastal terraces. This pattern is well-documented across Spitsbergen (Eurola and Hakala 1977). However, on Bjørnøya, where the cliff bases are submerged, there is no opportunity for nutrient accumulation at the shore. Instead, ornithogenic tundra develops primarily above the cliffs—a distinct and rare pattern in the Arctic, that offers unique opportunities to study nutrient-driven terrestrial ecosystem processes. This above-cliff enrichment likely results from wind-driven transport of guano particles and aerosols inland, facilitated by the presence of plateau tundra immediately above the nesting colonies (Schmale and others 2013). In contrast, on West Spitsbergen—where most seabird colonies occur—the cliffs are generally much higher and often topped by rocky peaks rather than plateaus, which limit the development of tundra habitats above the colonies. Consequently, ornithogenic tundra typically develops below, rather than above, seabird cliffs in these areas. While wind-driven dispersal of guano particles and aerosols appears limited to a few locations with appropriate topography in the Arctic, this mechanism has been shown to operate at much broader scales in the Antarctic. There, aerosolized nutrients from dense penguin colonies and seal aggregations have been recognized as major drivers of terrestrial diversity at distances exceeding several hundred metres from the colony (Bokhorst and others 2019a). For this reason, the interaction between soil enrichment by seabird-derived nutrients and the development of plant communities above the colonies on Bjornoya constitutes a particularly valuable system for studying nutrient-driven processes shaping Arctic tundra ecosystems (Elvebakk 1985, 1989). Although ornithogenic effects on lush, below-cliff communities have been well documented, comparable studies of plateau tundra above Svalbard bird cliffs are lacking. Targeted research in these habitats could clarify how nutrient enrichment and abiotic stress interact to determine the broader spatial reach of seabird influence in Arctic tundra ecosystems.

'The bird cliffs show a large variation in plant communities, but only a small part of the variation has been described yet,' wrote Arve Elvebakk (Elvebakk 1994), a statement that remains relevant today. Although the impact of seabirds on Arctic vegetation has been documented, most studies have focused on areas below the cliffs (Elvebakk 1994; Eurola and Hakala 1977; Zmudczyńska and others 2009; Zwolicki and others 2016b, 2023), with little attention paid to the tundra vegetation developing above the colonies. Furthermore, the terrestrial ecology of Bjørnøya, including its unique plateau vegetation, has received limited research attention compared to other Svalbard islands (Engelskjøn 1987; Zmudczyńska-Skarbek and others 2017).

In this study, we aim to unravel how seabird-derived nutrient subsidies, most likely mediated by wind-driven transport, influence soil chemistry and plant community composition above bird cliffs on Bjørnøya. We hypothesise that the nesting activity of colonial seabirds, combined with prevailing wind patterns, plays a pivotal role in shaping above-cliff terrestrial ecosystems by facilitating nutrient delivery inland. Wind action could mobilize both particulate guano material and volatilized compounds, such as ammonium, which is known to easily volatilize under Arctic conditions (Wainright and others 1998). These transported nutrients are expected to enrich soils and influence the structure of tundra plant communities. We predict that seabird guano inputs enhance soil nutrient availability and drive distinct plant composition patterns, and that spatial variation in these effects reflects the strength and direction of nutrient dispersal. Furthermore, we use stable nitrogen isotopes (δ^{15}N) in soils and plant tissues as tracers of marine-derived nutrients, providing insights into the pathways and extent of seabird influence on terrestrial ecosystems (Wainright and others 1998; Evenset and others 2004). By combining soil chemistry, vegetation composition, and isotopic signatures, this study contributes to a broader understanding of how seabird-driven processes structure Arctic terrestrial ecosystems beyond the immediate footprint of seabird colonies.

METHODS

Study Area

Bjørnøya is the southernmost island of the Svalbard archipelago, located 397 km north of mainland Norway and 225 km south of the southern tip of Spitsbergen, at the boundary between the Norwegian and Barents Seas (Figure 1). Bjørnøya has a triangular shape, being about 20 km long and

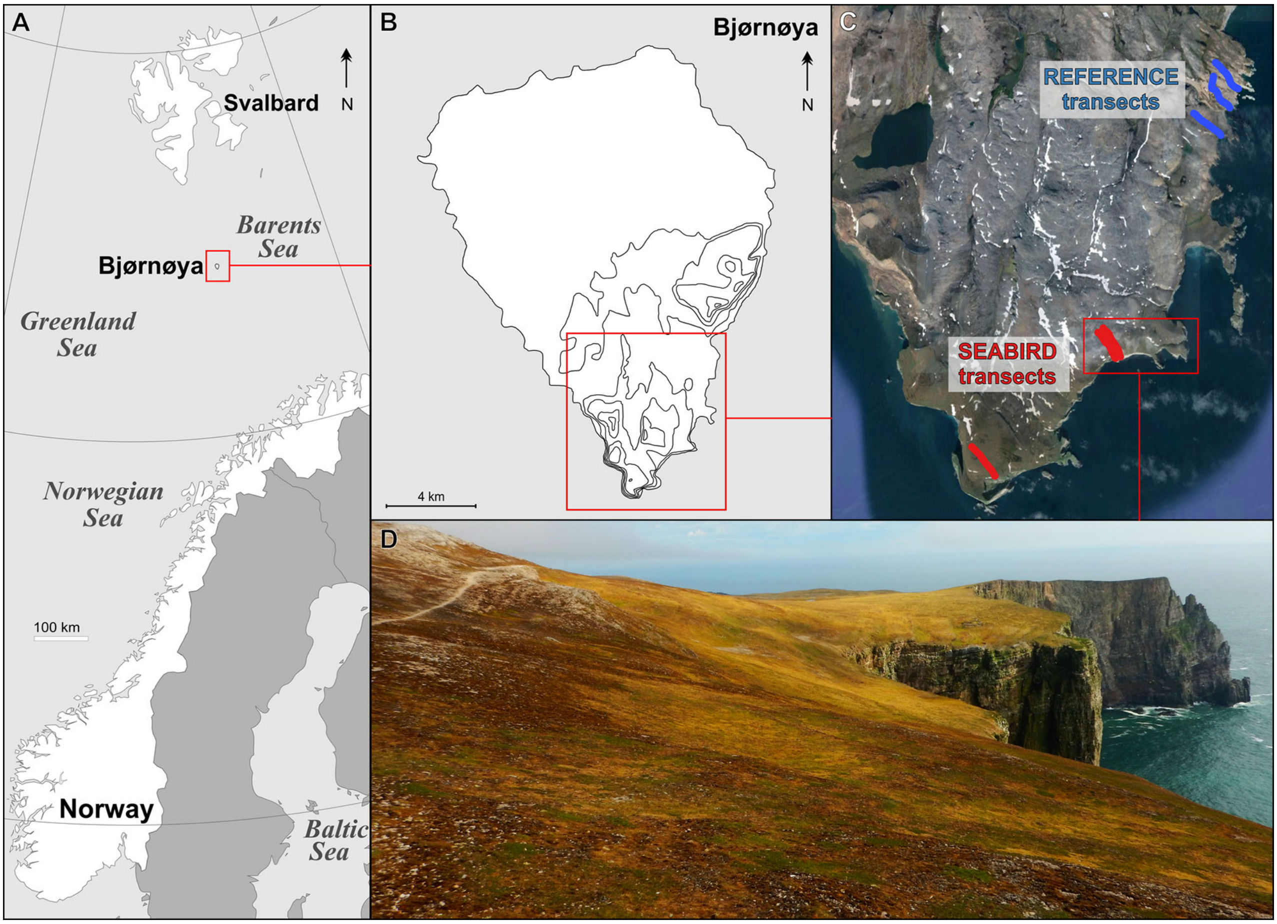

Figure 1. Location of SEABIRD and REFERENCE transects on Bjørnøya (Bear Island), Svalbard. **A** Regional map showing the position of Bjørnøya between mainland Norway and Svalbard in the Barents Sea. **B** Outline map of Bjørnøya with contour lines indicating elevation. **C** Satellite image of the south-eastern part of Bjørnøya showing locations of SEABIRD (red) and REFERENCE (blue) transects (© Google, Maxar Technologies). **D** Representative view of above-cliff tundra in the study area (Photo by Adrian Zwolicki). Red boxes in each panel indicate the area shown in the next panel.

15 km wide, and covers the area of 178 km^2. The southern part of the island is mountainous, with many plateaus, the highest being Miseryfjellet (536 m asl), while the remaining two-thirds of the area is flat and strewn with shallow lakes. The island's coastline is characterized by steep cliffs, the highest in the south, caverns, and isolated rock pillars. The geology of Bjørnøya is heterogeneous, dominated by clastic rocks (sandstone, mudstone, shale, conglomerate) and carbonate rocks (dolomite, limestone), particularly in the southern region where the study was conducted (Mørk and others 2014; Dallmann and Krasilscikov 1996).

Bjørnøya experiences a pronounced maritime Arctic climate. The mean annual air temperature is −1.39 °C and total annual precipitation averages 396 mm (Owczarek and others 2020). The island is subject to persistent strong winds, with wind speeds reaching Beaufort scale 6 or higher on approximately 178 days per year (Nuttall 2005). Mean wind speeds range between 6 and 8 m s^{-1}, predominantly blowing from the northwest and northeast; as shown in the wind rose (Supplementary Figure S1) and frequency table (Supplementary Table S2) (The Norwegian Meteorological Institute 2024). These wind patterns are crucial for the dispersal of seabird-derived nutrients across the island's plateau.

BirdLife International has designated Bear Island as an Important Bird Area due to its exceptionally large seabird colonies. The island supports breeding populations of Brünnich's guillemots (*Uria lomvia*, ca. 100,000 pairs), common guillemots (*U. aalge*, ca. 72,000 pairs), black-legged kittiwakes (*Rissa tridactyla*, ca. 10,000 pairs), and glaucous gulls (*Larus hyperboreus*, ca. 2000 pairs) (Fauchald and others 2015; BirdLife International 2025). Atlantic puffins (*Fratercula arctica*) are also present, with at least several hundred pairs, although estimates are likely conservative (Fauchald and others 2015). Little auks (*Alle alle*) are known breeders, but their population size remains uncertain due to methodological challenges (BirdLife International 2025). Other breeding species include black guillemots (*Cepphus grylle*), northern fulmars (*Fulmarus glacialis*), purple sandpipers (*Calidris maritima*), red phalaropes (*Phalaropus fulicarius*), Arctic skuas (*Stercorarius parasiticus*), and great skuas (*Stercorarius skua*) (BirdLife International 2025).

Vegetation on Bjørnøya is primarily composed of hygrophilous and chionophilous communities dominated by cryptogams (mosses and lichens), with dwarf willows, grasses, and herbs forming minor components. The most common vascular plant species include *Saxifraga oppositifolia*, *Festuca rubra*, *Saxifraga caespitosa*, *Cochlearia groenlandica*, *Salix polaris*, and *Silene acaulis*, characteristic of the Arctic tundra (Engelskjøn 1987).

Ethical Statement

All soil and plant samples were collected under the permission granted by the Governor of Svalbard (reference no. 22/00325-3, RiS-ID 11887). No protected species were sampled, and all fieldwork was conducted in accordance with the relevant guidelines and regulations.

Sampling

The field study was conducted in July 2022 on the south-eastern coast of Bjørnøya. Data and samples were collected along six 450-m-long transects, each starting close to the cliff edge and extending perpendicularly inland (Figure 1A, B). Three transects were located above seabird colonies (SEABIRD transects; mainly guillemots and kittiwakes), while three REFERENCE transects were established approximately 3 km north, beyond the influence of seabird colonies. This distance was chosen based on the absence of seabird colonies on the cliffs and the presence of barren or extremely poor vegetation, displaying the botanical characteristics of Arctic desert. These features indicate minimal or no influence of seabird nutrient inputs at these sites.

Each transect consisted of ten 1 × 1 m sampling plots, placed at 50-m intervals. Within each plot, we recorded plant species composition at the lowest taxonomic level possible, the percentage ground cover of total vegetation, vascular plants, cryptogams, and lichens, as well as the cover of each vascular plant species individually.

From each sampling plot, we collected approximately 700 cm^3 of soil from the surface to a depth of about 10 cm. Additionally, we collected tissue samples (about 5 g, mostly green leaves) of the most dominant vascular plant species (for example, *S. oppositifolia*, *F. rubra*, *S. caespitosa*, and *C. groenlandica*) for stable isotope analyses. Plant samples were cleaned in the field laboratory on the island to remove soil particles and debris, then dried at 70 °C using a laboratory drier. Dried samples were transported in plastic zip bags to the home laboratory for further analyses. In total, we obtained 60 soil samples and 60 plant tissue samples, corresponding to the 60 vegetation plots.

Physical and Chemical Soil Properties

The collected soil samples were air-dried, crushed, and sieved through a 2-mm mesh to remove coarse particles. Prior to chemical analysis, samples were homogenized using an agate mortar. Soil pH was measured potentiometrically in distilled water at a 1:2.5 w/v ratio (Thomas 1996). Total carbon (TC), total inorganic carbon (TIC), and total nitrogen (TN) contents were determined using a Vario Macro Cube CHN elemental analyser (Elementar Analysensysteme GmbH, Langenselbold, Germany). Each soil sample was analysed in triplicate, and the results were averaged. Total organic carbon (TOC) content was calculated as the difference between TC and TIC.

The chemical composition of soils was analysed using Inductively Coupled Plasma-Optical Emission Spectrometry (ICP–OES). The content of exchangeable K^+ was determined by flame atomic absorption spectrometry (FAAS) after extraction with 1 M ammonium acetate (Sumner and Miller 1996). Phosphate (PO_4^{3-}) content was measured colorimetrically with a Specord 50 UV–Vis spectrophotometer (Analytik Jena) after extraction with 1 M NH_4Cl (Kuo 1996). Ammonium (NH_4^+) and nitrate (NO_3^-) ion contents were also determined colorimetrically with a Specord 50 UV–Vis spectrophotometer after extraction with 2 M KC (Mulvaney 1996). Soil moisture content was determined by the gravimetric method.

Stable Isotope Analyses

To assess the nitrogen stable isotope ratios ($\delta^{15}N$) of both soil and vascular plant samples, all samples were initially ground using a vibrating mill (LMW-S, Testchem) to achieve a grain size of less than 0.03 mm. Prior to this, soil samples were sieved through a 0.25-mm mesh to remove coarse minerals. Due to parallel measurements of carbon stable isotope ratios in other studies, requiring the elimination of inorganic carbon, soil samples were decarbonated by adding 1 M HCl until no visible effervescence (CO_2 release) was observed. The nitrogen isotope ratio was determined using a continuous flow elemental analyser (MicroVario, Elementar, Germany) coupled with an IRMS mass spectrometer (Isoprime100, Isoprime, UK). Results were expressed using conventional $\delta^{15}N$ notation in ‰ (Kelly 2000), according to the equation:

$$\delta X_{\text{sample}} = \left[\frac{(X/x)_{\text{sample}}}{((X/x)_{\text{standard}})} - 1 \right] \times 1000 \qquad (1)$$

where X is the heavy isotope (^{13}C, ^{15}N, or ^{34}S), x is the lighter isotope (^{12}C, ^{14}N or ^{32}S) and $(X/x)_{\text{sample}}$ and $(X/x)_{\text{standard}}$ are the ratios of both stable isotopes in the sample and the standard, respectively.

Certified reference materials from the International Atomic Energy Agency (IAEA) were used for calibration, specifically IAEA N-1 (ammonium sulphate; $\delta^{15}N = 0.4 \pm 0.2$‰; mean ± SD). Laboratory glycine (Sigma-Aldrich; $\delta^{15}N = 2.4 \pm 0.3$‰) was analysed as an internal quality control every 15 samples. Replicated measurements of different batches of a replicate spread every 15 samples provided standard deviations of ± 0.3‰ for $\delta^{15}N$ values.

Statistical Analyses

Prior to analysis, we applied a square-root transformation to vegetation composition data and natural logarithm (Log_e) transformations to most soil parameters to reduce skewness in variable distributions. Soil pH was not transformed, given its logarithmic nature by definition. No transformation was applied to total carbon (TC) and total inorganic carbon (TIC), as their distributions approximated normality. After transformation, all soil parameters were standardized (z-score normalization) to mitigate the influence of differing units.

In our analyses, we used several predictors, including the ‘SeabirdImpact’ factor with two levels (SEABIRD and REFERENCE), the discrete variable ‘Distance’ representing plot distance from the cliff edge, and the continuous variable $\delta^{15}N$ soil signature as an indicator of seabird-derived fertilization. Three groups of response variables were considered: (i) soil physical and chemical properties, (ii) $\delta^{15}N$ signatures in vascular plant tissues, and (iii) vegetation composition.

To visualize ordination patterns in the multivariate data, we employed non-metric multidimensional scaling (nMDS) with Bray–Curtis similarity for vegetation composition and metric multidimensional scaling (mMDS) with Euclidean distance for soil characteristics (Clarke and others 2006). Differences between SEABIRD and REFERENCE plots were tested separately for vegetation and soil data using PERMANOVA models, with distance from the cliff included as a covariate and 999 permutations (Anderson 2017).

To identify the contributions of individual components to dissimilarity between groups, we used similarity percentage analysis (SIMPER). Differences in β-diversity between SEABIRD and REFERENCE communities were explored with a distance-based test for homogeneity of multivariate dispersions (PERMDISP) based on deviations from centroids and 999 permutations.

The relationships between vegetation composition and soil parameters was analysed using distance-based redundancy analysis (dbRDA). Soil vectors were fitted onto dbRDA ordinations based on Pearson correlations. Distance-based linear models (DistLM) with 999 permutations were used to test the influence of soil variables on vegetation composition, using exhaustive model selection based on Schwarz’s Bayesian Information Criterion (BIC) (Neath and Cavanaugh 2012).

To further distinguish vegetation communities and determine environmental thresholds, we conducted a linkage tree analysis (LINKTREE) coupled with the similarity profile (SIMPROF) routine (Clarke and others 2008). All multivariate analyses, including cluster analysis, SIMPER, LINKTREE, and DistLM, were conducted using PRIMER v7 with the PERMANOVA + add-on (Anderson 2008; Clarke and Gorley 2015).

To evaluate the directional influence of seabird-derived nutrients on vegetation, we employed structural equation modelling (SEM) using the lavaan package in R (Rosseel 2012). The model structure was based on findings from DistLM and isotopic analyses and tested a cascade of effects: distance from the cliff affecting soil $\delta^{15}N$, which in turn influenced a latent soil fertility variable (constructed from total nitrogen and phosphorus), plant $\delta^{15}N$, and total vegetation cover. Vegetation composition was represented by the first axis of an nMDS ordination (nMDS1) based on Bray–Curtis similarities. The model included a residual covariance between vegetation composition and total cover, while non-significant covariances were fixed to zero for parsimony. All variables were standardized prior to modelling, and completely standardized path coefficients (std.all) were extracted using the semTools::standardizedSolution() function. Maximum likelihood estimation with 1000 bootstrap draws was used to obtain standard errors and account for potential non-normality. Model visualization was performed using semPlot::semPaths(). To reduce the risk of overfitting, the model included only theoretically justified paths.

Use of AI Tools

During manuscript preparation, AI-based tools (ChatGPT, OpenAI) were used to assist with language editing for clarity and grammar. All content was written and verified by the authors. No AI tools were used for data analysis or content generation.

RESULTS

Seabird Influence on Soil Properties

There was a clear and statistically significant difference in soil parameters between the SEABIRD and REFERENCE plots (Table 1, Figure 2A). The SeabirdImpact factor explained a greater proportion of variation in soil characteristics than distance from the cliff (Sq. root = 3.15 vs. 0.69), indicating a strong seabird-driven alteration of soil conditions. The interaction between SeabirdImpact and Distance was also significant, indicating differences in the strength of soil gradients between SEABIRD and REFERENCE transects (Sq. root = 1.46) (Table 1). Descriptive statistics for all soil variables, including within-treatment variability, are provided in Supplementary Table S3.

SIMPER analysis confirmed a distinct separation between sites, with a relatively high average squared distance (Av. Sq. Dist. = 61.7). Approximately, forty per cent of these differences were attributed, in decreasing order of importance, to higher total nitrogen (TN) content, higher total organic carbon (TOC) content, higher concentrations of ammonium (NH_4^+) and nitrate (NO_3^-) ions, and higher soil moisture in SEABIRD transects compared to REFERENCE transects. Conversely, higher concentrations of Mg, Ba, Na, Mn, and higher pH values were observed in REFERENCE transects (Figure 2B, Supplementary Table S4).

Vegetation Composition Across Seabird and Reference Plots

The composition of plant communities differed significantly between SEABIRD and REFERENCE plots, with the SeabirdImpact factor explaining the largest portion of variation (Sq. root = 24.4; Table 1). These compositional differences were clearly shown in the nMDS ordination plots, which illustrate spatial separation between SEABIRD and REFERENCE plots (Figure 3A, B). In addition, plant composition varied significantly with distance from the cliff (Distance, Sq. root = 12.1), and this shift was more pronounced along SEABIRD than REFERENCE transects (SeabirdImpact × Distance, Sq. root = 8.5; Table 1, Figure 3C).

The average dissimilarity in plant composition between SEABIRD and REFERENCE areas, as calculated by SIMPER, was high (65.7%). Total vegetation cover was significantly higher in SEABIRD plots than in REFERENCE plots (median:15% vs. 87.5%; $W = 124$, $P < 0.001$). Mosses and lichens contributed 31% and 11%, respectively, to the total dissimilarity, with average transformed abundance values of 7.56 vs. 2.61 for mosses and 2.79 vs. 1.64 for lichens (Figure 3A, D; Supplementary Table S3).

Among the 17 vascular plant species analysed, seven showed significant differences in abundance. Specifically, *S. oppositifolia* (Figure 3B), *F. rubra*, *S.*

Table 1. Results of PERMANOVA Testing the Influence of Seabirds (SeabirdImpact factor), Distance from the Cliff (Distance), and Their Interaction on Soil Physical and Chemical Properties and Vegetation Composition

Response	Predictor	df	SS	MS	Pseudo-*F*	P (perm)	Sq. root
Soil properties	SeabirdImpact	1	317.7	317.7	16.4	0.001	3.15
	Distance	1	48.2	48.2	2.5	0.053	0.69
	Seabird × distance	1	83.7	83.7	4.3	0.006	1.46
	Residuals	56	1084.4	19.4			4.40
	Total	59	1534.0				
Plant communities	SeabirdImpact	1	19,413.0	19,413.0	12.6	0.0001	24.41
	Distance	1	10,256.0	10,256.0	6.6	0.0001	12.05
	Seabird × distance	1	3700.8	3700.8	2.4	0.0277	8.48
	Residuals	56	86,305.0	1541.2			39.26
	Total	59	119,680.0				

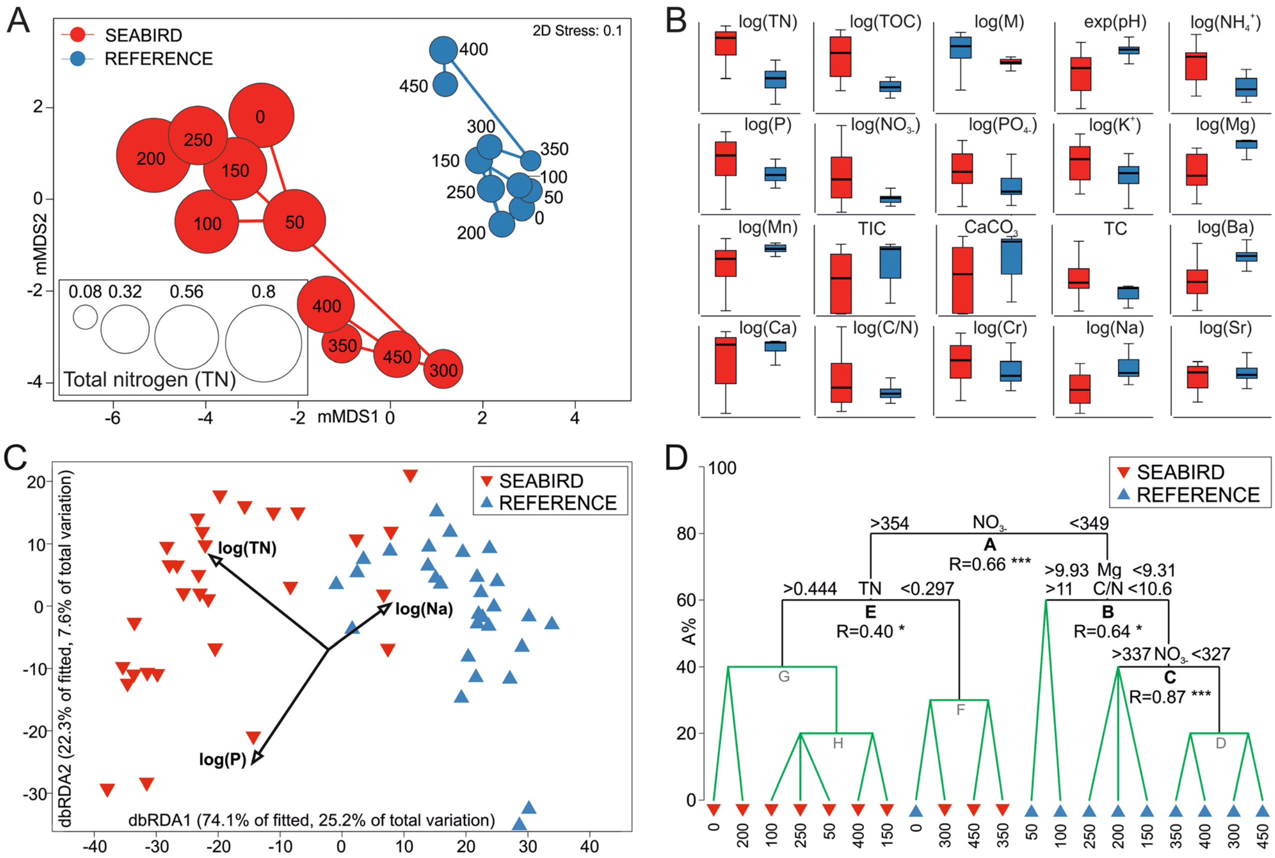

Figure 2. **A** Metric multidimensional scaling (mMDS) ordination plot illustrating multivariate differences in soil characteristics between SEABIRD and REFERENCE transects, based on centroids calculated for each distance. **B** Boxplots showing differences in individual soil parameters between SEABIRD and REFERENCE plots for the 20 variables most strongly associated with vegetation composition.

caespitosa, and *C. groenlandica* had higher average abundance in SEABIRD transects, whereas *S. polaris* and *S. acaulis* were more abundant in REFERENCE plots (Figure 3B, D; Supplementary Table S4).

Vegetation–Soil Relationships

Of the 26 soil parameters individually tested, 20 were identified as significant predictors of plant community composition based on marginal tests (Supplementary Table S5). Using Bayesian Information Criterion (BIC) for model selection, the optimal combination of predictors included three key soil variables: total nitrogen (TN), sodium (Na), and total phosphorus (P) contents (Table 2). This model explained a substantial portion of the variation in vegetation composition (BIC = 447.4; $R^2 = 0.34$), and the resulting dbRDA ordination clearly differentiated SEABIRD from REFERENCE plots based on these three soil parameters (Figure 4A). A detailed comparison of the top ten competing models is provided in Supplementary Table S6.

Vegetation–Soil Heterogeneity and Environmental Drivers

Vegetation heterogeneity was analysed using LINKTREE clustering constrained by soil parameters, with significant divisions confirmed by the SIMPROF test. The main division (A; B% = 89) separated SEABIRD from REFERENCE plots and was associated with elevated soil nitrate concentrations in SEABIRD-influenced areas ($NO_3^- >$ 354 mg kg^{-1} dry mass) (Figure 4B). Within SEABIRD plots, further heterogeneity was driven primarily by total nitrogen content, with division E (B% = 56) distinguishing higher TN concentrations closer to the cliff. In REFERENCE plots, vegetation differences were structured by magnesium concentrations and the C/N ratio (division B), followed by nitrate content (division C).

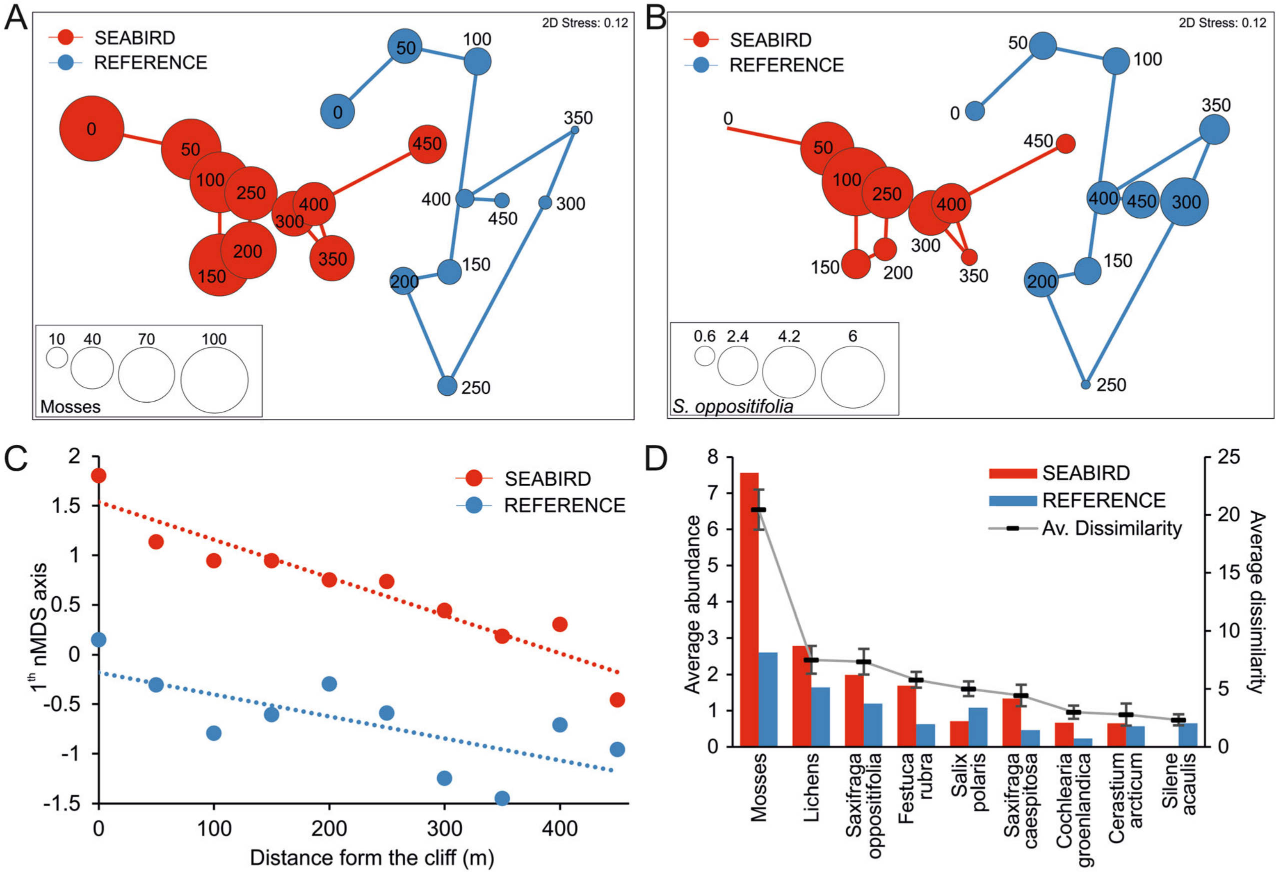

Figure 3. Non-metric multidimensional scaling (nMDS) ordination plots illustrating variation in vegetation composition between SEABIRD (red) and REFERENCE (blue) transects. **A** Bubble sizes represent the relative cover of mosses. **B** Bubble sizes represent the relative abundance of Saxifraga oppositifolia. **C** Significant interaction between SeabirdImpact and Distance factors, based on the first nMDS axis. **D** SIMPER results for the eight vegetation components contributing most to dissimilarity between SEABIRD and REFERENCE plots, showing mean abundance (bars) and average dissimilarity (line).

Table 2. The Results of the Distance-based Linear Model (DistLM) Sequential Test Showing Optimal Predictors for the Vegetation Composition Among 26 Soil Parameters

Soil properties	BIC	SS	Pseudo-F	P (perm)	Explained %	Cumulative %
LOG(TN)	448.16	27,894.0	17.63	0.0001	23.3	23.3
LOG(Na)	450.10	3230.6	2.08	0.0412	2.7	26.0
LOG(P)	447.36	9529.2	6.75	0.0001	8.0	34.0

Stable Isotopes as Indicators of Seabird-Derived Nutrients

We found significantly higher δ^{15}N values in both soil and vascular plant tissues in SEABIRD plots compared to REFERENCE plots (soil PERMANOVA: pseudo-$F = 32.84$, df = 1, $P < 0.001$; plant tissue PERMANOVA: pseudo-$F = 18.85$, df = 1, $P < 0.001$; Supplementary Table S7). Soil δ^{15}N values—which serve as an ecological tracer of marine-derived nitrogen input from seabird guano—were strong predictors of vegetation composition (explaining 17% of variation), soil properties (10%), and plant tissue δ^{15}N (26%). In sequential DistLM models, Distance did not emerge as a significant predictor of soil properties or plant tissue δ^{15}N after soil δ^{15}N was entered as the first predictor (Table 3). In marginal tests, Distance was a significant predictor for plant tissue δ^{15}N and vegetation composition, but not for soil properties

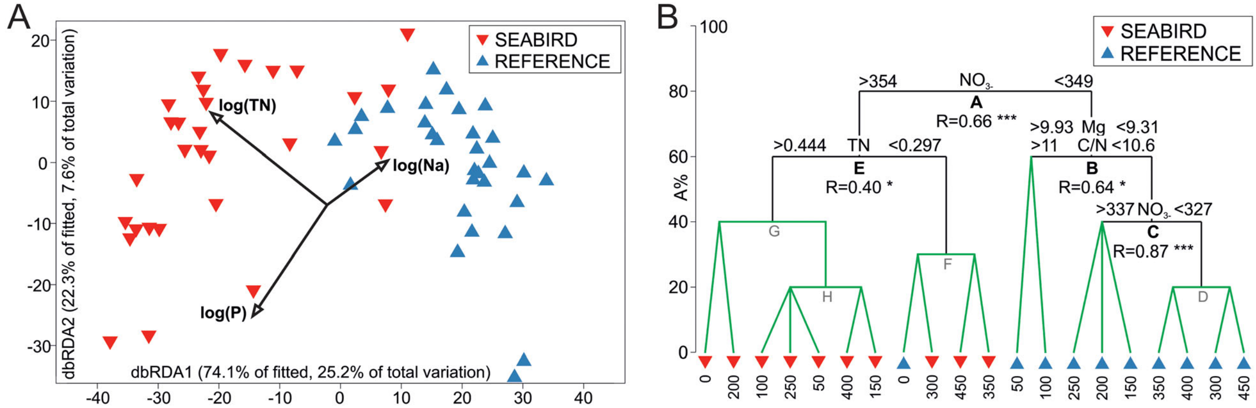

Figure 4. **A** Distance-based redundancy analysis (dbRDA) ordination of vegetation composition constrained by the three best soil predictors: total nitrogen, sodium, and phosphorus. **B** LINKTREE diagram showing distinct clusters of vegetation centroids based on environmental thresholds. Green clades represent homogeneous vegetation groups confirmed by the SIMPROF test.

(Supplementary Table S8). This finding is consistent with the PERMANOVA results, which also found no significant effect of distance on soil chemistry (Table 1.). The lack of a marginal distance effect for soils likely reflects the absence of a strong distance-related nutrient gradient in REFERENCE plots, and the fact that other factors may structure soil chemistry in those areas. A strong negative correlation between distance from the cliff and soil δ^{15}N (that is, between the two predictors in the model) further supports this relationship ($r = -4.08$; df = 58; $P < 0.001$).

Integrated Effects of Seabirds on the Tundra Ecosystem

The structural equation model (SEM) revealed a clear pathway of seabird influence on tundra vegetation (Figure 5). Soil δ^{15}N decreased with increasing distance from the cliff ($\beta = -0.47$, $P = 0.001$) and was positively associated with both plant δ^{15}N ($\beta = 0.86$, $P < 0.001$) and a latent soil fertility variable defined by total nitrogen and phosphorus ($\beta = 0.53$, $P < 0.001$). In turn, soil fertility strongly affected vegetation composition ($\beta = -0.68$, $P < 0.001$) and total vegetation cover ($\beta = 0.86$, $P < 0.001$). A residual covariance between vegetation composition and total cover ($\beta = -0.71$, $P < 0.001$) indicated additional shared variance not explained by fertility alone.

The model showed acceptable overall fit (CFI = 0.927, TLI = 0.883, SRMR = 0.078), although the RMSEA was moderately elevated (0.180), likely due to model complexity relative to sample size. The SEM structure is presented in Figure 5 and detailed in Supplementary Material S9.

DISCUSSION

Seabird colonies are well known for creating ornithogenic tundra below cliffs through concentrated guano deposition (Eurola and Hakala 1977; Zwolicki and others 2013). Here, we demonstrate that their influence also extends above cliffs, where no direct deposition occurs. On Bjørnøya, isotopic evidence and soil chemistry reveal that marine-

Table 3. Results of Distance-based Linear Models (DistLM) Testing the Explanatory Power of Soil δ^{15}N and Distance from the Cliff for Variation in Vegetation Composition, Soil Properties, and δ^{15}N Values in Plant Tissues

Response/model	Predictor	BIC	SS	Pseudo-F	P	Explained %	Cumulative %
Plant communities	Soil δ^{15}N	452.9	20,289.0	11.84	0.0001	0.17	0.17
	Distance	454.4	4231.9	2.535	0.0195	0.04	0.20
Soil properties	Soil δ^{15}N	196.3	153.5	6.45	0.0004	0.10	0.10
	Distance	198.2	50.1	2.15	0.0749	0.03	0.13
δ^{15}N in plant tissues	Soil δ^{15}N	39.2	34.7	19.59	0.0002	0.26	0.26
	Distance	39.5	6.2	3.68	0.058	0.05	0.31

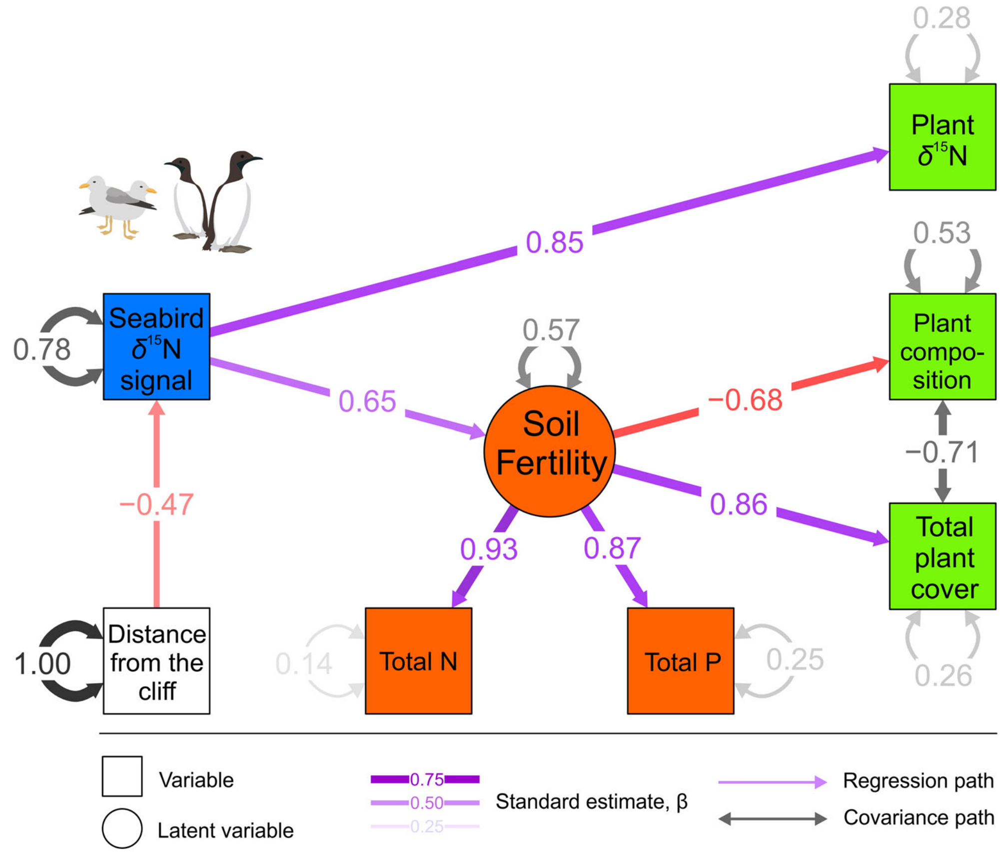

Figure 5. Structural equation model (SEM) that illustrated the relationships among distance from the cliff, seabird-derived nitrogen input (δ^{15}N in soil), soil fertility, and vegetation structure above seabird cliffs on Bjørnøya. Soil fertility was modeled as a latent variable defined by total nitrogen (N) and total phosphorus (P). Solid arrows represented significant standardized path coefficients (based on 1000 bootstrapped samples), with red indicating negative relationships and purple indicating positive relationships. Doubleheaded grey arrows represented residual covariances. The seabird δ^{15}N signal was used as a tracer of nutrient input from seabirds. Model fit indices: RMSEA = 0.180, CFI = 0.927, TLI = 0.883, SRMR = 0.078.

derived nitrogen is redistributed inland, most likely via wind (Schmale and others 2013; Zmudczyńska-Skarbek and others 2017), enriching soils and altering tundra vegetation. However, unlike classical ornithogenic systems, this above-cliff community is not dominated by nitrophilous grasses but by stress-tolerant mosses and *S. oppositifolia* (Zmudczyńska and others 2009; Opała-Owczarek and others 2018). These findings highlight a distinct pathway of seabird-driven ecosystem modification, where nutrient input interacts with harsher and drier abiotic conditions to shape a unique form of tundra vegetation above the cliffs.

Seabird Nutrient Influence Above Cliffs

Above-cliff areas affected by seabird activity showed pronounced changes in both soil chemistry and vegetation structure. Soils in SEABIRD plots were notably enriched in total nitrogen, organic carbon, phosphorus, and mineral nitrogen forms (NH_4^+ and NO_3^-), mirroring the nutrient signatures commonly reported for ornithogenic tundra (Zwolicki and others 2013; Zmudczyńska-Skarbek and others 2017). Although direct guano deposition above the cliffs is likely rare compared to sites below the colony, the soil chemical resemblance to typical ornithogenic environments suggests efficient nutrient transfer through indirect mechanisms, such as dry deposition of wind-blown guano aerosols or sea spray (Schmale and others 2013; Mizutani and Wada 1988). While indirect, wind-mediated dispersal appears to be the primary mechanism for nutrient transfer above the cliffs, we cannot fully exclude the possibility of occasional direct guano deposition from birds in flight, especially close to the cliff. Furthermore, increased soil moisture and higher soil pH values recorded in SEABIRD plots likely reflect the insulation effects from greater plant biomass—primarily mosses—-which enhance water retention and moderate soil temperature fluctuations (Gornall and others 2007; Bokhorst and others 2010). Increased soil moisture can enhance post-depositional δ^{15}N fractionation (Mizutani and Wada 1988; Bokhorst and others 2019b), but this effect is minor compared to the dominant influence of seabird nutrient input. The high concentrations of total nitrogen, phosphorus, and other nutrients in SEABIRD soils confirm that guano deposition remains the main driver of enrichment, while fractionation only slightly alters the isotopic signal.

Vegetation composition and cover also markedly differed between SEABIRD and REFERENCE plots. Contrary to the classical ornithogenic tundra model—where intense nutrient input typically favours dominance of fast-growing vascular plants while diminishing cryptogam abundance (Eurola and Hakala 1977; Zwolicki and others 2016a)—we documented a coexistence of substantial moss and lichen cover alongside enriched vascular plant diversity in SEABIRD areas. Species such as *S. oppositifolia*, *F. rubra*, *S. caespitosa*, and *C. groenlandica* were more abundant in these nutrient-enriched plots, indicative of a positive response to moderate nutrient enhancement. Conversely, the REFERENCE plots were predominantly occupied by stress-tolerant species, notably *S. acaulis* and *S. polaris*, adapted to nutrient-poor, moisture-limited, and wind-exposed conditions characteristic of Arctic plateaus (Molenda and others 2012; Körner 2003; Willard 1979). The cushion growth form of *S. acaulis*, in particular, provides advantages in such harsh abiotic environments by minimizing wind exposure and enhancing moisture retention (Jones and Richards 1962; Molenda and others 2012).

The coexistence of nutrient-demanding and stress-tolerant species in SEABIRD plots likely results from the interplay between moderate nutrient availability and persistent abiotic stress. In contrast to areas with intense, direct guano deposition—where cryptogams frequently decline—the diffuse and moderate nutrient input above cliffs on Bjørnøya still allows mosses and lichens to thrive. Mosses appear to play a key facilitative role here, likely stabilizing soils, enhancing moisture retention, and buffering temperature extremes (Oechel and Van Cleve 1986; Gornall and others 2007). This facilitation could specifically benefit *S. oppositifolia*, a shallow-rooted species commonly inhabiting nutrient-poor substrates but capable of exploiting improved microsite conditions (Opała-Owczarek and others 2018). Although mosses are typically vulnerable to winter freezing, particularly in wind-exposed sites with limited snow cover (Bokhorst and others 2008, 2010), their success in these plots likely reflects both enhanced moisture availability and the microclimatic buffering afforded by dense vegetation.

Vegetation–Soil Relationships and Heterogeneity

Multivariate analyses revealed clear differences in soil–vegetation relationships between seabird-influenced (SEABIRD) and background (REFERENCE) tundra. Distance-based redundancy analysis (dbRDA) and DistLM identified total nitrogen (TN), sodium (Na), and phosphorus (P) as primary soil predictors explaining vegetation composition. Nitrogen and phosphorus are well-established key drivers shaping Arctic plant communities, especially under ornithogenic nutrient enrichment (Croll and others 2005; Zwolicki and others 2016a, 2023; Ellis and others 2006). Sodium enrichment, though less frequently highlighted, likely reflects marine aerosol deposition or correlates indirectly with seabird-driven nutrient inputs (Mizutani and Wada 1988; Chen and others 2022). These soil properties thus appear to integrate both direct seabird fertilization and indirect feedbacks through enhanced plant biomass and organic matter accumulation (Gornall and others 2007; Bokhorst and others 2010).

The LINKTREE analysis further emphasized contrasting soil-driven vegetation patterns. In SEABIRD plots, vegetation composition was primarily influenced by total nitrogen, consistent with fertilization effects typical of seabird colonies (Ellis and others 2006; Mulder and others 2011; Zwolicki and others 2013, 2023). Conversely, REFERENCE vegetation was structured by magnesium concentrations and carbon-to-nitrogen ratios—factors indicative of nutrient limitation and local geochemical substrates (Walker and Chapin 1986; Chapin and others 1993; Beermann and others 2015). Interestingly, magnesium, calcium, and sodium levels were unexpectedly elevated in REFERENCE soils, which likely reflects underlying geological differences: dolomitic bedrock in REFERENCE plots (Russehamna Formation) contrasted with clastic sedimentary substrates of SEABIRD areas (Miseryfjellet and Ymerdalen Formations; (Dallmann 1993; Dallmann and Krasilscikov 1996; Worsley 2008). This highlights the critical role of geochemical background when interpreting nutrient patterns and vegetation responses in coastal tundra ecosystems, and shows how seabird nutrient inputs can override local mineral constraints to restructure vegetation-environment relationships.

δ^{15}N as Tracers of Seabird-Derived Nutrients

Nitrogen isotope ratios (δ^{15}N) in soil and plant tissues provided robust evidence for the assimilation of seabird-derived nitrogen into the above-cliff tundra ecosystem. We observed significantly elevated δ^{15}N values in soils and vascular plants within SEABIRD plots compared to REFERENCE plots, a signature typical of ornithogenic nutrient enrichment (Bokhorst and others 2019b; Lindeboom 1984; Zwolicki and others 2016a, 2016b; Szpak and others 2012). High δ^{15}N values in seabird-affected soils primarily result from post-depositional isotopic fractionation processes during guano decomposition, rather than from seabirds' high trophic positions alone. Specifically, the preferential volatilization of isotopically lighter ammonia ($^{14}NH_3$) enriches the residual nitrogen pool in heavier ^{15}N (Mizutani and Wada 1988; Wainright and others 1998).

Soil δ^{15}N emerged as a strong predictor of variation in both soil chemistry (10%) and vegetation composition (17%), and explained over a quarter (26%) of the variability in plant tissue δ^{15}N. These results indicate effective uptake of seabird-derived nitrogen by terrestrial vascular plants and confirm the integrative role of δ^{15}N as a sensitive tracer of marine nutrient pathways (Szpak and others 2012; Zwolicki and others 2016b). The strong isotopic coupling between soil and plants further underscores that seabird influence on nutrient cycling extends considerably inland, mediated by indirect transport mechanisms such as wind redistribution or aerosol deposition (Wainright and others 1998; Schmale and others 2013). These findings confirm that δ^{15}N effectively traces seabird-derived nitrogen from soil to plants, illustrating how marine nutrients influence tundra vegetation well beyond the immediate vicinity of bird colonies, with isotopic signals detected up to 450 m inland from the cliff edge. This is broadly comparable to the spatial scale reported in Antarctic studies, where Bokhorst and others found ornithogenic effects extending several hundred meters to over a kilometre from penguin and seal colonies, though local topography and colony size may modulate the distance of ornithogenic influence (Bokhorst and others 2019a, 2019b).

Nutrient Cascades and Transport Pathways

The distinct vegetation communities observed above cliffs on Bjørnøya highlight a clear cascade of seabird-derived nutrient influence despite the absence of direct guano deposition. Our structural equation model supported a robust, pathway whereby marine-derived nitrogen—traced by elevated soil δ^{15}N—enhanced soil fertility, defined as a latent construct encompassing total nitrogen and phosphorus. In turn, enhanced fertility drove significant changes in both vegetation composition and total vegetation cover. The SEM results quantify a clear inland nutrient cascade, where seabird-derived nitrogen enhances soil fertility, and in turn, alters vegetation composition and cover.

Our approach addresses limitations of previous research on Bjørnøya (Zmudczyńska-Skarbek and others 2017), where SEM analyses identified seabird impacts on soil and vegetation but excluded central nutrient indicators (for example, δ^{15}N, total nitrogen) from final models, leaving the principal nutrient pathways unresolved. By explicitly integrating δ^{15}N isotopes as tracers of marine input and combining multiple soil variables into a complete fertility construct, our model strongly elucidates the fundamental ecological mechanisms linking seabird colonies with terrestrial plant communities.

Efficient nutrient transport from seabird colonies to the plateau tundra is most plausibly explained by wind-driven redistribution of guano particles and aerosols. Bjørnøya's prevailing northwestern and northeastern winds (MET Norway; Supplementary Materials S1–S2) consistently interact with cliff faces, generating turbulent airflow capable of entraining fine, desiccated guano particles. As guano dries, it becomes increasingly friable and susceptible to aerial transport. Turbulent winds produce updrafts and separation zones at the cliff edge, effectively transporting and depositing nutrients inland (Tamura and Kareem 2013; Lange and others 2017). Although guillemots rarely overfly inland plateaus—likely deterred by turbulence above steep cliff margins (Greenwood 1964; Shepard and others 2019)—our results demonstrate clear inland nutrient influence indicative of atmospheric transport.

Additionally, nutrient dispersal may be facilitated by fog and sea spray aerosols. Seabird guano contains soluble ions readily incorporated into atmospheric moisture droplets (Schmale and others 2013). Notably, ammonium and nitrate ions easily form soluble salts transported efficiently in aerosols

(Zapp and others 2000). Conversely, phosphate ions, being less soluble due to higher negative charge, exhibit limited aerosol mobility (Ball and others 2011). These solubility differences likely underlie the spatial mismatch observed in soil nutrient distributions, with nitrogen reaching further inland compared to phosphorus.

While we do not directly measure transport processes, our results demonstrate inland nutrient enrichment patterns consistent with atmospheric redistribution. This lends support to the original hypothesis by Summerhayes and Elton (1923) of a seabird-driven nutrient cycle on Bjørnøya, and highlights how seabirds can extend their ecological influence beyond colony boundaries through indirect nutrient pathways.

Seabirds as Arctic Ecosystem Engineers

The ecological role of seabird colonies extends significantly beyond their direct fertilization effects on soil and vegetation. By facilitating nutrient transfer from marine to terrestrial ecosystems, seabirds sustain broader trophic interactions within Arctic landscapes. This influence is exemplified by the migratory ecology of the Svalbard barnacle goose, nearly the entire population of which—around 35,000 individuals—utilizes Bjørnøya as a crucial refuelling station during autumn migration (Owen and Gullestad 1984; Owen and Black 1989). Geese arriving from breeding grounds on Spitsbergen remain on Bjørnøya for several weeks to graze the terrestrial vegetation and replenish energy reserves before continuing to their wintering habitats in northern Britain. The island's unique geographic position between Spitsbergen and mainland Europe underscores its critical importance as a migratory stopover, an ecological role made possible by sustained seabird nutrient inputs that enhance tundra productivity.

However, the intensive seasonal grazing by barnacle geese also places substantial pressure on the vegetation, potentially leading to rapid degradation without ongoing nutrient replenishment (Kuijper and others 2006; Jakubas and others 2008). Goose herbivory and nutrient cycling through defecation create dynamic feedbacks that further modify plant–soil interactions (Greve Alsos and others 1998; Kuijper and others 2006). These complex interactions illustrate a cascading ecological dependency, in which seabirds indirectly support higher trophic levels by maintaining productive foraging habitats crucial for migratory herbivores.

Consequently, seabird colonies function as keystone ecosystem engineers (Wardle and others 2004; Jones and others 1994), structurally and chemically modifying their environment in ways that persist beyond their immediate presence. By facilitating nutrient transfer across ecosystems, seabirds enhance landscape-scale ecological connectivity and productivity (Croll and others 2005; Mulder and others 2011). Given ongoing climate-driven shifts in Arctic species distributions and migration patterns, incorporating inland seabird nutrient transfer into ecosystem assessments may improve predictions of tundra responses and help guide biodiversity conservation in polar environments.

Study Limitations and Future Directions

While our findings demonstrate a robust seabird-driven nutrient cascade shaping tundra vegetation, several limitations should be acknowledged. First, our conclusions about nutrient transport mechanisms rely on indirect evidence from spatial patterns in δ^{15}N and soil chemistry. Direct measurements of guano aerosol dispersal, wind dynamics, and nutrient deposition would greatly enhance mechanistic understanding (Wainright and others 1998; Schmale and others 2013). Additionally, this study was confined to a single location and one sampling period, limiting broader generalizations. Multi-year and multi-site studies across diverse Arctic settings are needed to capture spatial and temporal variability in tundra ecosystems (Polis and others 1997; Soininen and others 2015).

Our stable isotope analyses were limited to soils and vascular plant tissues. Extending this approach to terrestrial invertebrates and non-marine vertebrates would provide valuable insight into the wider transfer of seabird-derived nutrients through the terrestrial food web—a promising direction for future research on Bjørnøya and in similar systems. Furthermore, expanding this framework to include additional seabird species and geomorphological contexts will also be critical for developing pan-Arctic assessments of seabird-mediated nutrient dynamics and their ecological consequences under environmental change.

This study demonstrates that seabird colonies facilitate the redistribution of marine-derived nutrients well beyond cliff edges, altering soil chemistry and plant community composition on plateau tundra. The resulting spatial nutrient gradients, marked by elevated δ^{15}N signatures that decline with distance from colonies, reflect the inland reach of ornithogenic enrichment. These above-cliff habitats support structurally diverse plant communities shaped by the combined effects of nutrient input and abiotic stress, and may also function as important foraging areas for migratory herbivores, contributing to ecosystem connectivity. To advance understanding of these processes, future research should directly quantify wind-driven nutrient dispersal and assess the generality of these patterns across different Arctic settings and seabird species.

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DATA AVAILABILITY

Data are available at: https://doi.org/10.5281/zenodo.16669316.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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