

RESEARCH ARTICLE

Marine-derived nutrients shape the functional composition of High Arctic plant communities

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Handling Editor: Johannes Rousk**Abstract**

1. Low temperatures and nutrient limitation have shaped Arctic plant communities, which are now affected by biome-wise changes in both climate and nutrient cycling. Rising temperatures are favouring taller plant species with more resource-acquisitive traits across the Arctic tundra. Simultaneously, declines in seabird populations may reduce subsidies of marine-derived nutrients to terrestrial ecosystems, potentially favouring more resource-conservative plant traits. It is crucial to understand the consequences of these concurrent changes in climate and marine-derived nutrient inputs from seabirds for the functional composition and roles of Arctic plant communities.
2. We use a 'space-for-time approach' to compare the functional composition of vascular plant communities across two elevational gradients in High Arctic Svalbard, one where climate is the major environmental driver and one influenced by nutrient input from a seabird colony. We assess changes in 13 traits related to plant size, leaf economics and nutrient cycling along the two gradients, and we also explore the relative contributions of species turnover and intraspecific variation to total trait variation across and between the gradients.
3. Elevation *per se* had little impact on the plant functional composition. Instead, plants at the top of the seabird nutrient gradient, closest to the nesting sites, were taller and had resource-acquisitive trait values, such as larger and thicker

For affiliations refer to page 1617.

[Correction added on 22 May 2025, after first online publication: Vigdis Vandvik and Aud H. Halbritter have been added as co-corresponding author.]

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leaves and higher leaf nutrient contents. Enriched soil $\delta^{15}\text{N}\text{‰}$ signatures at these sites correlated with resource-acquisitive values of leaf area, specific leaf area, leaf dry matter content, leaf phosphorous content and with enriched leaf $\delta^{15}\text{N}\text{‰}$ signatures. This variation in leaf economic traits and isotopes was largely driven by intraspecific variation at the nutrient gradient, whereas species turnover dominated at the reference gradient.

4. Our results are consistent with marine-derived nutrient subsidies from seabirds being a major driver of functional trait variation in Arctic vegetation. Ongoing declines in seabird populations may therefore affect terrestrial primary producer communities in the Arctic and beyond, with potentially important but unknown implications for biodiversity, consumer and decomposer communities, and ecosystem processes.

KEYWORDS

Bjørndalen, intraspecific trait variation, nutrient enrichment, plant functional traits, seabirds, species turnover, Svalbard

1 | INTRODUCTION

Arctic ecosystems are at the forefront of global environmental change, with temperatures rising at rates four times the global average (Box et al., 2019; Constable et al., 2022; Post et al., 2009; Rantanen et al., 2022). Simultaneously, Arctic ecosystems are affected by unprecedented declines in seabird populations of approximately 70% between 1950 and 2010 globally (Paleczny et al., 2015). Seabird declines are expected to continue, driven by the combined impacts of invasive alien species, fisheries and climate change (Dias et al., 2019; Gibson et al., 2023; Will et al., 2020). Both climate warming and reduced seabird populations can affect biodiversity and the ecological functioning of terrestrial plant communities across the Arctic tundra, as these changes alter key environmental constraints regulating plant growth. Climate warming alleviates temperature limitation, leading to increased growth, vegetation cover and a shift towards dominance of taller species (Bjorkman et al., 2018; Myers-Smith et al., 2019). Less understood is which consequences reduced transport of marine-derived nutrients as a result of declines in seabird populations will have for otherwise nutrient-limited Arctic vegetation (Haag, 1974; Hobbie et al., 2002).

In the Arctic, vegetation near colonies of nesting seabirds stands out as *green islands* amidst otherwise barren landscapes. Near seabird colonies, nutrients, such as nitrogen, and phosphorus are deposited as droppings, feathers, egg shells and remains of deceased birds (Anderson & Polis, 1999; Duda et al., 2020; Ellis, 2005; Gabrielsen et al., 1991; Grant et al., 2022; Wojciechowska et al., 2015; Zwolicki et al., 2013). Marine-derived nutrients are thus a supplementary input to the terrestrial ecosystem and affect the distribution, succession, community composition and functional traits of Arctic plants (Croll et al., 2005; Duda et al., 2020; Ellis, 2005; Grant et al., 2022; Magnússon et al., 2014; Wojciechowska et al., 2015; Zwolicki et al., 2016). Marine-derived nutrients impact across trophic levels,

for example by decreasing the availability of preferred food for herbivores (Jakubas et al., 2008), and can be traced throughout the terrestrial food web using isotope signatures (González-Bergonzoni et al., 2017; Hentati-Sundberg et al., 2020; Kristiansen et al., 2019). Some Arctic plants, such as polar scurvygrass (*Cochlearia groenlandica*), respond positively to marine-derived nutrients with increased population densities and leaf size near nesting seabirds (Wojciechowska et al., 2015; Zmudczyńska-Skarbek et al., 2015). In contrast, other plant species decrease with marine-derived nutrients, as they are outcompeted by plants better suited to exploit high nutrient availability (Duda et al., 2020).

Temperature and nutrient status are major determinants of the functional composition of plant communities. Globally, the realized above-ground functional trait expressions of plants can be summarized across two major axes of variation; plant size and the 'leaf economic spectrum' characterizing the shift from 'slow' resource-conservative leaf economics (i.e. low specific leaf area (SLA), high leaf dry matter content (LDMC) and low nitrogen content) to 'fast' resource-acquisitive trait strategies (i.e. high SLA, low LDMC and high nitrogen content; Bruelheide et al., 2018; Díaz et al., 2016; Joswig et al., 2022; Maire et al., 2015; Ordoñez et al., 2009; Simpson et al., 2016; Thomas et al., 2020; Wright et al., 2004). In Arctic tundra, temperature is a main driver of plant height, with warmer climates favouring taller species or individuals. In contrast, leaf economic traits do not respond consistently to temperature (Bjorkman et al., 2018; Thomas et al., 2020) but vary with nutrient availability (Helsen et al., 2014; Joswig et al., 2022; Suding et al., 2005; Xia & Wan, 2008). These findings suggest that marine-derived nutrients may be important drivers of functional trait variation in Arctic plant communities, in particular leaf economics, above and beyond the impacts of temperature.

Isotope signatures are proxies for leaf, plant and ecosystem nutrient and hydrological cycling. The ratio of ^{15}N to ^{14}N ($\delta^{15}\text{N}\text{‰}$) indicates processes related to the nitrogen cycle, including nitrogen

fixation and acquisition (Craine et al., 2015), and is used to determine the trophic position of organisms (Post, 2002). Organisms occupying higher trophic levels in marine ecosystems (e.g. seabirds) have enriched $\delta^{15}\text{N}\text{‰}$ signatures compared with those occupying lower trophic levels (Kelly, 2000). Enriched $\delta^{15}\text{N}\text{‰}$ signatures from seabird excreta can be used to trace marine-derived N throughout terrestrial food webs (Anderson & Polis, 1999; Caut et al., 2012; Erskine et al., 1998; Mizutani & Wada, 1988; Wainright et al., 1998). $\delta^{13}\text{C}\text{‰}$ signatures are indicators for plant water status, with enriched values indicating higher water-use efficiency (Farquhar et al., 1982; Pérez-Harguindeguy et al., 2013).

The functional response of plant communities to environmental change is driven by species turnover (i.e. including changes in species identity and relative abundance) and/or trait variation within species (Violle et al., 2012). Generally, about one quarter of total plant trait variation is attributed to intraspecific variation, but this can exceed 50% for some leaf economic traits, such as leaf nitrogen content (Jónsdóttir et al., 2022; Siefert et al., 2015; Thomas et al., 2020). For species-poor, High Arctic plant communities, intraspecific trait variation is relatively more important, and this may explain the high ecological resilience of these systems whereby taxonomic community composition persists and maintains functioning even under rapidly increasing temperatures (Jónsdóttir et al., 2022). Although marine-derived nutrients from seabirds alter individual Arctic plant species traits (Wojciechowska et al., 2015; Zmudczyńska-Skarbek

et al., 2015) and increase the productivity of terrestrial vegetation (González-Bergonzoni et al., 2017), there is a need for studies that address functional responses of Arctic plants to marine-derived nutrient inputs at the community level.

We study how marine-derived nutrients from seabirds and microclimatic variation across elevation affect the functional composition of Arctic plant communities in terms of plant size, leaf economics and leaf isotope signatures. Traits were selected to capture plant responses to (micro)climate, soil abiotic factors and nutrient availability. We compare community-weighted trait means across two elevational gradients in High Arctic Svalbard (Figure 1); one influenced by nutrient input from seabirds, the other without (hereafter: nutrient and reference gradient). Because the seabirds nest atop a steep slope, nutrient input increases with elevation. Elevation does not always capture all microclimatic variation that impacts plant traits (Bruehlheide et al., 2018; Kemppinen & Niittynen, 2022; Opedal et al., 2015; Thomson et al., 2021). We therefore measure soil temperature, moisture, nitrogen and carbon, and $\delta^{15}\text{N}\text{‰}$ as a proxy for seabird influence (Caut et al., 2012). Finally, we quantify the relative contribution of intraspecific trait variation to total trait variation between the gradients for each trait. We predict that:

1. Marine-derived nutrients from seabirds shift vascular plant community traits towards faster leaf economics. We thus expect more resource-acquisitive trait values (e.g. higher SLA

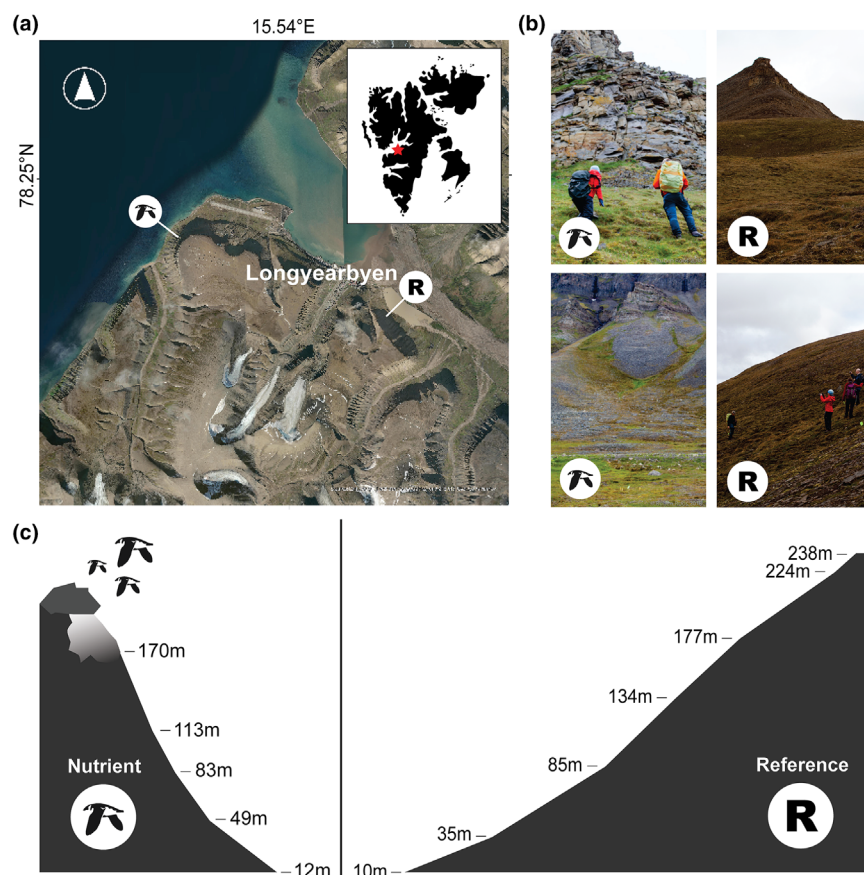


FIGURE 1 Location of the elevational gradients included in this study, one near nesting seabirds (nutrient; bird symbol) the other without seabirds (reference; R) (a). Images of the nutrient (left) and reference gradient (right) (b). Images were taken at the same time of year. Elevation profiles of the two gradients (c). Elevation markers indicate where sites for plant community trait analyses were established.

and nitrogen content and lower LDMC) at higher elevation in the nutrient gradient, but an opposite trend in the reference gradient where trait variation is driven mainly by climate.

- Size traits increase with temperature, whereby microclimate will be relatively more important than elevation.
- Intraspecific variation contributes most to total trait variation at the nutrient gradient and for leaf economic traits.

2 | METHODS

2.1 | Study localities and design

This study was conducted across two elevational gradients near Longyearbyen in High Arctic Svalbard (Vandvik et al., 2023). One gradient (nutrient gradient) was located at a coastal, north-west facing slope near Bjørndalen (78.24°N, 15.35°E). Here, a seabird colony of approx. 3500m² consists of little auk (*Alle alle*, 3000–4000 pairs) and some pairs (10–20) of black guillemots (*Ceppus grille*), fulmars (*Fulmarus glacialis*) and glaucous gulls (*Larus hyperboreus*). While little auks mainly feed on zooplankton (*Calanus* species), the other seabird species eat amphipods and fish species (Lønne & Gabrielsen, 1992; Mehlum & Gabrielsen, 1993). The seabirds nest amidst rocky outcrops and talus slopes underneath a steep cliff, where their excreta accumulate. Nutrient subsidies are therefore expected to decrease downslope (Duda et al., 2020; Finne et al., 2022; Hargan et al., 2017). The other gradient (reference gradient) lacks the influence of seabirds and was located about two kilometres inland near Lake Isdammen, along a north-east facing slope of Lindholmhøgda (78.20°N, 15.72°E, Figure 1a,b). The reference gradient was placed inland because other coastal slopes were occupied by seabirds or inaccessible. Vascular plant communities at the two gradients are rich in graminoids, forbs and deciduous dwarf shrubs (Vandvik et al., 2023). Barnacle geese (*Branta leucopsis*) and pink-footed geese (*Anser brachyrhynchus*) graze the lowlands below the reference gradient, but because of their terrestrial foraging, they are unlikely to subsidize marine nutrients. There were no signs of goose grubbing in our plots. Both gradients have similar bedrock (Dallmann, 2015) and are grazed by Svalbard reindeer (*Rangifer tarandus platyrhynchus*).

At the nutrient gradient, five sites were selected at elevations ranging from 12 to 170m above sea level (m a.s.l., Figure 1c). At the reference gradient, seven sites were established at elevations ranging from 10 to 238m a.s.l. At each site, seven 75 × 75 cm vegetation plots were established except for at the highest site at the reference gradient. Here, four plots were established due to limited vegetation cover. Plot selection was performed to include plots with similar microtopography (Thomson et al., 2021), minimizing differences related to factors other than elevation and seabirds, for example no plots were placed in snowbeds, streams, scree, exposed ridges or areas covered exclusively by non-vascular vegetation. Plot dimensions were selected as appropriate in relation to plant size and vegetation structure, capturing both common and rare species (Halbritter

et al., 2020). Plots were placed 5m apart. See Table S1 in Supporting Information for the replication statement.

2.2 | Soil parameters

Volumetric soil water content (–7.5 cm depth) was recorded on 19 July 2018 using a hand-held time-domain reflectometry sensor (FieldScout TDR 300; Spectrum Technologies, Plainfield, IL, USA). Three measurements per plot were averaged in further analyses. Soil temperature (–7.5 cm depth) was recorded every 4 h from 19 July until 10 August 2018 with miniature temperature sensors (ThermoChron iButtons, San Jose, CA, USA) at 36 plots along the reference gradient and 31 along the nutrient gradient. At each site, temperature loggers were installed in at least four plots. To measure soil nutrients and isotopes, 5 cm deep soil cores (5.7 cm diameter) were taken at the end of July to early August 2022. Three soil samples were taken at each site, but only two were taken at the middle site at the nutrient gradient ($n = 35$). Soil samples were dried at 60°C. Stones and roots were sieved out (2 mm) and samples homogenized. Carbon and nitrogen content were analysed using dry combustion at the CLIPT-lab at the University of Oslo (Matejovic, 1997). Soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios (‰) were analysed using a Flash 1110 Element Analyzer with a no-blank autosampler connected to a Delta V plus isotope Ratio Mass spectrometer (Thermo Fischer Scientific) at the FARLAB at the University of Bergen.

2.3 | Estimating community species composition

The species composition of vascular plant communities was surveyed for each plot in July 2018 as described by Vandvik et al. (2023). In short, we visually estimated the cover of each plant species with >1% cover to the nearest 1% for each plot. Species identification followed the SvalbardFlora (Elven et al., 2020). Taxon names were standardized using the TNRS R package v0.3.6 (Maitner & Boyle, 2021) based on the Taxonomic Name Resolution Service (Boyle et al., 2013), Tropicos (Missouri Botanical Garden, 2012), The Plant List (TPL., 2013) and USDA (USDA NRCS, 2015) databases.

2.4 | Trait measurements for vascular plants

Plant material was collected and analysed as described by Vandvik et al. (2023). In brief, plant functional traits were measured for three whole individuals or ramets of each plant species covering more than 1% in each plot. Plant samples were collected adjacent to the plots to avoid destructive sampling. For clonal plants, physically separated individuals were sampled. After collection, plants were stored in ziplock bags with moist paper towels in the dark at +6°C and were processed within 4 days. From each plant, we sampled at least three intact and fully developed leaves. Sampled leaves included petioles and stipules but excluded sheaths for graminoids. For *Equisetum*

species, where the stem is the main photosynthetic organ, the top 8 cm section of stem, including any side branches, was used for trait analyses.

We selected 13 functional traits related to plant size, leaf economic spectrum and nutrient cycling across trophic levels (Díaz et al., 2016). The size traits were as follows: plant height, dry leaf mass, leaf area and leaf thickness. The leaf economic traits were: LDMC, SLA, leaf C, N and P content, and C:N and N:P ratios. The nutrient cycling traits were: leaf $\delta^{15}\text{N}\%$ and $\delta^{13}\text{C}\%$. Chemical analyses were performed at the University of Arizona (Vandvik et al., 2023). In total, 9262 trait measurements were performed (reference: 5737, nutrient: 3525) on a total of 1074 leaf samples (708, 366). Because it was not possible to conduct nutrient and isotope analyses for all samples due to insufficient biomass, 454 (240, 214) leaf samples were analysed, for a total of 2980 chemical measurements.

2.5 | Data analyses and statistics

All analyses were performed in R v4.2.2 (R Core Team, 2022). To test whether soil microclimate, nutrients or isotopes differed between the nutrient and reference gradient or changed with elevation, we ran separate mixed-effects models for each soil parameter. Models included nutrient input (N) as a factor differentiating the two gradients and elevation (E) as a continuous variable to account for changes with elevation and distance to the seabird colony, and their interaction (Nx E). Elevation was included as a quadratic term, as this improved the model fit (lower AIC). Site was included as a random effect to account for the study design. We performed a likelihood-ratio test for each model, testing the effect of marine-derived nutrients, elevation and their interaction. For each soil parameter, we compared models by sequential removal of fixed effects terms using the *anova* function.

To calculate community-weighted means for each plant trait, we used a bootstrapping approach using the *traitstrap* package (v0.1.0; Maitner et al., 2023; Telford et al., 2021), with hierarchical trait imputation to fill missing datapoints (Figure S1). To produce a trait distribution (Enquist et al., 2015; Wiczyński et al., 2019) per trait and plot, the data were resampled 100 times, and the resulting distribution means were averaged to determine the overall community-weighted trait mean per plot. Trait values for size traits, such as plant height, shoot length, leaf area, dry mass and leaf thickness were log-transformed before analyses (Kerkhoff & Enquist, 2009).

To test the effect of elevation and seabird influence on community-weighted plant traits, we ran mixed-effects models for each community-weighted plant trait using the same modelling approach described for the soil parameters above. As the model with the quadratic elevation term produced a singular fit for SLA, we used a linear elevation term in the model. To test the effect of soil moisture and temperature on community-weighted traits, we ran the same model with soil temperature and soil moisture as explanatory variables (soil nutrients were not included as these were not available at the plot level). Quadratic terms produced the best model

fit for both explanatory variables. As soil temperature or soil moisture explained significant variation in only 3 and 5 out of 13 traits, respectively, we used elevation as a predictor in further analyses (Figure S2). To test how seabird influence trait responses to marine-derived nutrients, we ran the model with soil $\delta^{15}\text{N}\%$ as a predictor.

To quantify the effect of marine-derived nutrients and elevation on the multivariate taxonomic and functional composition of vascular plant communities, we performed principal component analysis (PCA) using the *rda* function in the *vegan* package (v2.6.4) (Oksanen et al., 2020). For plant functional composition, we used scaled and centred community-weighted trait means but excluded C:N and N:P due to collinearity. To visualize taxonomic and functional composition across elevations, we plotted centroids for each elevation and connected the centroids. We plotted 95% confidence intervals based on a t-distribution as ellipses for each gradient using the *stat_ellipse* function in *ggplot2* (Wickham, 2016). To test the effect of nutrient input and elevation and their interaction in the PCA, we used permutation tests with pseudo-*F* ratios and the *adonis2* function from the R package *vegan* with 999 permutations and Euclidean distances. Finally, we plotted soil temperature, moisture and isotopes, and the loadings of each species or trait as a vector.

To calculate the relative contribution of intraspecific trait variation versus species turnover to total plant trait variation in response to marine-derived nutrients, we calculated a *fixed* (species turnover effects) and *specific* (intraspecific and turnover effects) value for each trait and plot across both gradients (Lepš et al., 2011). To calculate the *fixed mean*, we first calculated the average trait value for each species from all observations (i.e. one value per species, based on the trait data from both gradients). We then used these species' means to calculate community-weighted trait values for each plot. The *specific mean* was calculated using trait values for species within each plot using bootstrapping described above. The difference between the fixed and specific mean trait value thus quantifies the contribution of intraspecific variation. To quantify the contribution of intraspecific variation and species turnover to the variation in community-weighted trait values at the nutrient and reference gradient separately, we decomposed the Sum of Squares from ANOVAs (Lepš et al., 2011). Three separate ANOVAs per gradient were performed: fixed, specific and the difference between fixed and specific trait variation. Then, we calculated the proportions of variability for intraspecific variation and species turnover by dividing their Sum of Squares by the total Sum of Squares for total variation. The average contribution of intraspecific variation and species turnover was calculated for each plant size trait, leaf economic trait and isotope signatures.

2.6 | Permissions

The research project is registered within the Research in Svalbard portal (RiS-10935) (Svalbard Science Forum, 2025). Sampling of leaves and soil was allowed by the Governor of Svalbard under the Svalbard Environmental Protection Act, section 29.

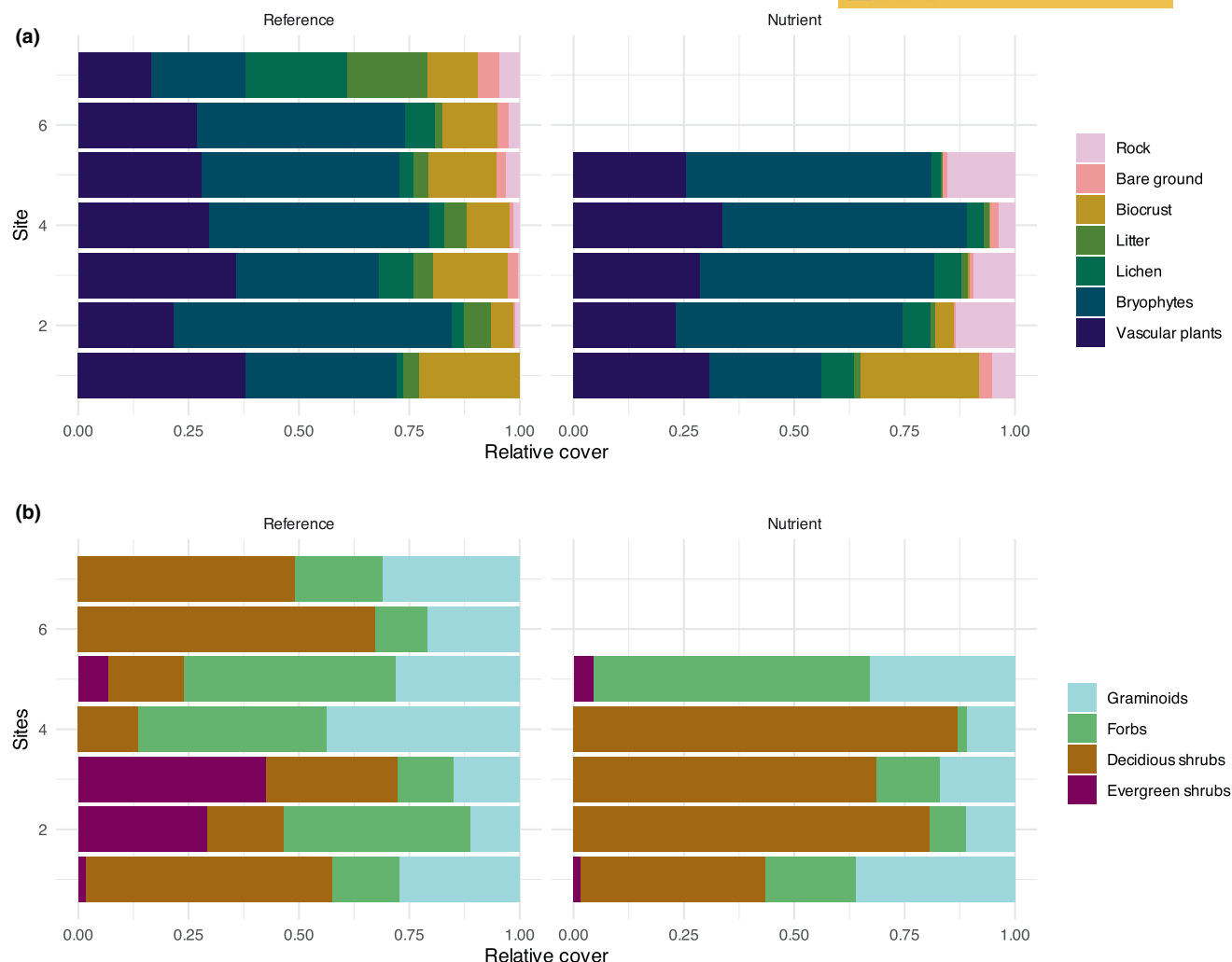


FIGURE 2 Average relative cover of different vegetation components (a) and average relative cover of vascular plant growth forms (b) across the reference and nutrient gradient. Site refers to the different elevations, where 1 is the lowest elevation and 7 is the highest.

3 | RESULTS

3.1 | Vegetation communities and plant growth forms

Both gradients supported continuous and relatively dense vegetation, dominated by bryophytes and vascular plants (Figure 2). Lichens were most common at the highest elevation at the reference gradient. Biocrust was more common at the reference gradient, except for the lowest elevation at the nutrient gradient (Figure 2). Average cover of bryophytes was 1.5 times higher at the nutrient compared with the reference gradient ($70.5 \pm 4.6\%$ vs. $47.8 \pm 2.3\%$, respectively). Vascular plant cover was similar between the gradients ($41.7 \pm 2.4\%$ and $32.4 \pm 2.2\%$, respectively). Forbs, graminoids and deciduous shrubs generally dominated, while evergreen shrubs were only abundant at low-to-intermediate elevations at the reference gradient. At the highest elevation at the nutrient gradient, vascular plant communities were dominated by forbs and graminoids (Figure 2). In total, 31 plant species were registered, 18 of which were found at the nutrient gradient and 28 at the reference gradient

(Table S2). Plant species richness per plot was lower at the nutrient gradient than at the reference gradient (6.5 ± 0.1 vs. 9.6 ± 0.1).

3.2 | Soil microclimate and nutrients

Mean soil temperature differed by almost 2°C between the nutrient and reference gradient (mean $\pm$ standard error: $6.5 \pm 0.2^\circ\text{C}$ vs. $8.4 \pm 0.2^\circ\text{C}$, respectively), with the lowest values at mid elevations and the highest at low and high elevations at both gradients (Table S3, Figure S3). Soil moisture was $21.8 \pm 2.2\%$ at the nutrient and $24.7 \pm 1.1\%$ at the reference gradient, decreasing with elevation across both gradients, but more strongly along the nutrient gradient (Table S3, Figure S3). Total soil carbon ($11.6 \pm 2.2\%$ vs. $6.2 \pm 0.8\%$) and nitrogen content ($0.5 \pm 0.07\%$ vs. $0.2 \pm 0.02\%$) were higher at the nutrient than at the reference gradient. Soil nitrogen content increased with elevation across the nutrient gradient and decreased with elevation at the reference gradient (Table S3, Figure S3). Soil $\delta^{13}\text{C}$ was enriched at the reference gradient ($-26.5 \pm 0.2\text{‰}$) compared with the nutrient gradient ($-27.8 \pm 0.1\text{‰}$), while soil $\delta^{15}\text{N}$ was

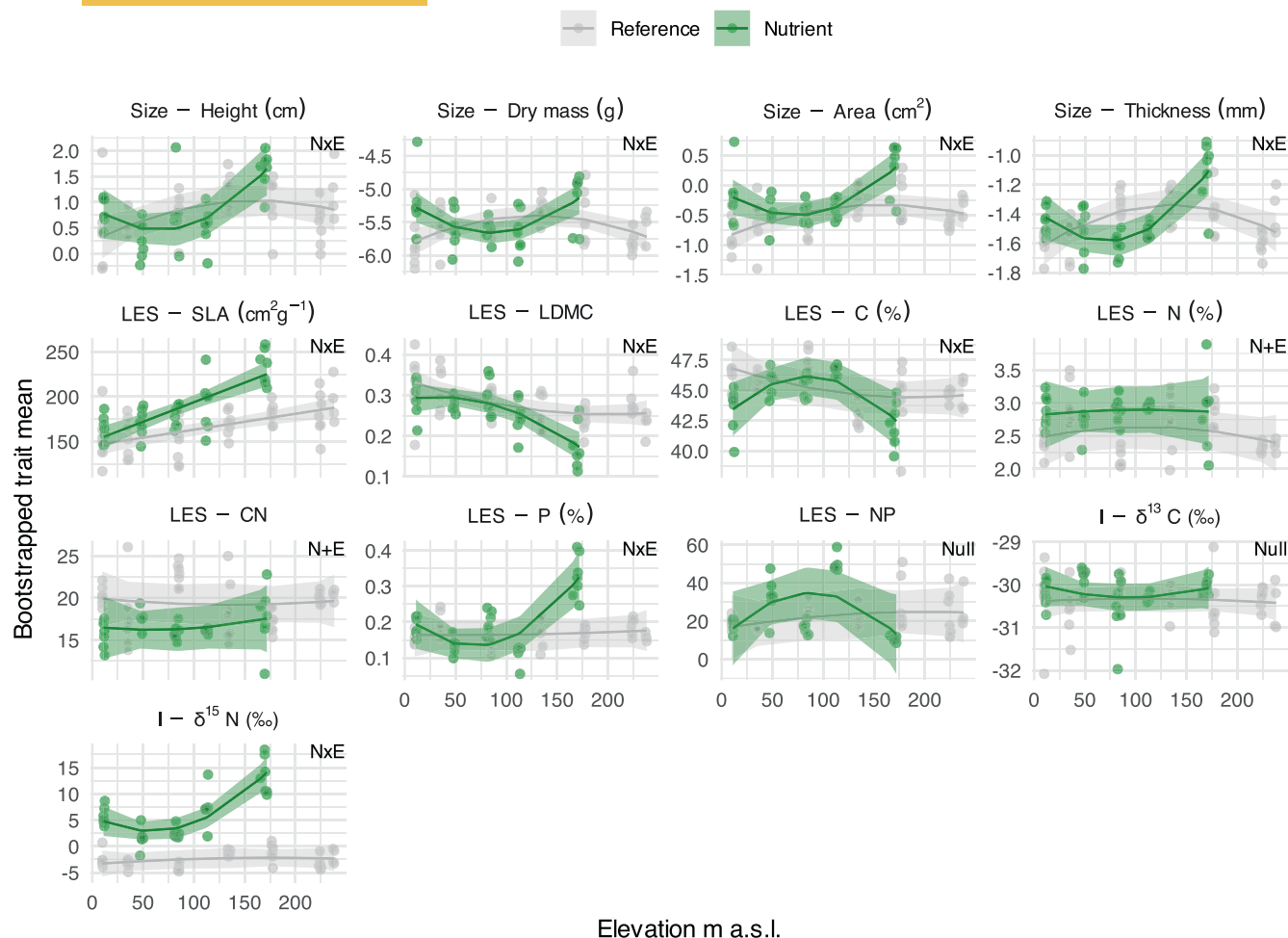


FIGURE 3 Bootstrapped community-weighted plant traits across the nutrient gradient (green) and reference gradient (grey). At the nutrient gradient, proximity to seabirds increases with elevation. Traits measured relate to plant size ('Size'), the leaf economic spectrum ('LES') and isotopes related to nutrient cycling ('I'). Shaded areas denote 95% CIs. Letters in upper-right corners denote significant trait differences between gradients ('N'), across elevation ('E'), between gradients and with elevation ('N+E'), or their interaction ('N×E'). Points denote observations, lines represent model predictions. Mean trait values for both gradients can be found in [Table S5](#).

enriched at the nutrient gradient ($6.1 \pm 0.8\text{‰}$ vs. $1.3 \pm 0.2\text{‰}$) and increased across the nutrient gradient ([Table S3](#), [Figure S3](#)).

3.3 | Vascular plant community-weighted mean traits

Community-level size traits (plant height, dry leaf mass, leaf area and leaf thickness) showed contrasting responses to elevation between the gradients. At the nutrient gradient, trait values increased with elevation (but with a convex relationship). At the reference gradient, trait values showed humpbacked relationships, with the highest trait values at middle elevations ([Table S4](#), [Figure 3](#)). Leaf economic traits showed more diverse responses ([Table S4](#), [Figure 3](#)). Specifically, SLA and P% increased, and LDMC decreased with elevation across the nutrient gradient, while the responses were weaker or absent across the reference gradient. Leaf C% peaked at mid-elevation at the nutrient gradient but decreased with elevation at the reference gradient. Leaf N% and C:N ratio showed a minor and similar response

across elevation at both gradients, but leaf N% was generally higher and C:N ratio lower at the nutrient gradient. Leaf N:P ratio showed no significant responses to elevation or seabird presence (models with nutrients or elevation as explanatory variables did not explain more than the null model). Leaf $\delta^{15}\text{N}\text{‰}$ was enriched at the nutrient gradient and increased sharply with elevation but did not change across the reference gradient. Leaf $\delta^{13}\text{C}\text{‰}$ showed no significant response to elevation. For an overview of average community-weighted mean traits, see [Table S5](#).

For all traits except plant height, leaf P% and leaf N:P, using soil $\delta^{15}\text{N}\text{‰}$ as a predictor produced models with higher conditional R^2 -values than models using elevation ([Tables S4](#) and [S6](#)). Eight community-weighted mean leaf traits showed a significant response towards values associated with larger leaf size and more resource-acquisitive strategies with increasing soil $\delta^{15}\text{N}\text{‰}$ ([Figure 4](#), [Table S6](#)). Leaf area and leaf thickness increased, and SLA and LDMC shifted towards more resource-acquisitive values with enriched soil $\delta^{15}\text{N}\text{‰}$. Leaf P% correlated positively with soil $\delta^{15}\text{N}\text{‰}$, while N:P showed contrasting responses at the two gradients and had relatively low

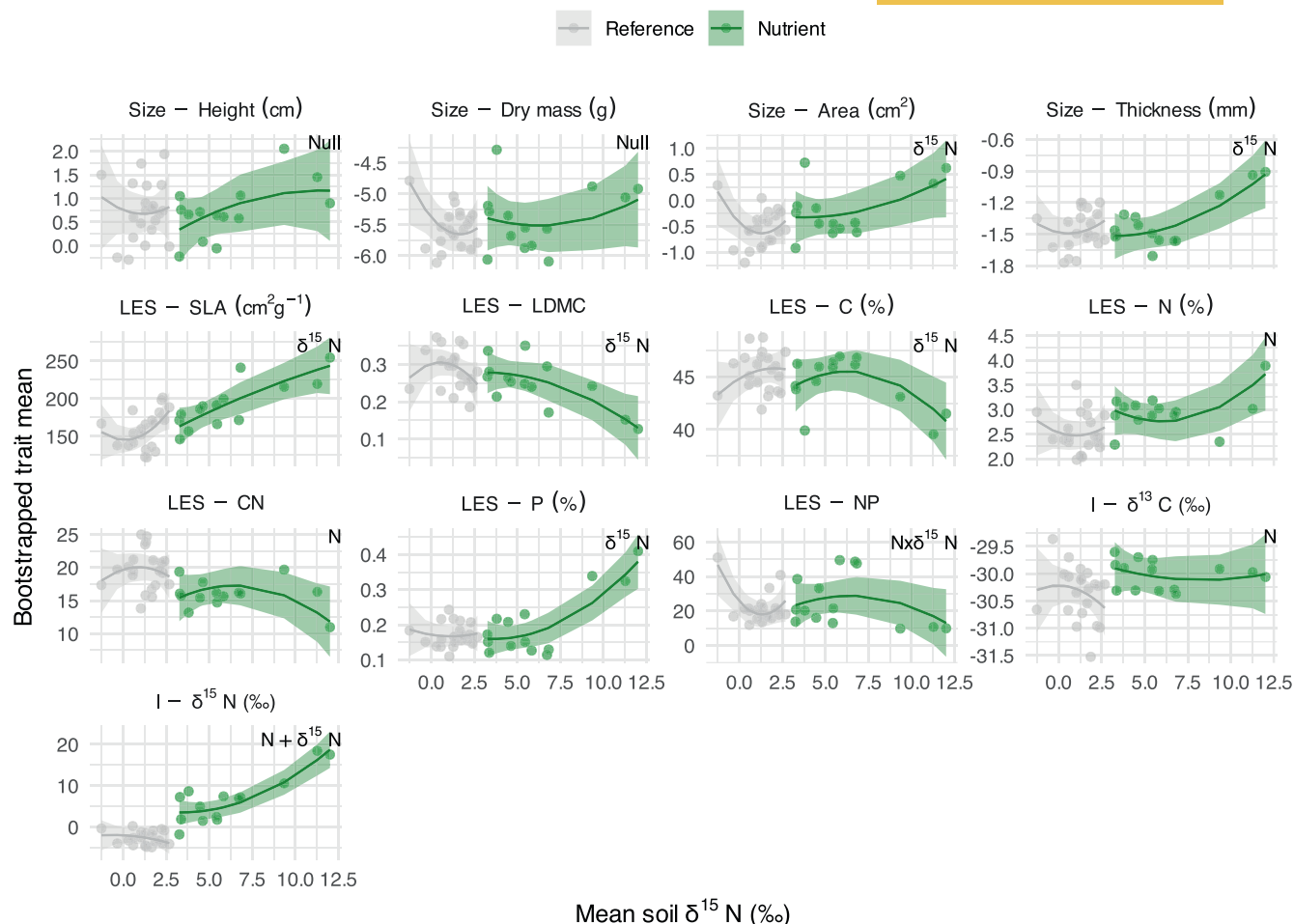


FIGURE 4 Bootstrapped community-weighted plant traits versus soil $\delta^{15}\text{N}\%$ signatures at the nutrient gradient (green) and reference gradient (grey). Traits measured relate to plant size ('Size'), the leaf economic spectrum ('LES') and isotopes related to nutrient cycling ('I'). Shaded areas denote 95% CIs. Letters in upper-right corners denote significant trait differences between gradients ('N'), with $\delta^{15}\text{N}\%$ (' $\delta^{15}\text{N}$ '), between gradients and with $\delta^{15}\text{N}\%$ ('N+ $\delta^{15}\text{N}$ ') or their interaction ('N $\times\delta^{15}\text{N}$ '). Points denote observations, lines represent model predictions.

values at sites with the most enriched soil $\delta^{15}\text{N}\%$ values. Leaf C% showed a concave response with resource-conservative values at intermediate soil $\delta^{15}\text{N}\%$ values. N% was higher and C:N lower at the nutrient gradient, but these traits showed no significant response to soil $\delta^{15}\text{N}\%$. Similarly, $\delta^{13}\text{C}\%$ signatures were higher at the nutrient gradient but showed no clear responses to soil $\delta^{15}\text{N}\%$. Leaf $\delta^{15}\text{N}\%$ was higher at the nutrient gradient and increased with enriched soil $\delta^{15}\text{N}\%$. Plant height and leaf dry mass showed no significant response to soil $\delta^{15}\text{N}\%$ (Figure 4, Table S6).

3.4 | Vascular plant taxonomic and functional community composition

The taxonomic composition of vascular plant communities differed between gradients and across elevation (i.e. proximity to the bird nests, Table S7). The first PC axis (explaining 35.6% of variation) distinguished the site closest to the seabirds, characterized by a high abundance of *Cerastium arcticum* and *Oxyria digyna*

and low abundance of *Salix polaris*, from lower-elevation sites at the nutrient gradient and all sites at the reference gradient. The second PC axis (13.2%) separated out lower-elevation plots characterized by *Bistorta vivipara* and *Dryas octopetala* at both gradients (Figure S4).

For functional composition, the first two PC axes explained 46% and 14.3% variation, which we considered sufficient to justify focusing primarily on those two axes when interpreting the PCA results (but see Figure S5). Differences in trait composition between sites and gradients were driven by the highest site at the nutrient gradient, related to higher values for size and leaf economic traits (Figure 5a,b, Tables S8 and S9). Size traits (towards the upper right of the diagram) and leaf economic traits (towards the lower right) form near-perpendicular trait axes in ordination space (Figure 5b). Vectors for soil C% and N%, but most strongly soil $\delta^{15}\text{N}\%$, aligned with leaf N% and SLA towards one side of the diagram, suggesting that increases in these soil parameters are associated with resource-acquisitive trait values and nutrient inputs from seabirds. Vectors for soil temperature, moisture, and $\delta^{13}\text{C}\%$ were poorly associated

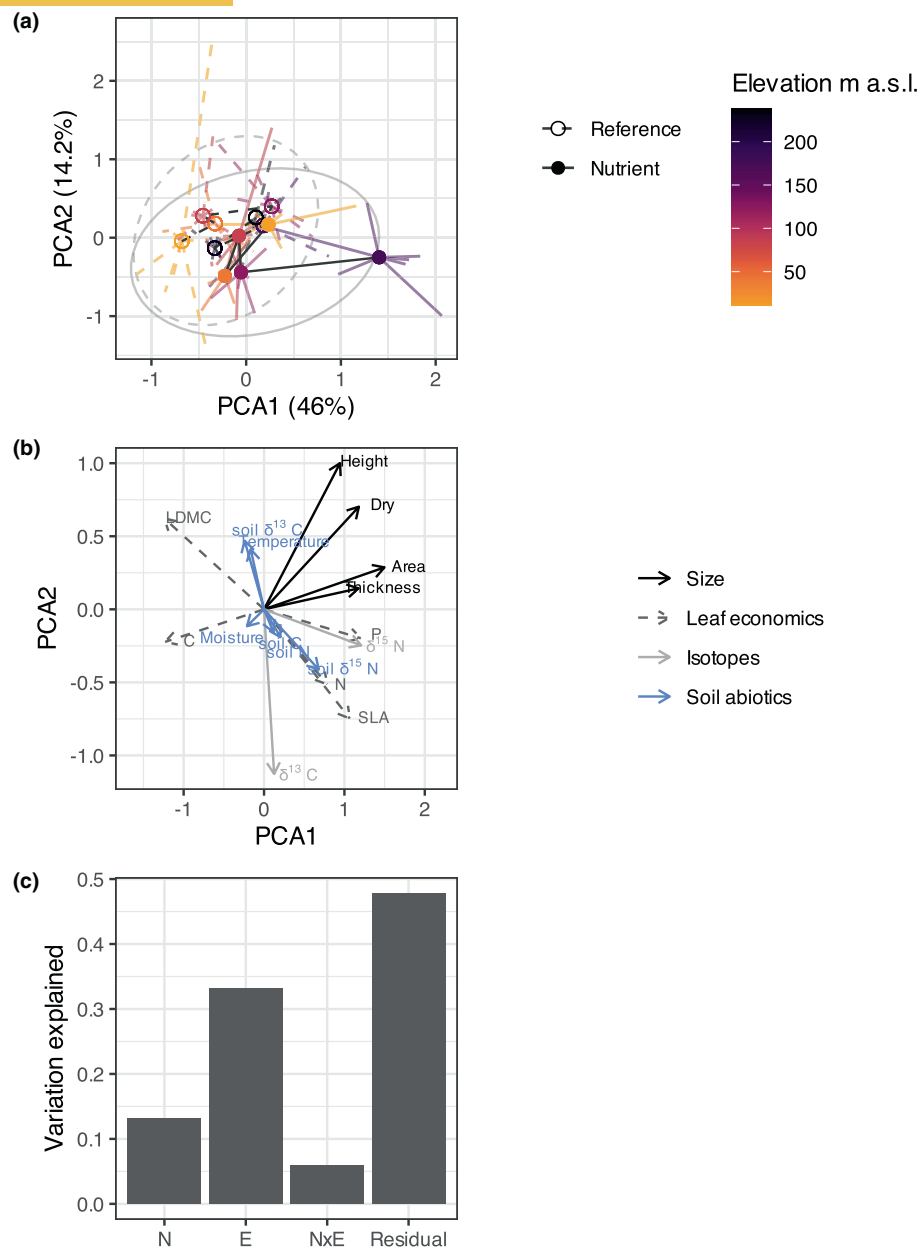


FIGURE 5 Functional composition of plant communities across both gradients based on a joint PCA-analysis (a). Loadings for size traits (in black), leaf economic traits (dashed dark grey), leaf isotope signatures (solid light grey) are plotted as vectors (b). Soil parameters (blue) are projected passively to the plot. Variation explained (R^2) by gradient (N), elevation (E), their interaction and unexplained (residual) variation (c).

with trait axes (Figure 5b). The permutational multivariate analysis of variance showed that elevation explained 33.2%, nutrient input 13.1%, and their interaction 0.6% of variation. 47.8% of variation was unexplained.

3.5 | Contributions of intraspecific variation and species turnover to plant functional trait variation

The relative contribution of intraspecific variation to total trait variation differed between gradients and among traits (Table S10). At both gradients, species turnover was the main source of variation

for size traits, accounting for 52.5%–70.3% of observed variation in plant height, leaf dry mass, area and thickness. The contribution of species turnover to size-related traits was consistently higher at the nutrient gradient (Figure 6a,b). Leaf economics and isotopes were mostly driven by intraspecific variation at the nutrient gradient (59.3% and 55.8%), but were driven primarily by species turnover at the reference gradient (54.6% and 67.1%, respectively; Figure 6a). Intraspecific variation varied among the measured leaf economic traits at the nutrient gradient, with a notably strong contribution to variation in N:P ratio, P%, SLA and N%, whereas C%, C:N ratio and LDMC were driven largely by species turnover (Figure 6b). For $\delta^{15}N$ %, the contribution of intraspecific variation was substantially

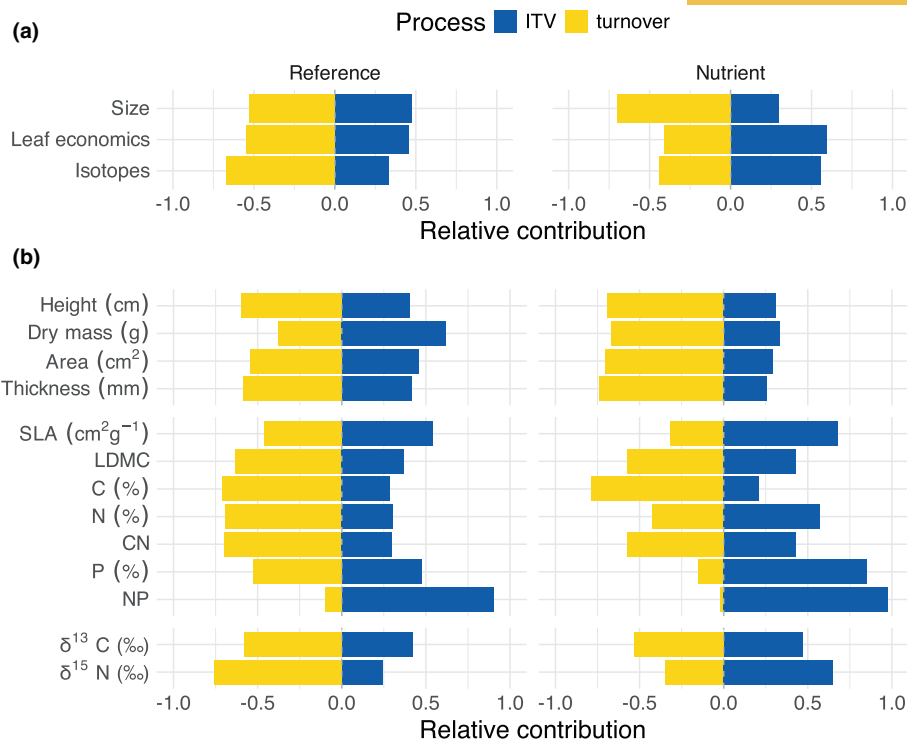


FIGURE 6 Relative contributions of intraspecific trait variation (ITV) and species turnover (visualized as negative values) to total explained trait variation for each gradient, standardized to 1 for traits related to size, leaf economics and isotope signatures (a) and all individual traits (b). Traits in (b) are sorted by the groups in (a). Unstandardized proportions are presented in Table S10.

larger at the nutrient than at the reference gradient, while $\delta^{13}\text{C}\%$ was similar for both gradients (Figure 6b).

4 | DISCUSSION

This study shows that marine-derived nutrients from seabirds modulate the functional composition of vascular plant communities in the High Arctic. Plant community composition varied between and across the nutrient and reference gradient. However, taxonomic turnover was not complete, and species found near the seabirds (e.g. *Oxyria digyna*, which responds positively to seabird influence; Eurola & Hakala, 1977) are also found elsewhere in Svalbard (Elven et al., 2020). Stronger turnover and more unique community composition can be expected at seabird colonies with higher population densities or in wetter conditions than studied here (Eurola & Hakala, 1977). Piscivorous rather than zooplanktivorous seabirds may further increase availability of soil nutrients, such as phosphorus (Zwolicki et al., 2013), and impact plant community composition more strongly.

Marine-derived nutrient subsidies, represented by enriched soil $\delta^{15}\text{N}\%$ signatures, associated with more resource-acquisitive trait values (e.g. larger and thicker leaves, higher SLA and lower LDMC) and plant communities closest to seabirds featured distinct functional compositions. In addition, soil $\delta^{15}\text{N}\%$ signature was a better predictor of community-weighted mean traits across the gradients than elevation or soil microclimate. Trait variation

across both gradients was oriented along two perpendicular axes, one related to plant size and the other to leaf economics. Both axes correlated poorly with soil microclimate, but leaf economics traits (most notably leaf N% and SLA) were positively associated with soil $\delta^{15}\text{N}\%$ signatures, suggesting they relate to seabird influence. More resource-acquisitive trait values near seabirds correspond to earlier studies reporting that increased nutrient availability supports more acquisitive trait values at the species (Poorter & De Jong, 1999) and community level (Jager et al., 2015; Mason et al., 2012). Enriched leaf $\delta^{15}\text{N}\%$ signatures were also found for *Oxyria digyna* growing under a seabird cliff in a nearby location in Svalbard (Zmudczyńska-Skarbek et al., 2015) and in vegetation on islands in the Bering sea (Wainright et al., 1998). Leaf $\delta^{13}\text{C}\%$ isotopes were typical for C3 plants (Choy et al., 2010; Hawke & Newman, 2007) and did not respond to marine-derived nutrients, indicating that water-use efficiency was not affected.

Soil microclimate and nutrients varied significantly between and across the gradients but poorly explained patterns in trait variation. Elevation was a better explanatory factor for plant community traits than soil temperature or moisture, which implies that a diverse complex gradient of biotic and abiotic conditions, including the influence of seabirds, drives the observed variation in plant traits across elevation. We discuss some of these dynamics below.

Bryophytes are important components of Arctic vegetation (Lindo & Gonzalez, 2010; Mateo et al., 2016; Turetsky et al., 2012). Depth and density of the bryophyte layer affect vascular plants through soil microclimate (Gornall et al., 2011). At the nutrient

gradient, bryophyte cover was higher than at the reference gradient. We hypothesize that such extensive bryophyte cover could have contributed to the lower soil temperatures observed at the nutrient gradient, keeping soils cooler and potentially reducing active layer depth (Porada et al., 2016; Schuur et al., 2024). Future studies on the effects of seabird declines should also include functional and taxonomic assessments of primary producers other than vascular plants as they constitute an important component of Arctic vegetation and impact soil microclimate and ecosystem processes (Gornall et al., 2011; Jaroszynska et al., 2023; Roos et al., 2021; Salazar et al., 2024; Van Zuijlen et al., 2020).

In absence of seabirds, the reference gradient can be regarded as a classic elevational gradient, where theory predicts a decrease in temperature with elevation and a subsequent shift towards resource conservative strategies (Sundqvist et al., 2013). However, we found that soil temperature peaked at intermediate elevations, that soil temperature and moisture were poor predictors of plant traits, and that some traits (e.g. SLA) had more resource-acquisitive values at high elevation. Such counter-intuitive responses to elevation and temperature are also found in studies from alpine systems (Lynn et al., 2023; Roos et al., 2019) and suggest that leaf economic traits do not respond linearly to elevation or growing season temperatures, in contrast to traits related to plant size (Bjorkman et al., 2018; Lynn et al., 2023; Rissanen et al., 2023). We hypothesize that microtopography determines the microclimate Arctic plants experience (Kemppinen et al., 2021; Opedal et al., 2015), and that air and soil temperatures therefore may not reflect actual leaf temperatures, which ultimately drive photosynthetic rates (Michaletz et al., 2015).

Steep slopes and dark rocks may create favourable growing conditions during periods of low sun angle in High Arctic spring and summer (Eidesen et al., 2018). In addition, rocks can shelter plants from the wind in otherwise open landscapes, allowing higher leaf temperatures and photosynthetic activity than expected from ambient air temperature. Near rocks, snow may accumulate and increase snow depth, which is known to be a major driver of Arctic and alpine plant community composition (Kemppinen et al., 2021; Niittynen et al., 2020). Sheltered microclimatic conditions can also promote a more favourable onset of snowmelt and thereby a longer growing season, which may support plants with resource-acquisitive trait strategies.

Intraspecific variation in the sampled plant communities was relatively high compared with global values (Siefert et al., 2015), yet comparable to other studies in Svalbard (Jónsdóttir et al., 2022). Similar to earlier studies, the contribution of intraspecific variation differed among traits, and was largest for traits associated with nutrient status, such as leaf N% and N:P (Henn et al., 2018; Roos et al., 2019; Thomas et al., 2020). In addition, intraspecific variation was more important at the nutrient gradient compared with the reference gradient for leaf economic traits and $\delta^{15}\text{N}\%$, whereas intraspecific variation was most important for size traits at the reference gradient. One explanation is that seabird droppings contribute to more heterogeneous availability of nutrients

(both spatial and temporal), which is reflected by higher intraspecific variation in traits related to nutrient acquisition and usage. This suggests that plant communities respond through plasticity of the existing species rather than through species turnover. These findings contribute to a growing understanding that intraspecific trait variation is an important mechanism for alpine and Arctic plant community responses to ongoing environmental changes (Bjorkman et al., 2018; Jónsdóttir et al., 2022), contributing to their resilience. This is particularly relevant for the geographically isolated and species-poor Svalbard flora (Elven et al., 2020). Significant changes in taxonomic and functional composition may be expected when new species are introduced to Svalbard and manage to colonize the archipelago under ameliorated climatic conditions (Artsdatabanken, 2023).

Seabird populations are in global decline (Palczyński et al., 2015) and subsequent reductions in nutrient subsidies cannot be seen separately from other drivers of environmental change currently impacting Arctic ecosystems (Box et al., 2019). Permafrost thaw affects nutrient availability in Arctic soils, leading to increased leaf nutrient content and plant biomass (Jasinski et al., 2022; Keuper et al., 2012; Salmon et al., 2016). In contrast to fertilization by seabirds, permafrost thaw concurs with wetter soil conditions, promoting significant shifts in plant community compositions (Errington et al., 2024). Experimental studies demonstrate that warming amplifies the effect of increased nutrient availability on Arctic and alpine plant communities (DeMarco et al., 2014; Klanderud & Totland, 2005; Scharn et al., 2022). In the experiments, released nutrient limitation supports taller and faster-growing plant species at the expense of species with more resource-conservative trait strategies. Climate warming may thus counteract the effects of reduced marine-derived nutrient inputs from seabirds, but we note that these processes occur on different spatial and temporal scales. More studies are needed to understand the spatiotemporal variation in the impacts of marine-derived nutrients from seabirds on plant communities, in the Arctic and across broader geographic contexts, and how these interact with other aspects of global environmental change.

AUTHOR CONTRIBUTIONS

Aud H. Halbritter, Pernille Bronken Eidesen, Brian J. Enquist, Ingibjörg S. Jónsdóttir, Jonathan J. Henn, Julia Kemppinen, Pekka Niittynen, Ruben E. Roos and Vigdis Vandvik conceived the ideas and designed the methodology. Inge Althuizen, Polly Bass, Matiss Castorena, Pernille Bronken Eidesen, Brian J. Enquist, Geir Wing Gabrielsen, Aud H. Halbritter, Siri Vatsø Haugum, Jonathan J. Henn, Ingibjörg S. Jónsdóttir, Julia Kemppinen, Kari Klanderud, Simone I. Lang, Kai Lepley, Yaoqi Li, Mary C. Linabury, Marc Macias-Fauria, Brian S. Maitner, Yadvinder Malhi, Sean T. Michaletz, Barbara M. Neto-Bradley, Molly Ng, Pekka Niittynen, Karolína Pánková, Ruben E. Roos, Marcus P. Spiegel, Richard J. Telford, Eleanor R. Thomson, Vigdis Vandvik and Lucely L. Vilca-Bustamante collected the data. Aud H. Halbritter curated and analysed the data. Aud H. Halbritter, Julia Kemppinen, Pekka

Niittynen, Ruben E. Roos and Vigdis Vandvik led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the OSF repository: <https://doi.org/10.17605/OSF.IO/SMBQH> (Halbritter et al., 2025). Code for data curation and analyses is archived on <https://doi.org/10.5281/zenodo.15187982> (Halbritter, 2025).

STATEMENT ON INCLUSION

Our study brings together authors from many different countries, including scientists based in the country where the study was carried out. The author group consists of both early-career and senior researchers. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Replication statement for the study.

Table S2. Full plant species list for the nutrient and reference gradient.

Table S3. Model statistics for the best model after model selection for soil temperature, moisture, total carbon and nitrogen content, $\delta^{13}\text{C}\text{‰}$, and $\delta^{15}\text{N}\text{‰}$ in response to marine-derived nutrients from seabirds and elevation.

Table S4. Model statistics for plant community-weighted trait means.

Table S5. Community weighted mean and variance for each plant trait for the nutrient and reference gradient.

Table S6. Model statistics for plant community-weighted trait means versus soil $\delta^{15}\text{N}\text{‰}$.

Table S7. Results of permutation test of the PCA of plant community composition.

Table S8. Results of permutation test of the PCA of plant functional composition.

Table S9. PCA loadings for the first four PC-axes for each plant trait.

Table S10. Decomposition of the sum of squares for the total variation explained and the proportions for variation explained by species turnover, intraspecific variation, and their covariation.

Figure S1. Proportions of the data source levels traits imputed before bootstrapping.

Figure S2. Bootstrapped community weighted trait means across soil temperature and volumetric soil moisture content at the nutrient and reference gradient.

Figure S3. Soil temperature, soil moisture, total soil carbon and nitrogen content, $\delta^{13}\text{C}\text{‰}$, and $\delta^{15}\text{N}\text{‰}$ along elevation for the nutrient and reference gradient.

Figure S4. PCA of taxonomic plant community composition for the nutrient and reference gradient.

Figure S5. PCA of functional plant community composition (PCA3 vs. PCA4) for the nutrient and reference gradient.

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