RESEARCH ARTICLE

Forage quality in tundra grasslands under herbivory: Silicon-based defences, nutrients and their ratios in grasses

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Handling Editor: Kyle Tomlinson

Abstract

1. Herbivore-induced changes in both leaf silicon-based defence and nutrient levels are potential mechanisms through which grazers alter the quality of their own grass supply. In tundra grasslands, herbivores have been shown to increase nutrient contents of grasses; yet, it is an open question whether they also increase grass silicon-based defence levels. Here, we asked if, and to what extent, herbivores affect silicon content and silicon:nutrient ratios of grasses found in tundra grasslands.

2. We performed an herbivore-interaction field-experiment spanning four tundra-grassland sites. At each site, we established reindeer-open and reindeer-exclusion plots in tundra-patches that had been disturbed or not by small rodents during the previous winter, for a total of 96 plots. We randomly collected over 1,150 leaf samples of inherently silicon-rich and silicon-poor grass species throughout a growing season and analysed silicon, nitrogen and phosphorus contents of each leaf.

3. Small-rodent winter disturbance did not affect grass silicon content, but increased grass quality (i.e. lowered silicon:nutrient ratios) by enhancing nutrient levels of both silicon-rich (+20%–22%) and silicon-poor (+26%–34%) grasses. Reindeer summer herbivory increased the quality of silicon-rich grasses by decreasing their silicon content (–7%). However, the two herbivores together offset both these quality increments in silicon-rich grasses, thus reducing their quality towards the level of those found in the absence of herbivores and further enhancing their silicon:nutrient ratios (+13%–22%) relative to silicon-poor grasses.

4. *Synthesis*. We provide the first community-level, field-based assessment of how herbivory-driven changes in both leaf silicon-based defence and nutrient levels alter grass-forage quality in tundra grasslands. Herbivores did not promote a net silicon accumulation in grasses, but rather enhanced their overall quality. Yet, the magnitude of these quality increments varied depending on the herbivore(s)

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involved and differed between silicon-rich and silicon-poor grasses. Such differential herbivory-induced changes in grass quality between and within tundra-patches may mediate plant–herbivore interactions by altering herbivore forage patterns and food choices. In tundra-patches utilised by both herbivores, the quality of silicon-rich grasses was further decreased relative to that of silicon-poor grasses. This could provide an advantage against herbivory, potentially being one of the pathways through which tundra-grassland vegetation states dominated by silicon-rich grasses are maintained by herbivores.

1 | INTRODUCTION

Grasslands, including managed rangelands and pastures, cover approximately 40% of the Earth's land surface (Gibson, 2009) and have long been recognised as important hotspots for plant–herbivore interactions (Bardgett & Wardle, 2003). Grasses (Poaceae), which dominate grassland ecosystems worldwide, can employ silicon (Si) to avoid herbivory (Vicari & Bazely, 1993). Si, taken up in its soluble form (silicic acid) from the soil and deposited as sharp bodies of amorphous silica (phytoliths) in the leaf epidermis or in hairs and trichomes on the leaf surface (Hartley et al., 2015; Ma & Yamaji, 2006), increases the abrasiveness of grasses (Calandra et al., 2016; Massey et al., 2007a), thus acting as a feeding deterrent against herbivores (Cotterill et al., 2007). Moreover, high Si-content reduces both palatability and digestibility of grass leaves, thereby influencing herbivore feeding preferences for different grass species (Massey et al., 2006, 2007a, 2009) and decreasing herbivore fitness and performance (Abaturov & Dzapova, 2015; Massey & Hartley, 2009; Massey et al., 2008). Massey and Hartley (2006) found that experimentally enriched grass Si-content reduced the amount of nitrogen that field voles *Microtus agrestis* could absorb from foliage, leading to a decline in the growth rate of both juveniles and mature females. These findings indicate that changes in Si-content relative to levels of essential nutrients in forage grasses are likely to be critical for herbivores utilising grassland ecosystems. This could be particularly relevant in high-latitude regions, such as the tundra, where herbivores have a short time-window to access plants and hence any changes in plant quality may have large consequences for their fitness (Beard et al., 2019; Doiron et al., 2015; White, 1983). We have recently shown that, within a single summer, mammalian herbivores enhance plant nutrient dynamics in tundra grasslands (Petit Bon, Inga, et al., 2020). Here, we ask to what extent herbivores modify the quality of tundra grasses by altering their Si-content in relation to their nitrogen (N) and phosphorus (P) levels.

While the functional role of Si as a constitutive anti-herbivore defence in grasses is widely recognised, the circumstances Si uptake is triggered by mammalian herbivores remain unclear. McNaughton and Tarrants (1983) first proposed Si accumulation in grasses as an 'inducible defence' against mammalian herbivores in African Savannah grasslands. Subsequently, a series of greenhouse and field experiments (see review by Hartley & DeGabriel, 2016) have shown that similar patterns also hold in some commonly occurring European grass species (Huitu et al., 2014; Massey et al., 2007b; Reynolds et al., 2012; Ruffino et al., 2018). However, leaf Si-content varies greatly among grasses [usually ~0.1%–5% dry weight (%DW), but up to ~10%; Hodson et al., 2005], suggesting that species with intrinsically high (Si-rich) and low (Si-poor) levels of Si may differ in their use of Si-based defences. As well, grass Si-content has been related to soil Si (Cornelis & Delvaux, 2016; Quigley et al., 2017), nutrient (Minden et al., 2021; Quigley et al., 2020) and water availability (Quigley & Anderson, 2014), and mechanisms of Si uptake, which can be both active (i.e. transporter-mediated) and passive (i.e. transpiration), differ between species (Ma & Yamaji, 2006), likely contributing further to the observed differences in Si utilisation by grasses. Perhaps for these reasons some grass species do not show Si accumulation following herbivory (Kindomihou et al., 2006), whereas others require high frequency and intensity of damage for Si induction (Massey et al., 2007b; Reynolds et al., 2012). Unsurprisingly, many other functions for Si have been identified in addition to protecting plants from herbivory, such as conferring resistance to pathogens and alleviating the impacts of several abiotic pressures, for example, water and temperature stress and nutrient deficiency (Cooke & Leishman, 2011, and references therein).

In cold ecosystems with a short growing season, evidence for Si changes in grasses following herbivory is inconsistent and variations in Si-content have been mainly ascribed to species, genotypes and locations (Soininen et al., 2013). Yet, in tundra-grassland communities, Si levels in grasses (range across seven species: ~0.2%–5.1% DW; Soininen et al., 2013) are comparable to those found in grasses dominating grasslands further south (range across five species: ~0.3%–5.5% DW; Massey et al., 2007a). As well, unpalatable, Si-rich tundra grasses have been shown to be maintained by the grazing activity of

large ungulates (Austrheim et al., 2007; Bråthen & Oksanen, 2001; Ravolainen et al., 2011), while palatable, Si-poor tundra grasses often lose their dominance when the grazing pressure is high (Bråthen et al., 2007; Bråthen & Oksanen, 2001). This suggests that, also in tundra grasslands, grasses might benefit from high Si-content in the presence of herbivores. However, whether tundra grasses also have the ability of increasing foliar Si in response to herbivory is unknown.

Tundra grasslands are habitat to a range of herbivores with different spatial and temporal dynamics. Small rodents, such as voles and lemmings, have major impacts on the functioning of most Arctic ecosystems (Ims & Fuglei, 2005). During peak abundances, which can occur both in summer and winter, small rodents visibly disturb the vegetation (Hambäck et al., 1998; Ims & Fuglei, 2005). Such disturbance also represents a major pathway through which small rodents affect tundra plant-community nutrient levels (Petit Bon, Inga, et al., 2020; Tuomi et al., 2018). In contrast, *Rangifer* (reindeer/caribou) show large-scale spatial dynamics through their migratory behaviour and their impacts by grazing and trampling on vegetation are more likely to be seasonal (Bernes et al., 2015; Tuomi et al., 2021). The extent to which these herbivores, that often co-occur in space, but less often in time (Ims et al., 2007; Ravolainen et al., 2011), concomitantly alter Si-based defence and N and P levels in tundra grasses will ultimately determine changes in the quality of their pastures.

We studied both absolute changes in grass Si-based defence and changes relative to nutrient levels following winter disturbance by small rodents and summer herbivory by reindeer in tundra grasslands. We asked (a) to what extent herbivores modify leaf Si-based defence levels in grasses and (b) to what extent such changes can alter grass quality in terms of leaf Si:N and Si:P ratios throughout a short Arctic summer. A full-factorial field experiment was undertaken within four sub-Arctic/alpine tundra grasslands in northern Norway. We combined quasi- and full-experimental study designs (Shadish et al., 2002), where reindeer summer herbivory was experimentally excluded both within and outside tundra-patches that had been naturally disturbed by small rodents during the previous winter. At seven instances during the growing season, we collected a random selection of leaves from grass species that were previously classified as having either high or low Si-content (i.e. Si-rich and Si-poor grasses; see e.g. Ravolainen et al., 2011). At each instance, we quantified the community-level elemental composition of Si, N and P of both grass groups. We hypothesised that herbivores will have complementary impacts and promote an increase in Si-based defence levels of grasses. Yet, the enhanced grass N- and P-contents (Petit Bon, Inga, et al., 2020) made us expect altered grass quality (Si:N and Si:P ratios) to be dependent on the magnitude of changes in both leaf Si and nutrient levels.

2 | MATERIALS AND METHODS

2.1 | Study area

The study took place in the low alpine zone at 300–400 m a.s.l. at Ifjordfjellet (70°27′N, 27°08′E), Finnmark, Northern Norway (Figure 1a) during summer 2015. The region is generally snow-covered until mid-late June and primarily characterised by dwarf-shrub tundra-heaths (Walker et al., 2005). Rivers descending from the inland towards the coast have created large riparian sediment plains mainly dominated by grasslands interspersed with tall-shrub tundra (Bråthen et al., 2017). Ifjordfjellet is bisected by a fence built in 1950s to separate spring/fall migratory and summer pasture ranges for semi-domesticated reindeer *Rangifer tarandus tarandus* (Hætta et al., 1994). Yet, the two ranges reflect more an historical division than a current one; reindeer faeces counts in permanent plots show that reindeer also utilise migratory ranges in summer, although to a lesser extent than summer ranges (see Figure S1). Our study area encompassed both migratory and summer ranges within the Lágesduotter reindeer herding district, where a density of 4.8 reindeer/km^2 was estimated in summer 2015 (https://landbruksdirektoratet.no).

Due to historical differences in reindeer herbivory pressure, grasslands found on the two sides of the fence differ in their plant-community composition. Forb-rich grasslands characterise the migratory range, while grasses are more dominant in the summer range. The community of grasses also differs between the two ranges. Whereas Si-poor grasses are more common in migratory-range grasslands, Si-rich grasses are more abundant in summer-range grasslands. Overall, grasses accounted for approximately 63% of the total above-ground biomass in the study area (own data, see below).

At Ifjordfjellet, as in most of the Arctic tundra biome, migratory reindeer (caribou in North America) is the main large herbivorous mammal. Moose *Alces alces* is another wild large herbivore occasionally found within the study area. Small rodents (i.e. voles and lemmings) dominate among small herbivores. Tundra vole *Microtus oeconomus* is the most common species within tundra grasslands (Killengreen et al., 2007).

2.2 | Study design

Soon after snowmelt, we selected two grassland sites within each range (Figure 1b). Within each site, 12 pairs of 60 × 60 cm plots were established. Six plot-pairs were located in tundra-patches that showed evident signs of winter disturbance by small rodents (disturbed patches: Ro+), whereas the other six plot-pairs were located in undisturbed tundra-patches (undisturbed patches: Ro−). Within each pair, plots were randomly assigned to be accessible (open-grazed plots: Re+) or excluded (exclusion plots: Re−) to reindeer (Figure 1c). We used cages (70 × 70 cm area × 50 cm height) made of metal net (mesh-size 1.3 × 1.3 cm) to exclude reindeer herbivory in Re− plots throughout the summer. Gaps between the bottom part of the cage and the ground allowed small rodents to have free access into the cages. The number of small rodents within the study area was very low in early summer 2015, but it increased towards the end of the growing season (Figure S1). Small-rodent effects in summer are considered to be generally minimal and equal in all plots.
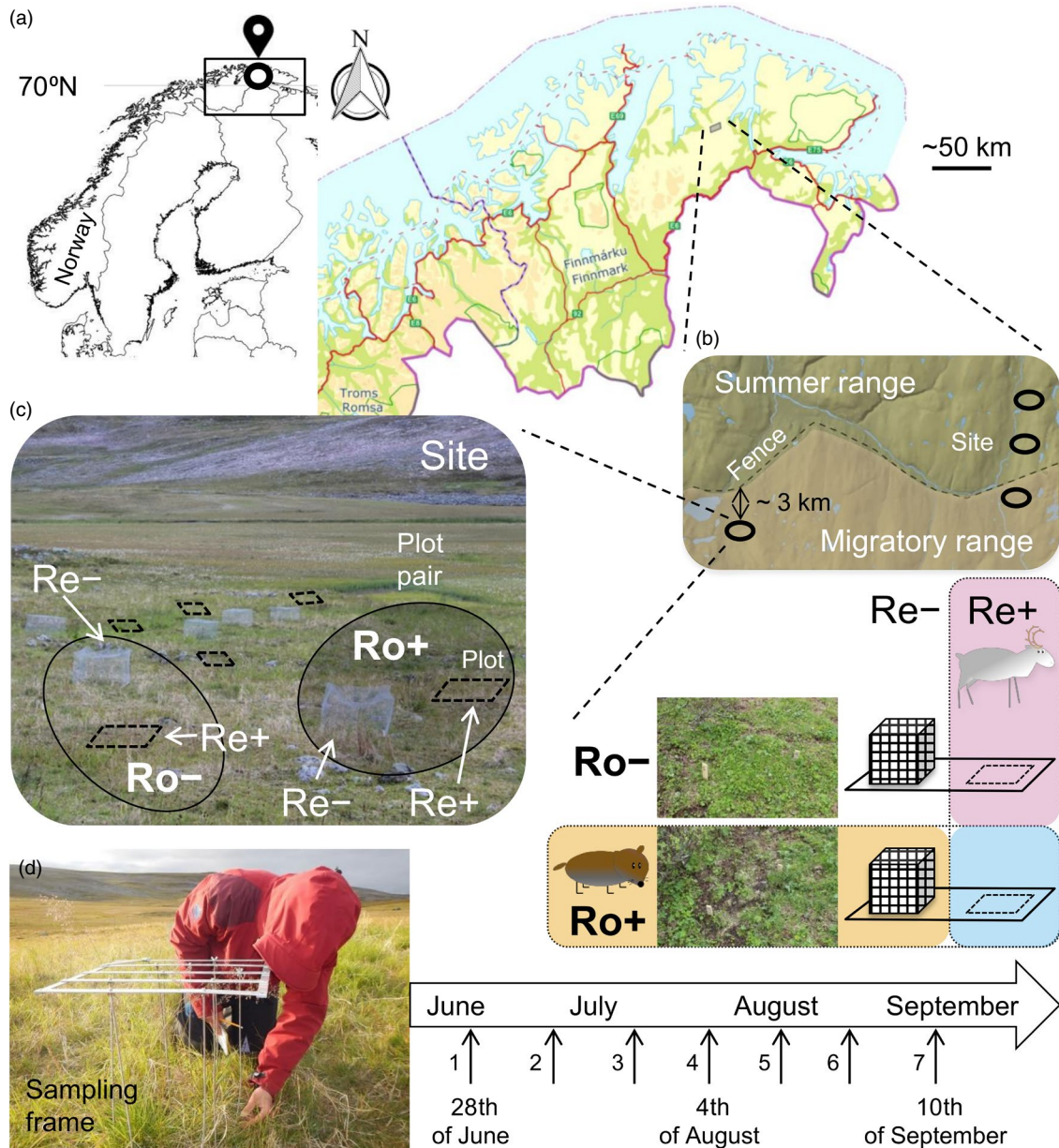
FIGURE 1 Study and sampling design. (a) Study location. (b–c) Hierarchical spatial structure of the study design. A full-factorial semi-randomised pair design was implemented in four tundra-grassland sites in which small-rodent winter disturbance and reindeer summer herbivory were used as quasi- and full-experimental factors, respectively (Shadish et al., 2002). In total, 96 plots were established (across grasslands, each herbivore-treatment combination was replicated 24 times). (d) Temporal structure of the sampling design. Leaf sampling was performed at seven instances from the start to the end of the growing season (on average, every 12 ± 1.3 days)

The selection of suitable tundra-patches for plot establishment followed three main criteria: (a) paired plots were maximum 3 m apart and distance to other plot-pairs was minimum 3 m, (b) plot-pairs within tundra-patches were similar in both plant-community composition and micro-topographical features, and (c) at least 80% of the Ro+ patch surface should show signs of small-rodent winter disturbance, whereas there should be no visible signs of disturbance in Ro− patches (Figure 1c). The scatter of small-rodent disturbed and undisturbed tundra-patches observed within our relatively homogeneous grassland sites points to a rather random fine-scaled spatial variation in winter herbivory (cf. Hambäck et al., 1998).

2.3 | Sampling design and sample processing

2.3.1 | Plant-community characterisation

At the peak of the growing season (3rd–5th of August), we used the point intercept method (PIM; Bråthen & Hagberg, 2004) to assess differences in above-ground plant-community composition between herbivore-treatment combinations. At each plot, we used nine pins attached to nine randomly selected pin placements on a metal frame (42 × 46 cm area × 40 cm height) consisting of 50 regularly distributed pin placements. Intercepts between the nine pins and vascular

plants were counted, and pooled into seven plant functional types (PFT; Si-rich and Si-poor grasses, forbs, sedges, horsetails, deciduous and evergreen shrubs). Intercept data were converted into PFT biomass [g/m² dry weight (DW)] following Bråthen and Hagberg (2004), with calibration coefficients given in Tuomi et al. (2018).

2.3.2 | Leaf elemental composition of grasses

Grasses were a priori assigned to either Si-rich or Si-poor grasses following previous studies (Soininen et al., 2013), further confirmed by foliar Si-content estimates provided by Smis et al. (2014) for grass samples collected in the same region. Accordingly (average and range of Si-content in brackets as provided by Smis et al., 2014), *Nardus stricta*, *Calamagrostis phragmitoides* and *Deschampsia cespitosa* were assigned to the group of Si-rich grasses [>1.5 (0.3–4.0) %DW silicon], while the others, of which common species are e.g. *Avenella flexuosa*, *Anthoxanthum* spp., *Phleum alpinum*, *Festuca ovina*, were assigned to the group of Si-poor grasses [<0.8 (0.1-1.5) %DW silicon]; species names follow the Pan-Arctic Flora, http://nhm2.uio.no/paf. This clear distinction in Si-content among grass species also suggests our goal, that is to examine how community-level Si-content and Si:N and Si:P ratios respond to herbivory, was best approached by grouping species in Si-rich and Si-poor grasses (see below for the procedure adopted). Since changes in the abundance of grasses in response to herbivory are likely to differ between species with inherently high or low Si-content (Massey et al., 2007a), a similar PFT classification has also been employed to disentangle herbivore effects on tundra plant-community composition (Bråthen & Oksanen, 2001; Ravolainen et al., 2011).

Leaf sampling was performed within each plot at seven sampling instances throughout the summer (Figure 1d), to span all grass-leaf developmental stages available to herbivores throughout the growing season. To guide leaf sampling, we used the metal frame also utilised for PIM (see above). The smaller size of the sampling frame compared to the plot size is assumed to minimise edge effects. We collected the uppermost plant-leaf touching each of the nine randomly selected pins if it belonged to a grass species. Additional leaves within a plot were collected whenever the first sampled leaf was not considered to be large enough for elemental content analyses (a minimum leaf area of 4 mm Ø, see below). This only occurred during the first sampling instance, when leaves were still very small. Pin placements were changed at each sampling occasion, and those used in the previous two rounds were excluded to reduce the possibility of sampling repeatedly the same grass individuals.

To obtain balanced estimates of Si, N and P levels for Si-rich and Si-poor grasses, we aimed at collecting at least one leaf sample for both groups of grasses within each plot at each sampling occasion. Consequently, when a group was not represented at a given plot using the procedure described above, we collected the required plant-leaf tissue as close as possible to one of the pins. In total, we collected 1,182 leaf samples (Si-rich grasses: 576, Si-poor grasses: 606) evenly distributed across herbivore-treatment

combinations and sampling instances (Figure S2). Grass species differed in abundance within our grasslands, and this was mirrored in the different number of samples obtained for each species (Figure S2). Given our random sampling design, we assume the large spectrum of collected samples to reflect the assemblage of Si-rich and Si-poor grass species.

During fieldwork, each sample was placed in a separate tea-filter bag. All samples were pressed with a plant-press within maximum 10 hr after collection and oven-dried flat at 60°C for 48 hr within 4 days of collection. Samples were cleaned from soil/dust particles and stored in their original bags in a dry and dark place at room temperature. Prior to analyses, all samples were oven-dried again at 60°C for 2 hr and cooled down in a desiccator.

All leaf samples were analysed for their element contents using near-infrared reflectance spectroscopy (NIRS) methodology with a FieldSpec 3 (ASD Inc.) in 350–2,500 nm range and equipped with a 4 mm light adapter for full-leaf scanning (Petit Bon, Böhner, et al., 2020). Narrow leaves were cut and stacked together to cover the minimum area needed for analyses. We took between 4 and 32 NIR measurements for each sample (on average 6.3 ± 3.2), depending on the size of the leaf. Each NIR measurement (in total 7,498) was converted to Si-, N- and P-content (%DW) using the prediction models based on milled and tableted plant samples (for Si-content, see Smis et al., 2014; for N- and P-contents, see Murguzur et al., 2019) and adjusted for full-leaf scanning (Petit Bon, Böhner, et al., 2020). We finally used the median of the NIR measurements of each sample for data analyses.

To determine whether soil water availability relates to grass elemental composition, we measured soil moisture in three random spots within each plot at each sampling instance (except occasion one, 28th–30th of June) using a SM150 moisture logger (Delta-T Devices). We then took the average of the three readings to obtain mean soil moisture at each plot.

2.4 | Statistical analyses

Statistical analyses were conducted in R ver. 4.0.3 (https://www.r-project.org) via VEGAN (Oksanen et al., 2020), LME4 (Bates et al., 2015), EMMEANS (Lenth, 2021) and GGPLOT2 (Wickham, 2016) packages.

First, a non-metric multidimensional scaling (NMDS; Legendre & Legendre, 2012) was implemented to explore PFT composition in tundra grasslands. The NMDS was based on Euclidean distances of the *log-transformed* + 1 relative PFT biomass at each plot. We tested statistically for differences in PFT composition between herbivore-treatment combinations using Permutational Multivariate Analysis of Variance (PERMANOVA). PERMANOVA was run on the Euclidean distance matrix and consisted of 10,000 restricted permutations to account for the hierarchical spatial structure of the study design (see below).

Prior to modelling, we explored the data following Zuur et al. (2010). In total, 31 (2.6% of the data) and 51 (4.3%) predicted median values for leaf Si- and P-contents, respectively, fell outside the calibration range of our prediction models (range for Si-content:

0.0008%–3.73% DW, Smis et al., 2014; range for P-content: 0.04%–0.70 %DW, Murguzur et al., 2019). We excluded these data from the analyses to avoid introducing statistical artefacts. However, since non-random patterns in missing values can bias statistical inference (Soininen et al., 2017), we explored possibly introduced trends in missing observations. We did not discover non-random missing-value patterns that could affect model estimates. We also checked if patterns in leaf element contents were consistent between migratory and summer ranges, which they were.

Data were analysed using linear mixed-effects models. 'Group of grasses' (Si-poor and Si-rich grasses), 'small-rodent winter disturbance' [undisturbed (Ro−) and disturbed (Ro+) tundra-patches], 'reindeer summer herbivory' [reindeer-exclusion (Re−) and reindeer-open (Re+) plots], and their interactions were used as predictors in full models with leaf Si-, N-, P-content and Si:N and Si:P ratios as response variables (five models in total). We considered the hierarchical spatial structure of the study design and the correlation among plot-level observations by specifying 'plot' nested in 'tundra-patch' nested in 'grassland-site' as nested random effects. However, 'plot' variance was always estimated as zero; thus, this term was removed from the models, as suggested by Bates et al. (2018). 'Sampling instance' was used as crossed random effect to account for the repeated sampling throughout the summer across all plots within the experiment (for details on the use of nested and/or crossed random effects, see Baayen et al., 2008; Bolker et al., 2009). This model structure allowed us to quantify if and to what extent herbivores affect overall (i.e. across-season) elemental composition of Si-rich and Si-poor grasses. We provide temporal patterns in leaf element contents to enable the assessment of both natural variability and variations in herbivore effects throughout the growing season. To avoid over parameterisation, we only fitted full models including random intercepts (Bates et al., 2018). We $log_e(y + 1)$-transformed leaf P-content, Si:N and Si:P ratios to meet homoscedasticity. Other transformations, such as the $log_e(y)$ and square-root(y), yielded comparable results.

The three-way 'grass group × small-rodent winter disturbance × reindeer summer herbivory' interaction was found to be statistically significant only in the full models fitted for leaf Si-content and Si:N ratio as response variables. Therefore, for the other three response variables, we also determined the model that produced the least unexplained variation given the constraint that all its interaction terms were statistically significant (i.e. most parsimonious models). Model simplification was performed using likelihood ratio test (models fitted using maximum likelihood – ML), following Bolker et al. (2009). Both full and most parsimonious models produced consistent results (and effect sizes), but differed in how they explained the model variance. We present results from full models, but include results from most parsimonious models in tables for completeness (model summaries in Tables S1–S5).

We originally tested 'soil moisture' as a covariate to determine whether it improved model fit. Soil moisture was not a significant predictor of any of the response variables, except in the models fitted for leaf N-content. Nevertheless, the inclusion of 'soil moisture' neither statistically changed other parameter estimates nor their biological interpretation. Thus, we excluded soil moisture from the models shown in Section 3.

Finally, we explored the relationships between Si and nutrient levels in grass leaves. Leaf N- and P-contents, in interaction with 'grass group × small-rodent winter disturbance × reindeer summer herbivory', were used as predictors in two separate linear mixed-effects models with leaf Si-content as response variable. The random-effects structure of the models was the same as above. After running these models, we found that results for the effects of herbivores on grass Si-content matched those from former analyses (as expected) and, more importantly, that the relationship between grass Si and nutrient levels was independent of herbivores. We consequently present results for the overall relationships between Si- and N- and P-contents in Si-rich and Si-poor grasses (model summaries in Tables S6 and S7).

Statistically significant effects (models fitted using restricted ML) were defined as having their 95% confidence interval (CI) not overlapping zero. Models were validated by assessing normality and homogeneity of variances in the residuals for the fixed effects and checking for approximate linearity between observed and fitted values.

3 | RESULTS

Relative PFT composition did not differ between herbivore-treatment combinations (Figure 2a). Overall, Si-rich and Si-poor grasses accounted for *c.* 23% and 40% of the above-ground biomass at our grasslands, respectively, and, together with forbs, they made up about 95% of the total biomass (Figure 2b). Small-rodent winter disturbance caused the strongest reduction in grass biomass (Si-rich grasses: —34%, Si-poor grasses: —50%), whereas the reduction caused by reindeer summer herbivory was less pronounced, yet considerable (Si-rich grasses: —19%, Si-poor grasses: —30%; Figure 2c). Grass biomass was similar in small-rodent disturbed tundra-patches regardless of reindeer herbivory (Figure 2c).

3.1 | Leaf element contents of grasses in the absence of herbivores

Our a priori subdivision of grasses in the two groups was a posteriori confirmed by their Si-content; Si-rich grasses had 65% higher Si-content than Si-poor grasses (Figure 3a; Figure S3). The two grass groups also differed in their N-content, but not P-content, with Si-rich grasses having 11% higher N-content than Si-poor grasses (Figure 3b,c). Si-rich grasses also had 52% higher Si:N ratio and 64% higher Si:P ratio compared to Si-poor grasses (Figure 3d,e).

3.2 | Effects of herbivores on leaf Si, N and P levels of grasses

Herbivores had mixed effects on grass Si-content (Figure 4a). Reindeer summer herbivory alone decreased Si-content of Si-rich grasses by 7%, whereas small-rodent winter disturbance alone or both herbivores together had no effects. Yet, Si-rich grasses
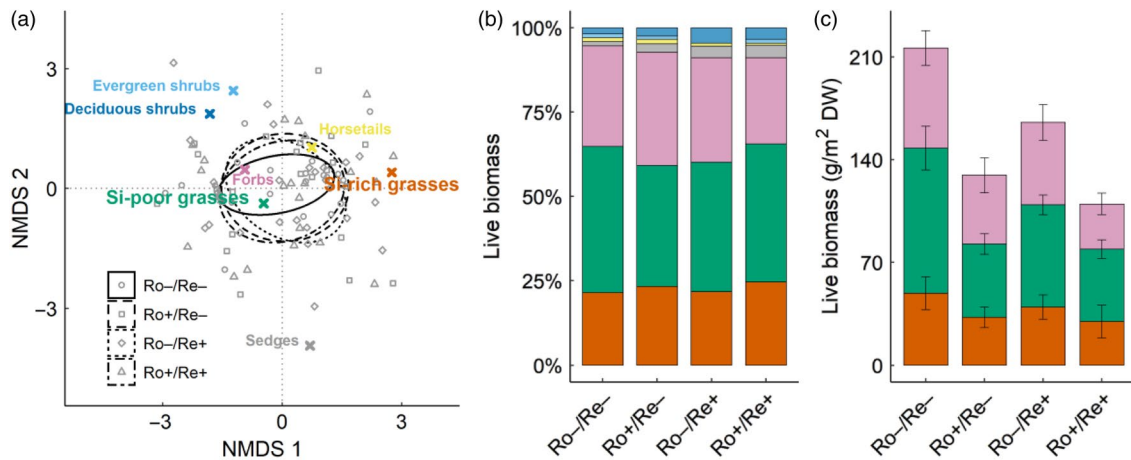
FIGURE 2 Plant functional type composition in tundra grasslands. (a) Two-dimensional NMDS ordination based on (b) relative PFT abundance within each herbivore-treatment combination ($n = 96$, stress = 0.146, Non-metric fit $r^2 = 0.98$, Linear fit $r^2 = 0.90$). Ellipses represent the 95% confidence interval for the standard deviation around group centroids: multivariate difference of herbivore-treatment means (F-statistics = 0.61, $p = 0.49$) and homogeneity of herbivore-treatment dispersions (F-statistics = 1.5, $p = 0.14$). (c) Biomass [g m^{-2} dry weight (DW)] of Si-rich grasses, Si-poor grasses and forbs (bars are standard errors of raw means)

impacted by both herbivores had higher Si-content than those affected by reindeer alone. Herbivores did not affect Si-content of Si-poor grasses relative to those in the absence of herbivores, but when impacted by both herbivores they had lower Si-content than those affected by small rodents alone.

Si-rich grasses had higher Si-content compared to Si-poor grasses under all herbivore-treatment combinations, but the size of this difference varied from 55% when affected by small rodents alone to 68% when affected by both herbivores together (Figure 5a).

Herbivores affected N and P levels in both Si-rich and Si-poor grasses, and effect sizes were larger compared to changes in Si-content. Small-rodent winter disturbance alone increased N-content of both grass groups by 22%–26% (Figure 4b) and P-content by 20% in Si-rich grasses and by 34% in Si-poor grasses (Figure 4c). Reindeer summer herbivory alone did not affect grass nutrient levels, but weakened the positive effects of small rodents on nutrient levels of Si-rich grasses; both herbivores together increased N-content of Si-rich grasses by 12%, that is, less than small rodents alone (Figure 4b), and did not modify their P-content (Figure 4c).

Herbivores altered the difference in N and P levels between Si-rich and Si-poor grasses observed in the absence of herbivores. Under either herbivore alone, N-content in Si-rich grasses was still 8%–12% higher than that of Si-poor grasses, but this difference was cancelled out in the presence of both herbivores (Figure 5b). P-content in Si-rich grasses still did not differ from that of Si-poor grasses under reindeer herbivory alone, but was 11% and 17% lower under small rodents alone and under both herbivores together, respectively (Figure 5c).

3.3 | Effects of herbivores on leaf Si:N and Si:P ratios of grasses

Through their differential effects on Si, N and P levels of Si-rich and Si-poor grasses, herbivores differently affected their Si:nutrient

ratios. Small-rodent winter disturbance alone decreased Si:N and Si:P ratios by 14%–20% in both grass groups (Figure 4d,e), whereas reindeer summer herbivory alone only decreased Si:N ratio of Si-rich grasses by 11% (Figure 4d). Both herbivores together did not affect Si:nutrient ratios of Si-rich grasses, but they decreased Si:N and Si:P ratios of Si-poor grasses by 21% and 28%, respectively (Figure 4d,e).

Si-rich grasses had higher Si:nutrient ratios compared to Si-poor grasses under all herbivore-treatment combinations, but this difference was greater under the impact of both herbivores. Together, herbivores increased the relative difference in Si:N ratio and in Si:P ratio between Si-rich and Si-poor grasses by 13% and 22%, respectively, compared to their difference in the absence of herbivores (Figure 5d,e).

3.4 | Relationships between leaf Si and nutrient levels in grasses

The relationships between Si-content and N- and P-contents differed between Si-rich and Si-poor grasses (Figure S4). Si-content was not related to N-content in either grass group, though the slope of the relationships still differed between Si-rich (negative) and Si-poor (positive) grasses. Conversely, Si-content had a strong negative association with P-content in Si-rich grasses, which contrasted with the absence of any relationships in Si-poor grasses.

4 | DISCUSSION

Here, we assessed the extent to which keystone Arctic herbivores, small rodents and reindeer, alter the summer quality of their own food supply by simultaneously modifying leaf Si-based defence and N and P levels of grasses found in tundra grasslands. Contrary to our prediction, herbivores did not elicit a net increase in grass Si-based defence levels, and reindeer summer herbivory alone even
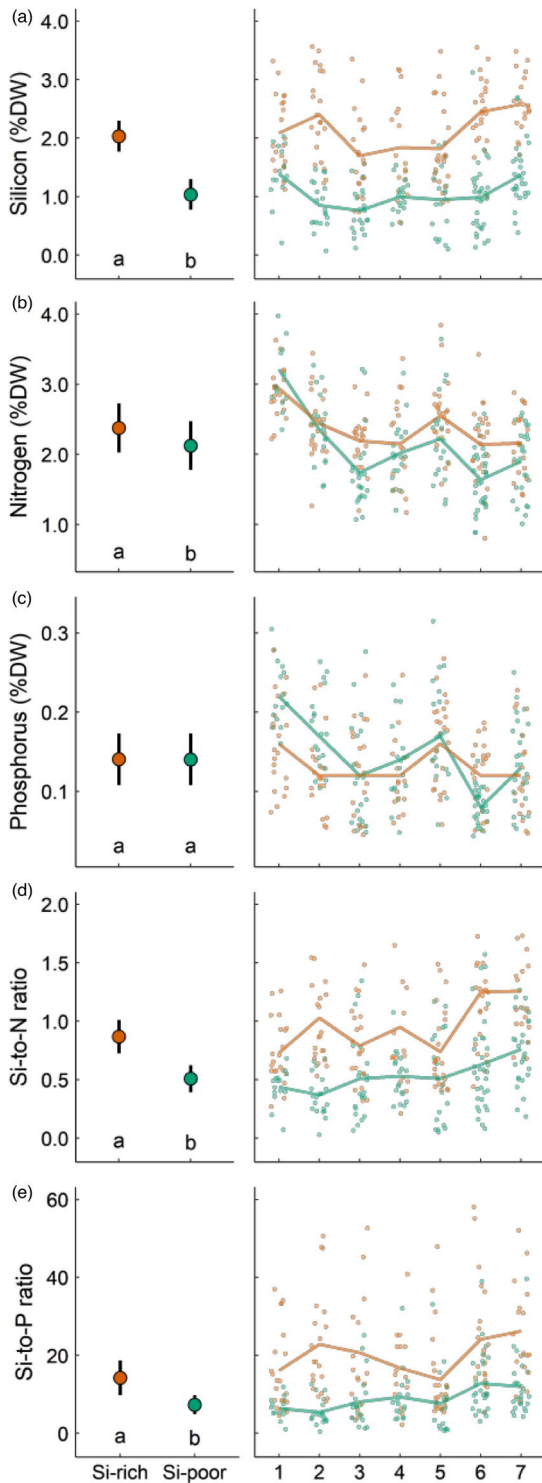
Baseline leaf elemental composition, that is, leaf element contents in the absence of herbivores, in Si-rich and Si-poor tundra grasses. (Left panels) Across-season model predictions and their 95% confidence intervals (CIs) and (right panels) observed temporal development (sampling instances 1–7) for (a) Silicon (Si), (b) Nitrogen (N), and (c) Phosphorus (P) contents (%DW) and (d) Si:N and (e) Si:P ratios of Si-rich and Si-poor grasses. In left panels, model predictions and their 95% CIs were extracted from each model for the contrast between Si-rich and Si-poor grasses in Ro−/Re− plots, and different letters indicate significant differences between grass groups. Model predictions and their CIs for leaf P-content and Si:N and Si:P ratios were back-transformed on the response scale prior to presentation. In right panels, dots show raw data from Ro-/Re- plots, which were jittered within each sampling occasion to reduce overlapping. Lines connect average leaf elemental composition throughout the summer

and they were stronger in Si-poor than in Si-rich grasses. This shows that herbivores in tundra grasslands interact with grasses in ways that ultimately give rise to tundra-patches of diverse nutritive values. Within these patches, the quality of Si-rich grasses was further decreased relative to that of Si-poor grasses in those affected by both herbivores. The ability of maintaining a lower quality might confer an advantage to Si-rich over Si-poor grasses against herbivores utilising tundra grasslands throughout the summer.

In direct opposition with our expectation, we did not find evidence of leaf Si accumulation in tundra grasses following herbivory. We studied herbivore effects in natural tundra-grassland ecosystems; one might expect that the magnitude of such herbivory is lower than that faced by grasses in laboratory-based studies (Reynolds et al., 2012) or in fenced enclosures (Huitu et al., 2014), where Si-based defence levels and herbivory have been shown to be related. For instance, in controlled feeding trials, Reynolds et al. (2012) found that a foliar damage of at least 20% was required to cause a substantial increase in Si uptake of *Deschampsia cespitosa* when exposed to vole herbivory, although a damage of 5%–7% already sufficed for short-lived, yet detectable, Si induction, also in field conditions (Ruffino et al., 2018). Though we did not measure leaf damage directly, we found herbivores to reduce peak-season biomass of Si-rich and Si-poor grasses by *c.* 19%–50%. Moreover, as compensatory re-growth in grasses often occurs after defoliation (McNaughton, 1983), such biomass reduction may even be an underestimate of realised herbivory rates at our sites. Hence, it appears that the grazing intensity in these grasslands would be high enough to cause grass Si accumulation.

In this study, we aimed at determining herbivore effects on grass Si-content over spatial and temporal extents relevant to herbivores, that is, across tundra grasslands and throughout the whole summer. Unsurprisingly, we found large variations in the Si-content of both Si-rich and Si-poor grasses. For instance, inconsistent Si responses of five tundra-grass species to both natural and experimental herbivory have been attributed to their large variability in Si-content (Soininen et al., 2013), which is particularly pronounced even within a few meters across the tundra landscape, also in the high Arctic

decreased the Si-content of inherently Si-rich grasses. As expected, herbivores generally increased grass N and P levels (Petit Bon, Inga, et al., 2020), though the assessment conducted here separately for Si-rich and Si-poor grasses showed further details on their responses. Grasses affected by herbivores often had lower (and anyway never higher) Si:nutrient ratios than grasses in the absence of herbivores, indicating that herbivory enhances the overall grass quality in these grasslands. Yet, these quality increments were larger following small-rodent winter disturbance than reindeer herbivory,
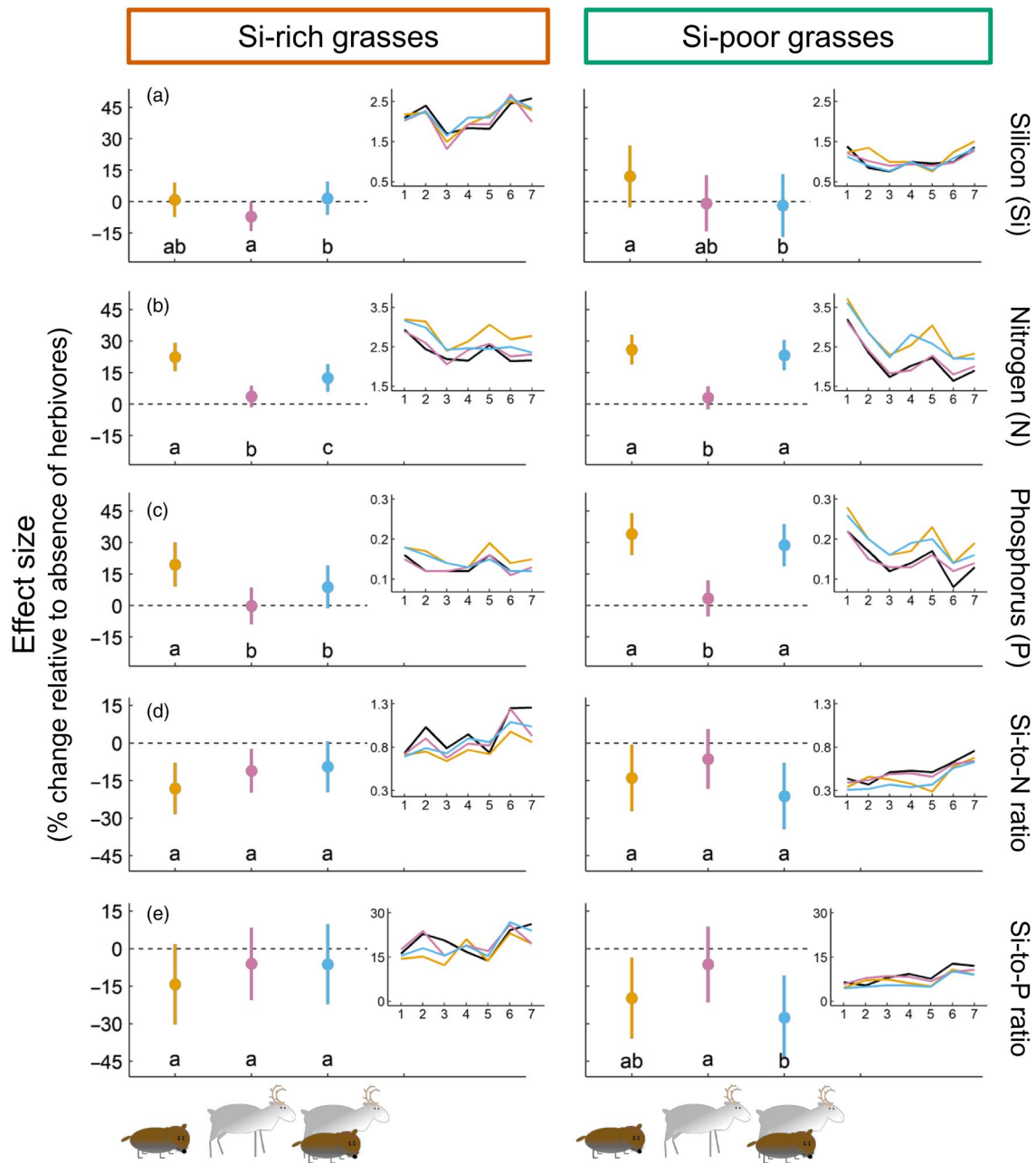
FIGURE 4 Effects of herbivores on leaf elemental composition of Si-rich and Si-poor tundra grasses. Effect sizes (as % change) and their 95% confidence intervals (CIs) for the effects of herbivores on leaf (a) Silicon (Si), (b) Nitrogen (N) and (c) Phosphorus (P) contents, and (d) Si:N and (e) Si:P ratios as contrasts to the absence of herbivores (Ro−/Re−) across the growing season. 'Ro−/Re−' is used as the reference level and is denoted with the black dashed lines at zero effect size (refer to Figure 3 for actual values of leaf elemental composition in the absence of herbivores). Thus, for example, a positive effect size with its 95% CI not overlapping the reference level indicates significantly higher leaf element contents in the presence of herbivores than in their absence. Different letters at the base of each panel indicate significant differences between herbivore-treatment combinations. The statistical significance and the direction of the two-way interaction between herbivores is reported as standardised coefficients with their 95% CIs in Figure 5, separately for Si-rich and Si-poor grasses ('Ro+ × Re+', right panels). Model estimates and their 95% CIs for leaf P-content and Si:N and Si:P ratios were back-transformed on the response scale prior to calculation of effect sizes. Insets display the observed temporal development in leaf elemental composition (%DW or ratios) throughout the summer (sampling instances 1–7), separately for each herbivore-treatment combination

(Petit Bon, Böhner, et al., 2020). Yet, Soininen et al. (2013) sampled grasses for Si-content analyses only once at the peak of the growing season. Furthermore, each of their samples consisted of several leaves merged together to obtain enough plant material for analyses.

Using near-infrared reflectance spectroscopy (NIRS) methodology, we were able to process a high number of samples, thus increase spatial and temporal resolution of our sampling design compared to previous studies, as well as quantify Si-content of single leaves.
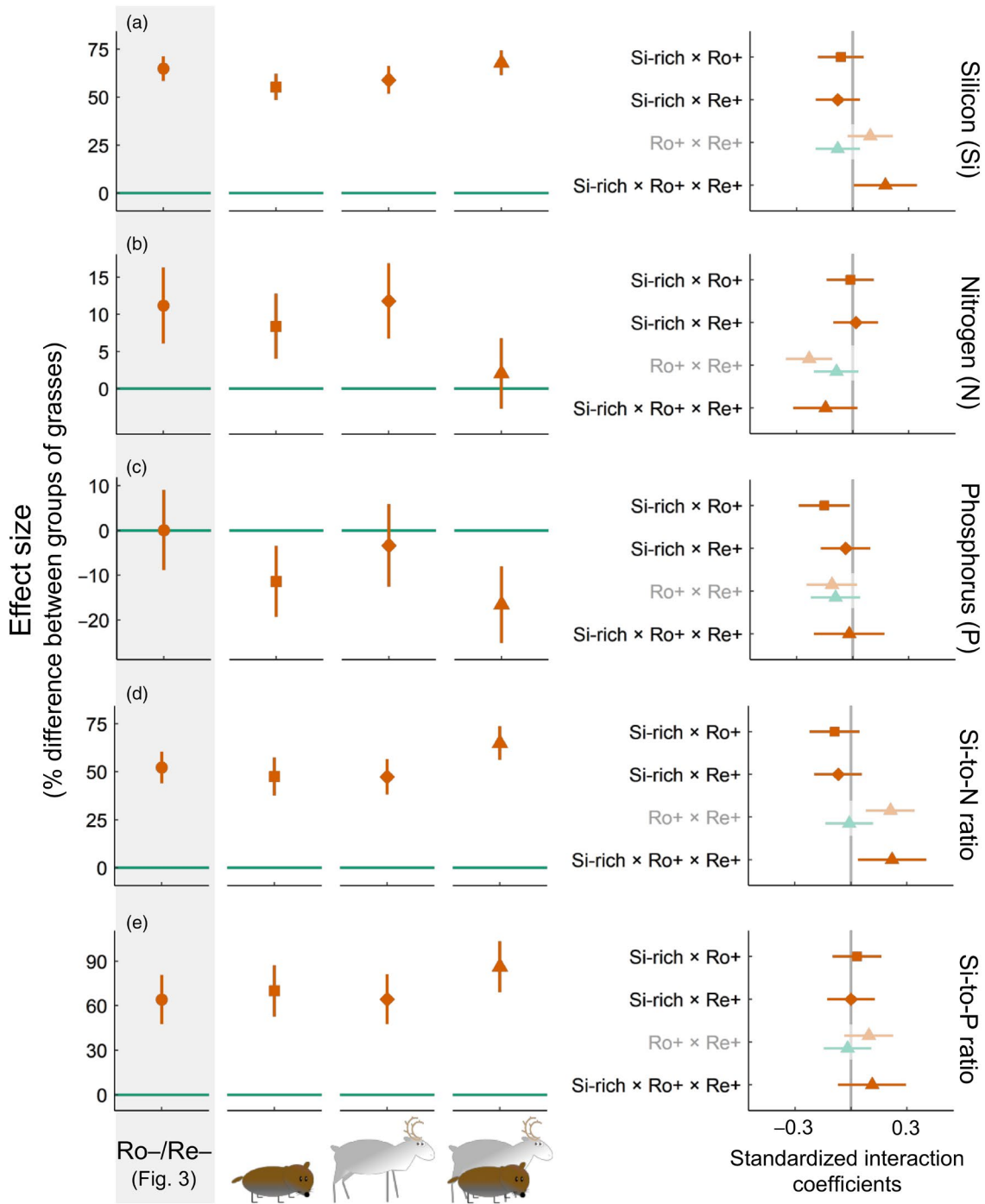
FIGURE 5 Effects of herbivores on the difference in leaf elemental composition between Si-rich and Si-poor tundra grasses. (Left panels) Effect sizes (as % difference) and their 95% confidence intervals (CIs) for the contrast between Si-rich and Si-poor grasses in (a) Silicon (Si), (b) Nitrogen (N) and (c) Phosphorus (P) contents, and (d) Si:N and (e) Si:P ratios across the growing season. 'Si-poor grasses' is used as the reference level and is denoted with the solid lines at zero effect size. Thus, for example, a positive effect size with its 95% CI not overlapping the reference level indicates significantly higher element contents in Si-rich grasses than in Si-poor grasses. (Right panels) The statistical significance and the direction of the interaction between Si-rich grasses and either herbivore alone (two-way interactions 'Si-rich × Ro+' and 'Si-rich × Re+') or in combination (three-way interaction 'Si-rich × Ro+ × Re+') is reported as standardised coefficients with their 95% CIs (symbol coding facilitates the match with left panels). Model estimates and their 95% CIs for leaf P-content and Si:N and Si:P ratios were back-transformed on the response scale prior to calculation of effect sizes

Our findings clearly indicate that herbivory does not cause a net increase in Si-based defence levels of grasses found in these tundra grasslands.

On a large scale, heterogeneity in factors other than herbivory can influence the production of Si-based defences by grasses (Hartley & DeGabriel, 2016). For instance, the availability of

dissolved-Si in soils is known to regulate grass Si accumulation (Cornelis & Delvaux, 2016; Quigley et al., 2017). As well, temperature (Liang et al., 2006) and nutrient availability and/or precipitation (Quigley et al., 2020) have been found to explain patterns of grass silicification. On a smaller scale, soil moisture can affect grass Si-content, as indeed experimental watering raised Si levels in the Serengeti grass *Themeda triandra* (Quigley & Anderson, 2014). Hence, a range of abiotic factors may modulate the extent to which Si acts as an 'inducible' defence against herbivores in tundra. Yet, soil moisture was not related to grass Si levels, although it varied considerably across tundra-patches [seasonal average and range: 55%volume (20%–90%); Petit Bon, Inga, et al., 2020], indicating that the fine-scale availability of water is unlikely to play a major role in grass silicification in tundra grasslands. Interestingly, at the level of single leaves, we found that Si-content relationships to nutrient levels were loose, except for a tight negative coupling with P-content in Si-rich grasses. This observation suggests that Si assimilation in inherently Si-rich tundra grasses may be partly mediated by available P, as it has recently been shown in the common European grass *Holcus lanatus* (Minden et al., 2021). However, it is presently not known whether and how environmental characteristics of tundra ecosystems impact on overall grass Si accumulation, nor if interactions with biotic factors are at stake (Hwang & Metcalfe, 2021), emphasising the need for additional research to disentangle their relative role.

The only net effect on grass Si-based defences was a 7% decrease in Si-content of Si-rich grasses following reindeer summer herbivory alone. Because Si cannot be remobilised after its deposition in leaves (Strömberg et al., 2016), it generally accumulates as the summer progresses, thus making grass Si-content to increase with both plant and leaf age (e.g. Motomura et al., 2002). This overall seasonal pattern also emerged from our data, although variations in natural conditions are often high (cf. Brizuela et al., 1986; Ruffino et al., 2018). Reindeer may have promoted overall lower Si-content in Si-rich grasses by keeping leaves in young phenological stages (Bañuelos & Obeso, 2000). In mid-summer, reindeer are often utilising the northernmost part of their pastures (i.e. areas further north of our grassland sites), potentially explaining why the decrease in grass Si-content was mainly observed at the start and end of the growing season. As multiple defoliation events (i.e. high grazing frequency) may be necessary for Si induction (Massey et al., 2007b), this pattern offers an alternative, yet not mutually exclusive, explanation for the lack of Si accumulation in our study. Noteworthy, the decrease in Si-content promoted by reindeer also reduced the Si:N ratio of Si-rich grasses. The capacity of herbivores to enhance plant quality in grassland ecosystems by increasing plant N and P levels, thus reducing carbon:nutrient ratios, is well acknowledged (Bardgett & Wardle, 2003), whereas their ability to increase the quality of grasses by reducing their Si-based defence levels is first shown here.

Si-rich grasses affected by both herbivores had higher Si-content than those affected by reindeer alone, though nearly identical Si-content than those in the absence of herbivores. This suggests that grass–reindeer interactions in small-rodent disturbed tundra-patches differed from those established in undisturbed patches (see above). The enhanced nutrient levels of forbs (Petit Bon, Inga, et al., 2020), but also the enhanced quality of Si-poor relative to Si-rich grasses (this study), in disturbed tundra-patches could have caused reindeer to prefer forbs (and eventually Si-poor grasses) and show less preferences for Si-rich grasses. Furthermore, small rodents may have increased forb exposure by reducing grass biomass, hence promoting reindeer grazing on the more nutritious forbs. Indeed, only the biomass of forbs, and not that of grasses, was found to be further reduced by reindeer in disturbed tundra-patches. 'Feeding facilitation' in herbivore assemblages originates when grazing by one species either improve forage quality or foster the access to forage of suitable quality for another species (Arsenault & Owen-Smith, 2002). Similar mechanisms also played out in a range of other ecosystems, including African Savannah grasslands (McNaughton, 1976) and temperate saltmarshes (van der Wal et al., 2000), where the herbivory by one herbivore profited the herbivory by another herbivore. Overall, these results are indicative of that the presence/absence of small rodents in winter could mediate (indirectly) the effects of reindeer on Si-content of Si-rich grasses in summer, and show that subtle, yet divergent, fine-scale changes in Si-based defence levels of grasses might occur across tundra-patches that differ in herbivory load.

Small-rodent winter disturbance alone strongly increased N and P levels in grasses (up to 34%), raising their quality by decreasing leaf Si:nutrient ratios (up to 28%). Conversely, the effects of reindeer summer herbivory alone were much weaker. Nonetheless, grass–rodent–reindeer interactions were clearly complex. At first, small rodents promoted overall larger quality increases in Si-poor compared to Si-rich grasses. Then, reindeer reduced/offset these quality increments in Si-rich, but not Si-poor, grasses. As a result, herbivore activities in these tundra grasslands led to the formation of a fine-scale mosaic of tundra-patches with different grass quality. As Arctic herbivores select forage plants at the scale of tundra-patch (Grellmann, 2002; Iversen et al., 2014), such herbivory-driven patchiness in grass quality may have implications for how herbivores themselves exploit the tundra landscape throughout the growing season. Importantly, however, grasses growing in the presence of herbivores never had lower nutrient levels and/or higher Si:nutrient ratios than grasses in their absence, clearly indicating that the nourishing state of grasses is increased by herbivore activities. Affecting grasses towards lower Si:nutrient ratios, thereby improving their nutrient-reward potential (Massey & Hartley, 2006), might benefit herbivores utilising tundra grasslands in summer.

There is yet a nutrient-mediated process that, together with changes in leaf Si-content, could confer a further competitive advantage to the already less palatable Si-rich grasses over Si-poor grasses when the herbivory load is high. Indeed, in the presence of both herbivores, Si-rich grasses maintained the lowest quality relative to Si-poor grasses, and this held true in terms of both absolute nutrient levels and Si:nutrient ratios. Because herbivores are highly selective and low-quality food items are often discarded when high-quality food is available (Augustine & McNaughton, 1998; Mulder, 1999), the lower nutritive quality of Si-rich grasses in

tundra-patches experiencing the grazing succession of small rodents in winter and reindeer in summer may act as a defence against herbivores (Augner, 1995), eventually making them more likely to target Si-poor grasses. 'Apparent competition' in plant communities refers to the indirect negative interactions between plant species (or PFTs) that are mediated by the activities of one or more herbivores (Holt & Bonsall, 2017; Sotomayor & Lortie, 2015). The establishment of such interactions between Si-rich and Si-poor tundra grasses may also partly explain why the persistence of tundra-vegetation states dominated by Si-rich grasses is often promoted by herbivores (Austrheim et al., 2007; Bråthen et al., 2007; Ravolainen et al., 2011). It is possible that, though herbivores do not cause a net Si increase in grasses, inherently Si-rich grasses can still be favoured under herbivory (Massey et al., 2007a) through herbivore-induced changes in Si-based defence relative to nutrient levels, which ultimately diminish the quality of Si-rich grasses relative to that of the already more palatable Si-poor grasses.

5 | CONCLUSIONS

The quality of plants is crucial for herbivore performance (White, 1983). Yet, plant quality can be difficult to quantify satisfactorily, as it depends on both plant defence and nutrient levels. Using NIRS methodology, we were able to provide estimates of Si-based defence relative to N and P levels for single tundra-grass leaves (Petit Bon, Böhner, et al., 2020), that is, at the bite-size level of the herbivores, and further scale up to the grass-community level. Our study provides the first community-level, quantitative assessment of the role of mammalian herbivores for the quality of grasses found in tundra grasslands.

High-latitude regions are experiencing the fastest rate of climate warming (IPCC, 2013), and there is extensive evidence that rising temperatures can reduce forage quality for herbivores by speeding up the seasonal decline in plant nutrient contents (Doiron et al., 2014; Zamin et al., 2017). By increasing N and P relative to Si-based defence levels in grasses, herbivores themselves could thus be a key factor counteracting the quality deterioration of their own forage in tundra grasslands. Importantly, however, the quality of the grass community was not homogeneously affected by herbivores. On the one hand, small rodents and reindeer created a foodscape of tundra-patches that differed in their palatability states, which, in turn, may influence herbivore forage patterns across grasslands. On the other hand, herbivore-induced changes in the quality of Si-rich relative to Si-poor grasses may alter herbivore diet choice, potentially affecting plant-community structure in tundra grasslands in the longer term.

CONFLICT OF INTEREST

There are no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

K.A.B. conceived the idea with contributions from M.P.B., K.G.I. and T.A.U., and all four collected the data; M.P.B. and K.G.I. processed the samples; M.P.B. analysed the data and led the writing of the manuscript with contributions from all authors; I.S.J. and K.A.B. financed the study with their research grants; K.A.B. supervised the research.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13790.

DATA AVAILABILITY STATEMENT

Data are available via DataverseNO UiT Open Research Data Repository https://doi.org/10.18710/FKAJVI

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How to cite this article: Petit Bon, M., Inga, K. G., Utsi, T. A., Jónsdóttir, I. S., & Bråthen, K. A. (2021). Forage quality in tundra grasslands under herbivory: Silicon-based defences, nutrients and their ratios in grasses. *Journal of Ecology*, 00, 1–15. https://doi.org/10.1111/1365-2745.13790