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Research article

Long-term nutrient addition and grazing exclusion determine flower abundance, diversity and community composition in high-latitude grasslands

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The abundance and composition of flowers within plant communities shape the resources available to flower-visiting insects. However, it remains unclear how nutrient enrichment and changes in grazing impact plant communities and their floral resources, and whether these effects contribute to ongoing pollinator decline. We investigated how the abundance, diversity and species composition of flowers (excluding graminoids) respond to long-term nutrient additions and grazing exclusion in two high-latitude grasslands (tundra and montane). We used two factorial experimental designs: 1) a nutrient experiment with additions of nitrogen (N), phosphorus (P), and potassium (K with micronutrients), and 2) a grazing experiment that included combined NPK addition with and without grazing exclusion. Flower abundance was assessed in 5 × 5 m experimental plots after 6–10 years of treatments. N and P interactively affected flower abundance, with N counteracting the positive effects of P. N reduced flower abundance in the montane grassland, whereas P and K increased it. Grazing exclusion increased flower abundance, with its effect amplified under NPK addition, but this joint treatment reduced flower species richness. Grazing exclusion reduced flower species diversity, with contrasting site-specific effects depending on NPK. N, P and K additions as well as grazing exclusion and NPK addition changed the composition of flower assemblages. At the montane grassland joint NPK addition and grazing exclusion led to strong dominance of forbs, such as *Anthriscus sylvestris* and *Geranium sylvaticum*, and grazing exclusion led to homogenisation of the flower community at the montane grassland. Our study demonstrate the importance of grazing and nutrients as key determinants of floral resources, which are vital for flower-visiting insects. We suggest that quantifying floral resources could contribute to ecosystem status assessment. Our findings offer insights for managing and conserving pollinator habitats in the face of environmental change.

Keywords: Arctic, species diversity, herbivory, Nutrient Network, nutrients, reindeer, vegetation change

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Introduction

The abundance and composition of flowering plants are essential for flower-visiting insects, as flowers are key resources providing them with nectar and pollen. A decline in floral resources can lead to reductions in insect abundance and diversity (Hoover et al. 2012), potentially triggering cascading effects in the food web. However, although floral resources play a crucial role in ecosystem functioning (Fontaine et al. 2006), and biodiversity maintenance (Ebeling et al. 2008), the drivers of floral assemblages, such as soil nutrients and grazing, remain poorly understood. This knowledge gap is particularly concerning, given the escalating global impacts of anthropogenic changes on biodiversity.

Human-induced enrichment of nutrients affects ecosystems worldwide (Vitousek et al. 1997). In general, nutrient enrichment has been shown to decrease plant diversity (Öckinger et al. 2006, Phoenix et al. 2006, Schoukens 2017, WallisDeVries and Bobbink 2017) through increasing aboveground biomass and favouring taller, fast-growing species that are superior in competition for light (Hautier et al. 2009, Borer et al. 2014a, Eskelinen et al. 2022). The effects of increased nitrogen (N) alone on plant communities are often profound, resulting in decreased species diversity (Jonasson 1992, Havström et al. 1993, Suding et al. 2005, Goulson et al. 2015, Storkey et al. 2015, David et al. 2019). These compositional shifts can lead to more uniform plant communities (Carvalheiro et al. 2013). Nitrogen can further affect reproductive traits including flowering, fruit, and seed production (Campbell and Halama 1993, Gerdol et al. 2000, Muñoz et al. 2005) as well as magnitude and duration of flowering (Burkle and Irwin 2009, Schemske and Horvitz 1988, Biederman et al. 2017). Along with nitrogen, increased availability of phosphorus (P) can accelerate N uptake by plants, which can increase plant biomass production (Chapin et al. 1986), cause changes in flowering plant composition, and lead to decreased flowering plant diversity (Wang et al. 2022) and flower or fruit output (Muñoz et al. 2005, Alatalo et al. 2022). While N and P are often profiled as primary limiting nutrients in northern grasslands, potassium (K) also plays an important role in physiological processes, such as osmotic balance, stomatal regulation, photosynthesis and enzyme activation, which are vital for growth and abiotic stress tolerance, and may influence community-level responses. In particular, K contributes to water-use efficiency, which may affect flower production (Johnson et al. 2022).

Moreover, nutrient levels can change flowering plant species composition, which also might include a shift from flowering forbs to grass dominance (Phoenix et al. 2012, Wang et al. 2022, Nelson et al. 2025).

In addition to nutrients, the abundance and diversity of floral resources for pollinators may depend on grazing. In grassland ecosystems, grazing can promote flowering plant species diversity through the suppression of dominant species, which reduces competitive exclusion and allows subordinate species to persist. Grazers also create small-scale disturbances, promoting heterogeneity in local soil and light conditions which gives opportunities for colonization from the species pool (Olff and Ritchie 1998, Eskelinen et al. 2022). The effect may also be reflected in increased flower abundance and diversity (Wentao et al. 2023).

Grazing can further mitigate the adverse effects of nutrient enrichment on flower species diversity (Borer et al. 2014a) and reduce the dominance of tall-growing tussock grasses or litter accumulation (Minervini Silva et al. 2024). Flowers can be the preferred food item for grazers because of their high nutritive value, and heavy grazing can lead to reductions in flower abundance or diversity (Gao et al. 2021, Veen et al. 2024). Flowers are particularly vulnerable to grazing also as they are positioned at the top of the plant canopy and are thus readily consumed. Lennartsson et al. (2012) showed that delaying grazing after peak flowering period, substantially increased the number of flowers and fruit production, compared to continuous grazing. These findings show that floral structures are sensitive to grazing and can be slow to reappear (Côté et al. 2004).

Grazer's effects on flowers may also depend on nutrients (Veen et al. 2024) or the type of herbivores, and whether they preferentially feed on flowers. For instance, compared to cattle grazing, sheep grazing may negatively affect floral abundance because of selective floral herbivory (Côté et al. 2004, Cutter et al. 2022). Taken together, nutrient addition and grazing exclusion, representing bottom–up and top–down processes, can have various and interactive effects on floral resources, and the effects may also depend on ecological contexts. Hence, more research is needed to unravel the ways in which the abundance and composition of floral resources for pollinators are determined by nutrient availability and grazing pressure across ecosystems varying in their species composition and environmental conditions.

To address this knowledge gap, we studied how the abundance, diversity and species composition of flowers (excluding graminoids), respond to long-term addition of nutrients (N, P and K) and grazing exclusion. We conducted two coordinated experiments at each of two high-latitude, cold-climate grassland sites – a low-productivity tundra grassland and a higher-productivity montane grassland – both used as reindeer summer pastures. The first was a 'nutrient experiment' with factorial additions of nitrogen (N), phosphorus (P), and potassium (K) with micronutrients. The second was a 'grazing experiment' that included factorial combinations of NPK addition with or without grazing exclusion. Both experiments were implemented using the same design at each site. We predicted that 1) the addition of N, P and K would increase flower abundance by alleviating nutrient limitation, but decrease flower species richness and/or diversity; 2) grazing exclusion would enhance flower abundance by reducing floral herbivory, while multi-nutrient (NPK) addition would enhance flower abundance by relieving nutrient limitation; 3) grazing would mitigate the negative effects of multi-nutrient (NPK) addition on flower species richness and diversity by preventing dominance of tall plants; 4) the addition of single nutrients (N, P, K) and multi-nutrients (NPK), along with grazing exclusion, would alter flower

assemblage composition; 5) multi-nutrient addition would cause homogenisation of flower assemblage composition e.g. by increasing the dominance of a few species and reducing local plant diversity; and 6) the expected nutrient addition and grazing exclusion effects on flowers would vary between sites due to differences in species composition, site conditions and the varying susceptibility of plant assemblages to grazing. Specifically, nutrient addition is likely to have a stronger impact on flower abundance in low-productivity grassland sites than in more productive ones, while within higher-productivity sites where taller plants are more susceptible for floral herbivory, grazing exclusion may lead to increased flower abundance.

Material and methods

Our study was conducted at two experimental sites within the Nutrient Network (NutNet), a coordinated global research network that addresses consumer and nutrient controls of grassland productivity and diversity. This network enables the study of plant communities using a standardized experimental design (Borer et al. 2014b). In 2013 and 2014, two experimental sites, following the NutNet experimental design, were established in NW Finnish Lapland, near Lake Kilpisjärvi (69°02'N, 20°48'E). The growing season in Kilpisjärvi is short (June–September), with a mean temperature of +11.4°C in July. The mean annual temperature is −1.7°C, and the mean annual precipitation is 546 mm (Finnish Meteorological Institute 2024).

The first site represents a low-productive tundra grassland (kilp.fi, 730 m a.s.l.), and the second site represents a moderately productive montane grassland (saana.fi, 600 m a.s.l.). Both sites are used for reindeer summer grazing. The tundra grassland is a tundra meadow above the treeline, characterized by graminoids such as *Agrostis mertensii*, *Anthoxanthum alpina*, *Carex bigelowii*, *Carex lachenalii* and *Festuca ovina*; low herbs such as *Antennaria dioica*, *Sibbaldia procumbens*, *Solidago virgaurea* and *Veronica alpina*; and creeping dwarf shrubs such as *Harrimanella hypnoides* and *Salix herbacea* and bryophytes. The aboveground standing crop of these plant communities (litter and live biomass including bryophytes) is on average, 251 g m^{-2} (pre-treatment data for 2013). The montane grassland is characterized by tall-statured forbs such as *Anthriscus sylvestris, Geranium sylvaticum*, *Ranunculus subborealis* and *Trollius europaeus*; legumes such as *Astragalus frigidus*; and graminoids such as *Anthoxantum alpinum, Poa alpigena* and *Poa alpina*. The aboveground standing crop of these plant communities (litter and live biomass, including bryophytes) is on average 387 g m^{-2} (pre-treatment data for 2014).

The most dominant herbivore at these sites is the semi-domesticated reindeer *Rangifer tarandus tarandus*, which grazes in the area from snowmelt in late May–June to August–September. The grazing intensity for the two sites was estimated as the offtake calculated as the % difference in biomass in grazing exclosures versus grazed controls at the end of the growing season (mean values for each year). The mean offtake at the montane grassland was 57%, standard deviation (SD) 8.4, for 2016–2023, and at the tundra grassland 35%, SD 14.6 for 2016–2023, Welch two sample t-test for the difference between sites $t = -3.7$, degrees of freedom (df) = 11.2, $p = 0.003$. The frequency of the reindeer visits at the sites was documented in 2023 using wildlife cameras placed at each site, showing the peak times of reindeer grazing in summer (Supporting information). In addition, Norwegian lemmings *Lemmus lemmus*, grey-sided voles *Myodes rufocanus* and mountain hares *Lepus timidus* can be encountered at the study sites but their herbivory on herbaceous plants is likely low compared to that of reindeer.

The following experimental designs were established at both sites: 1) a factorial nutrient (N, nitrogen, P, phosphorus and K, potassium with micronutrients) addition experiment, and 2) a factorial grazing exclusion experiment crossed with NPK additions. The experimental units were 5 × 5 m plots, and treatments were assigned in a randomized block design with four blocks per site. The nutrient experiment consisted of a control and a full factorial combination of three nutrient addition treatments: control, N, P, K, NP, NK, PK and NPK. Nutrient addition rates were 10 g m^{-2} $year^{-1}$. The addition of K was combined with a single addition of micronutrients following the NutNet design (Borer et al. 2014b). N, P and K addition treatments were applied annually. The N fertilizer was applied as granular urea, P fertilizer as triple super phosphate and K fertilizer as potassium sulfate. Micronutrients were applied once during the first year using a mix of the following elements (and their doses): boron (B; 0.1 g m^{-2}), calcium (Ca; 6 g m^{-2}), copper (Cu; 1 g m^{-2}), iron (Fe; 17 g m^{-2}), magnesium (Mg; 3 g m^{-2}), manganese (Mn; 2.5 g m^{-2}), molybdenum (Mo; 0.05 g m^{-2}), sulphur (S; 12 g m^{-2}), and zinc (Zn; 1 g m^{-2}). The grazing experiment consisted of a factorial combination of herbivore exclusion with NPK addition resulting in the following four treatments: control (no nutrients, mammals), grazing exclusion (no mammals, no NPK addition), NPK (mammals, NPK addition), NPK + Fence (NPK, no mammals). The fertilization treatment was the same as the all-nutrients-added treatment (NPK) in the multiple-nutrient experiment. The fences were 110 cm tall, with the lower 80-90 cm surrounded by a 1 cm mesh, and the upper part with visible 10 mm-wide polytape wires. The nutrient addition and grazing exclusion treatments started in 2014 at the tundra grassland and in 2015 at the montane grassland.

The flowers of plant species, excluding graminoids, were counted at the peak flowering times in 2020 (26 July–3 August) and in 2023 (9–13 July). The flower counts were estimated based on flower units, defined as approximately 1 cm^2 of flower surface, with at least one open flower (Carvalheiro et al. 2014); flowers smaller than 1 cm^2 were combined until they reached 1 cm^2 and were then counted as one unit. For some flowers, such as *Parnassia palustris* or *Geranium sylvaticum*, one floral unit corresponds to one flower, whereas for certain members of the Asteraceae family, such as *Solidago virgaurea*, one floral unit corresponds to one

capitulum. Flower units were first counted within 10 randomly placed 0.5 × 0.5 m quadrats (using a metal frame haphazardly thrown across different parts of the 5 × 5 m plot). Subsequently, flower units of infrequent species that did not occur within the ten small quadrats were counted from the entire 5 × 5 m plot area. The flower abundances were combined and presented on a square meter scale. This method was used independently in each sampling year (2020 and 2023), and the mean flower abundance per plot was averaged across the years. The species abundances were summed to obtain the total floral abundance per square meter. We calculated the flowering plant species richness (number of species 25 m^{-2}) and inverse Simpson's diversity index (Roswell et al. 2021, function *diversity()* in the 'vegan' package of R; Oksanen et al. 2022), which describes the effective number of species, and is less affected by rare species than species richness (Chase and Knight 2013).

We used mixed-effects models to test the effects of grazing exclusion and nutrient addition on flower abundance (flowers m^{-2}, log-transformed to normalize residuals) and diversity metrics (species richness and inverse Simpson index). The first models included site, nutrient (N, P and/or K) addition treatments, and their interactions as explanatory variables. As the grazing exclusion was only applied to NPK fertilized and unfertilized plots, we used these plots in a second model, and site, NPK addition and grazing exclusion treatments, and their interactions were included as fixed effects. In all models, we included block as a random effect. We first constructed full models with all interaction terms as predictors, followed by manual backward model simplification, where interaction terms with $p > 0.05$ were removed (Crawley 2012). All models were fitted in R software (www.r-project.org), using the *lmer()* function from the 'lme4' package (Bates et al. 2015, ver. 1.1-35.2). Post hoc pairwise comparisons of treatment effects were tested using the *contrast()* function of the 'emmean' package (Lenth 2025). Maximum likelihood (ML) estimation was used in the model simplification, and the final models were fitted using restricted maximum likelihood (REML). The normality and homoscedasticity of the models were verified using functions of the R package 'DHARMa' (Hartig 2018).

We used non-metric multidimensional scaling (NMDS; Minchin 1987) to describe the flower community composition responses to the experimental treatments. For the NMDS analyses, the function *metaMDS()* was used (R package 'vegan'; Oksanen et al. 2022), which automatically determines the best solution with the lowest stress value for a given dimensionality. The NMDS flower abundance data were standardized using Wisconsin double standardization (*metaMDS* option; Oksanen et al. 2022), with the Bray–Curtis dissimilarity measure, which is well-suited for community data. To test whether flower community composition differed in response to experimental treatments, we used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001, function *adonis2()* implemented in R package 'vegan'; Oksanen et al. 2022). We relativized the distance matrix by plot totals of flower abundance and expressed it as a Bray–Curtis dissimilarity. We then specified separate PERMANOVA models for the two sites and the two experimental designs 1) factorial N, P and K additions and 2) factorial NPK addition + Fence (e.g. grazer exclusion). The main effects were included as explanatory factors. In PERMANOVA models, block was used as a strata, and 999 permutations were performed.

To test biotic homogenisation of flower assemblages across treatments, we used permutational analysis of multivariate dispersion (Anderson et al. 2006) via the function *betadisper()* in R package 'vegan' (Oksanen et al. 2022). In this procedure, compositional heterogeneity of flower assemblages was quantified as the average distance of individual sample plots from a multivariate median within a treatment, with smaller distances corresponding to within-group homogenisation. The analysis was conducted with the 'spatial median' option and checked with bias correction enabled (bias.correction = TRUE). Finally, we identified species strongly associated with specific treatments or control plots. Species were identified using the function *multipatt()* of R package 'indicspecies' (De Cáceres and Legendre 2009), with the option 'IndVal.g' and significance level of 0.05 (999 permutations).

Results

Nutrient addition effects on flower abundance, species richness and diversity

Phosphorus addition alone exerted a positive effect on flower abundance, whereas this effect was counteracted by joint N addition (Fig. 1a, Table 1). Nitrogen addition alone reduced flower abundance at the montane grassland site, whereas it had a minimal effect on the tundra grassland (Fig. 1b, Table 1, see also the Supporting information for emmeans contrasts). The additions of both K and P had a positive effect on flower abundance (Fig. 1c, Table 1). Nutrient addition treatments and site explained 58 % (R^2 without random effects) or 69 % (R^2 with random effects) of the variation in flower abundance (Table 1).

N addition reduced flower species richness (Fig. 2, Table 1). N addition treatment and site accounted for 27 % (R^2 without random effects) or 47% (R^2 with random effects) of the variation in flower species richness (Table 1). The additions of N, P and K had an interactive effect on flower species diversity (Fig. 3a, Table 1), while the effects of P and K on flower species diversity depended on site (Fig. 3b, Table 1). P and K decreased species diversity at the tundra grassland (Supporting information; emmeans contrasts). The N, P and K addition treatments, along with site, explained 22 % (R^2 without random effects) or 31 % (R^2 with random effects) of the variation in flower species diversity (Table 1), but did not show significant (at $p = 0.05$ level) pairwise differences between treatments (Supporting information; emmeans contrasts).

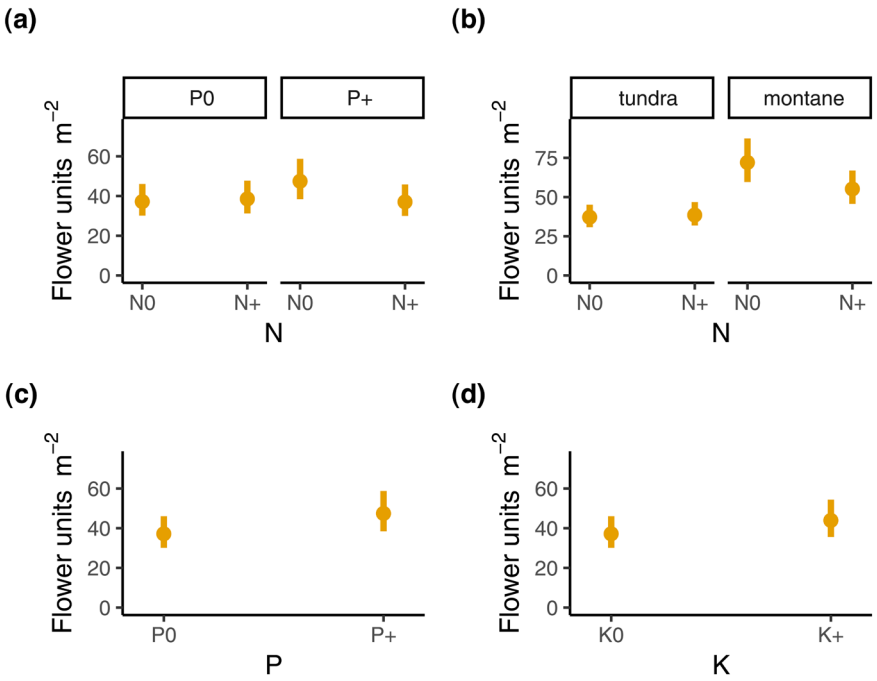


Figure 1. Predicted responses of flower abundance (flower units m^{-2}) to N, P and K additions at the tundra grassland and the montane grassland, based on the simplified mixed-effects model (Table 1). The predicted abundances were back-transformed from log-transformed values. Error bars represent 95% confidence intervals.

NPK addition and grazing exclusion effects on flower abundance, species richness and diversity

Grazing exclusion increased flower abundance, and this increase was stronger at the montane grassland than at the tundra grassland (Fig. 4, Table 2). Grazing exclusion and NPK addition interacted to influence flower abundance, with NPK addition strongly increasing flower abundance but only within grazing exclosures (Fig. 4, Supporting information; emmeans contrasts). Grazing exclusion, NPK nutrient addition treatments and site explained 88 % (R^2 without random effects) or 89 % (R^2 with random effects) of the variation in flower abundance (Table 2).

NPK addition reduced flower species richness less in grazed plots than in grazing exclosures (Fig. 5a, Table 2, Supporting information; emmeans contrasts). Grazing exclusion, NPK addition treatments and site explained 62% (R^2 without random effects) or 66% (R^2 with random effects) of the variation in flower species richness (Table 2). NPK reduced flower species diversity in the tundra grassland and increased it in the montane grassland (Fig. 5b, Table 2), whereas grazing exclusion reduced flower species diversity at both sites (Fig. 5b, Table 2, Supporting information; emmeans contrasts). Grazing exclusion, NPK addition treatments and site explained 55% (R^2 without random effects) or 58% (R^2 with random effects) of the variation in flower species diversity (Table 2).

Nutrient addition and grazing exclusion effects on flower assemblages

At the tundra grassland site, the flower assemblage responded to N, P and K addition treatments (Fig. 6a, Table 3), whereas at the montane grassland, K had no effect on flower assemblage species composition. In contrast, at the montane grassland, N and P had an interactive effect, and flower assemblages in plots receiving N and P were most distinctly separated from the controls (Fig. 6b). The nutrient addition treatments and block explained 52% (tundra grassland) or 63% (montane grassland) of the variation in the flower assemblage composition (Table 3). At both sites, nutrient addition treatments did not cause homogenisation of the flower assemblages (betadisper ANOVA tests; $p > 0.05$). Grazing exclusion and NPK addition significantly affected the composition of flower assemblages, both at the tundra grassland (Fig. 6c, Table 4) and at the montane grassland (Fig. 6d, Table 4).

More specifically, at the tundra grassland, grazing exclusion and NPK addition had an additive effect on the composition of flower assemblages (Table 4), and these treatments explained 72% of the variation in the flower assemblage composition. At the montane grassland, grazing exclusion and NPK addition had a significant interactive effect on the composition of flower assemblages (Table 4). Grazing exclusion and NPK addition treatments, along with block explained 72% (tundra grassland) or 86% (montane grassland) of the variation in the flower assemblage composition (Table 4). the tundra grassland, grazing exclusion and NPK addition treatments did not cause homogenisation of flower assemblages (betadisper ANOVA tests; $p > 0.05$), whereas at the montane grassland flower assemblages were more homogeneous in grazing exclosures than in unfenced plots (betadisper ANOVA test; $p = 0.02$, Supporting information).

Across both sites, 51 flowering plant species (excluding graminoids) were observed, of which 35 were found at the

Table 1. Summary of the simplified mixed-effects model for parameter estimates of the effects of N, P and K additions on the abundance of flower units (log-transformed), flower species richness and species diversity (inverse Simpson's index) at the tundra grassland (kilp.fi) and the montane grassland (saana.fi). The reference level of the Site factor is tundra grassland. σ^2 refers to within block variance and τ_{00} to between block variance. Intraclass correlation (ICC) indicates of the correlations within a block. Marginal R^2 describes the proportion of the variance explained by the fixed effects; conditional R^2 indicates the variance explained by both fixed and random effects (based on Nagagawa et al. 2017). Estimates with $p < 0.05$ excluded. The N × P × K interaction with a p-value > 0.05 was retained in the model simplification based on anova test ($p = 0.04$). p-values less than 0.05 are shown in bold.

	log (flower units)			**Species richness**			**Species diversity**		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	3.62	3.41 – 3.83	**<0.001**	15.81	14.50 – 17.12	**<0.001**	5.28	4.15 – 6.41	**<0.001**
Site	0.66	0.40 – 0.92	**<0.001**				-1.76	-3.19 – -0.34	**0.016**
N	0.04	-0.17 – 0.24	0.727	-3.31	-4.49 – -2.14	**<0.001**	-0.40	-1.71 – 0.90	0.537
P	0.24	0.08 – 0.41	**0.005**				-0.86	-2.29 – 0.57	0.232
K	0.17	0.05 – 0.28	**0.007**				-1.34	-2.77 – 0.09	0.065
Site × N	-0.30	-0.54 – -0.07	**0.013**				1.24	0.08 – 2.41	**0.037**
N × P	-0.28	-0.52 – -0.05	**0.020**				-0.80	-2.45 – 0.85	0.335
Site × P							1.42	-0.22 – 3.07	0.089
Site × K							2.36	0.71 – 4.01	**0.006**
N × K							-0.69	-2.34 – 0.96	0.402
P × K							0.96	-1.06 – 2.98	0.345
Site × P × K							-2.39	-4.72 – -0.06	**0.045**
N × P × K							2.18	-0.15 – 4.52	*0.066*
Random effects									
σ^2		0.06			5.53			1.35	
τ_{00}		0.02_{Blocks}			2.04_{Blocks}			0.16_{Blocks}	
ICC		0.27			0.27			0.11	
N		8_{Blocks}			8_{Blocks}			8_{Blocks}	
Observations		64			64			64	
Marginal R^2/ Conditional R^2		0.576/0.690			0.269/0.466			0.220/0.305	

tundra grassland and 36 at the montane grassland. The mean flower abundance of species under the different treatments are presented in the Supporting information. Using *multipatt* analyses, which identify species significantly associated with specific treatments, eleven species at both sites exhibited preferences for nutrient addition, grazing exclusion or for untreated control plots.

At the tundra grassland site, untreated control plots were characterized by *Antennaria dioica*, *Sibbaldia procumbens* and *Thalictrum alpinum*, while NPK fertilized plots were dominated by *Ranunculus subborealis* and *Rhodiola rosea*. At the montane grassland, control plots showed a prevalence of *Bistorta vivipara*, *Cerastium fontanum*, *Melampyrum sylvaticum* and *Parnassia palustris* characterized and *Anthriscus sylvestris*, *Silene dioica* and *Taraxacum* sp. dominated in the NPK fertilized plots (for more details see the Supporting information). At the tundra grassland, the abundances of flower units of tall herbs strongly increased in grazing exclosures: *Solidago virgaurea* (21-fold increase), and *Trollius europaeus* (27-fold increase) (Supporting information). Also at the montane grassland, flowers of tall herbs increased in grazing exclosures: *Anthriscus sylvestris* (no flowers in the grazed controls and, on average, 18.9 flower units m^{-2} in exclosures), *Geranium sylvaticum* (48-fold increase) and *Trollius europaeus* (6-fold increase) (Supporting information). The specific changes in flower abundances caused by grazing are clearly visible in the photos taken from the experimental sites, where tall herbaceous species bloom abundantly in the grazing exclosures (Supporting information). These blooming tall forbs include particularly members of *Geraniaceae* and *Apiaceae* at the montane grassland and *Asteraceae* at the tundra grassland (Supporting information).

Discussion

We found that the long-term experimental treatments of nutrient addition and grazing exclusion led to significant changes

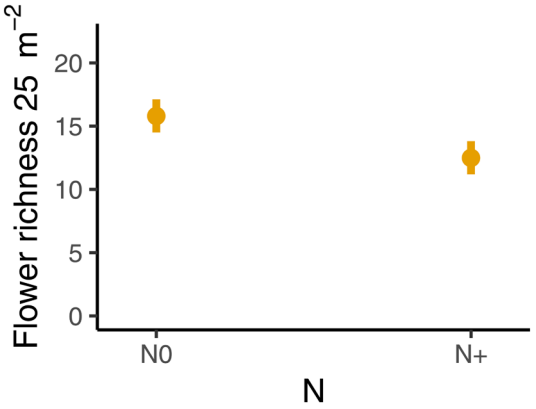


Figure 2. Predicted flower species richness (flower species 25 m^{-2}) in the control and N addition treatments across sites, based on the mixed-effects model (Table 1). Error bars represent 95% confidence intervals.

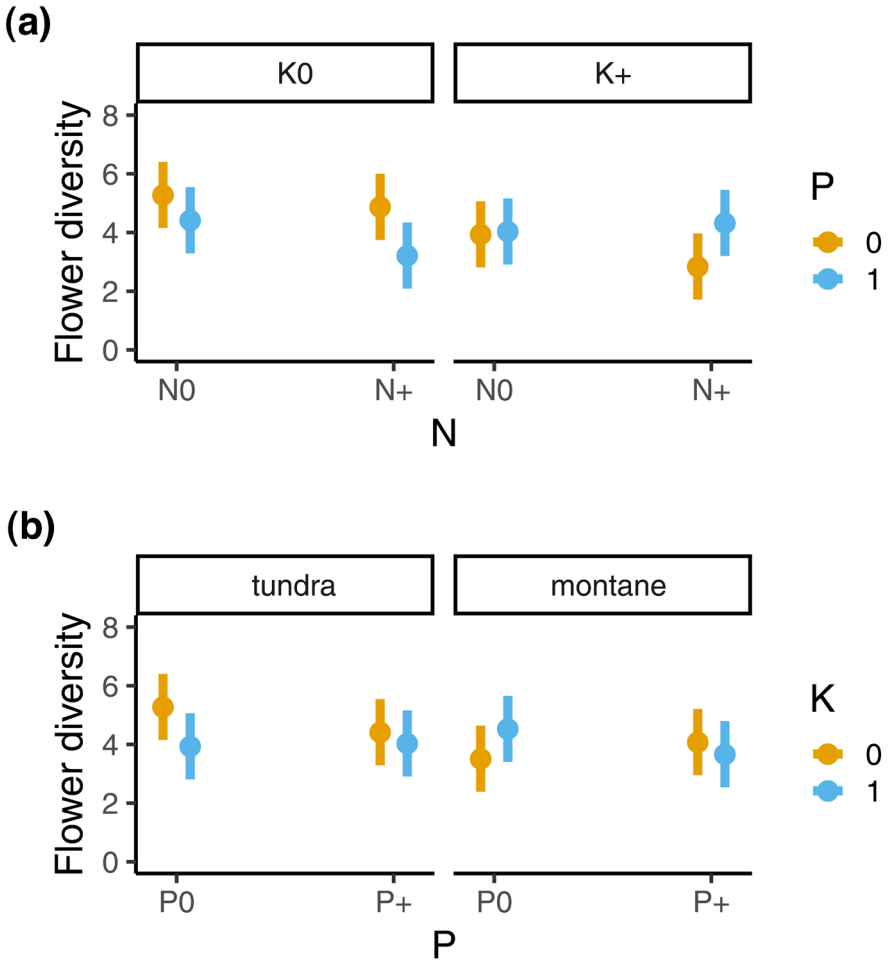


Figure 3. (a) Effects of nutrient addition on flower diversity (inverse Simpson index). (a) Predicted flower species diversity (inverse Simpson's index of the mean number of flower units m^{-2}) in the control, N, P and K additions across sites, based on the mixed-effects model (Table 1). (b) Predicted flower species diversity (inverse Simpson's index of the mean number of flower units m^{-2}) in the control, K and P additions in the tundra grassland, and montane grassland sites, based on the mixed model (Table 1). Error bars represent 95% confidence intervals.

in flowering plant communities, revealing how nutrient availability and grazing pressure shape floral resources essential for flower-visiting insects. Our findings demonstrate that both bottom–up (nutrients) and top–down (grazing) processes regulate floral resources, with effects varying depending on site conditions and flowering plant community characteristics. In the following, we discuss our main findings in light of our predictions described in the Introduction.

Multi-nutrient addition effects on flower abundance, species richness and diversity

Contrary to our initial prediction, the additions of N, P and K did not uniformly enhance flower abundance. Firstly, we found that N addition primarily had negative effects. This finding aligns with previous studies indicating that increased N availability reduces flower production (Burkle and Irwin 2010). However, our results also reveal that alleviating multi-nutrient co-limitation can either enhance or suppress flower abundance. Unlike in croplands, where N and P commonly co-limit plant production (Ringeval et al. 2021),

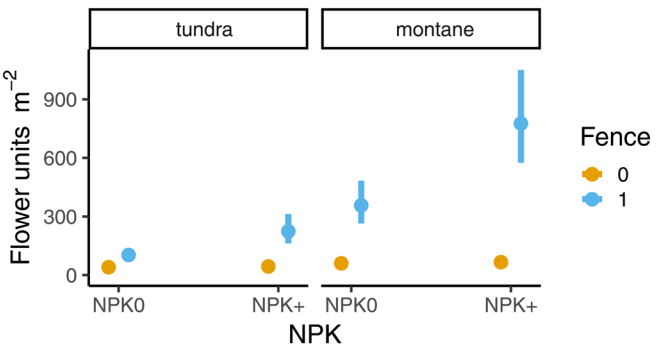


Figure 4. Predicted flower abundance (flower units m^{-2}) in controls, grazing exclusion (Fence), and NPK addition at the tundra grassland and montane grassland and their combined treatments based on the mixed-effects model (Table 2). Error bars represent 95% confidence intervals.

Table 2. Summary of the simplified mixed-effects model for parameter estimates of the effects of grazing exclusion and NPK addition on the abundance of flower units (log-transformed), flower species richness and species diversity (inverse Simpson's index) at the tundra grassland (kilp.fi) and the montane grassland (saana.fi). p-values less than 0.05 are shown in bold.

	log (flower units)			Species richness			Species diversity		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	3.71	3.38 – 4.05	**<0.001**	16.00	14.40 – 17.60	**<0.001**	5.26	4.45 – 6.07	**<0.001**
Site	0.40	0.00 – 0.79	**0.049**				-1.56	-2.59 – -0.53	**0.005**
Fence	0.93	0.49 – 1.36	**<0.001**	-0.32	-2.40 – 1.75	0.751	-1.85	-2.55 – -1.15	**<0.001**
NPK	0.09	-0.28 – 0.46	0.609	-3.25	-5.38 – -1.12	**0.004**	-0.67	-1.67 – 0.33	0.179
Site × Fence	0.84	0.31 – 1.37	**0.003**						
Fence × NPK	0.69	0.16 – 1.22	**0.013**	-3.44	-6.48 – -0.40	**0.028**			
Site × NPK							1.71	0.31 – 3.11	**0.018**
Random effects									
σ^2	0.13			4.29			0.91		
τ_{00}	0.01_{Blocks}			0.55_{Blocks}			0.07_{Blocks}		
ICC	0.06			0.11			0.07		
N	8_{Blocks}			8_{Blocks}			8_{Blocks}		
Observations	32			32			32		
Marginal R^2/ Conditional R^2	0.881/0.889			0.615/0.659			0.547/0.580		

these nutrients exhibited an antagonistic interaction effect. While P alone increased flower abundance, the joint addition of N and P did not result in any increase in flower abundance. This interaction effect likely arose from the development of strongly graminoid-dominated plant communities with sparse cover of flowering forbs under N and P addition (Supporting Information; see also Nelson et al. 2025). Interestingly, the effects of P and K differed from those of N and P. P and K additively increased flower abundance, suggesting that these nutrients can limit flower production without promoting graminoid overgrowth (Supporting information). These findings indicate that multi-nutrient additions can have stronger effects on flower abundance than single-nutrient applications. However, their effects can range from additive (P and K) to antagonistic (N and P), depending on nutrient identity.

Our results did not provide unequivocal support for our prediction that the additions of N, P and K would decrease flower species richness or diversity. Instead, N addition alone reduced flower species richness, whereas P and K had no significant effects. This suggests that the declines in flower species richness are primarily driven by increased N availability. The observed decreases in flower species richness likely result from the loss of low-statured forb species, such as *Antennaria dioica*, *Euphrasia wettsteinii*, *Pyrola minor* and *Sibbaldia procumbens*, that are inferior in the competition for light. These findings are compatible with previous research demonstrating that increased nutrient availability leads to lower overall plant species richness (Harpole et al. 2016, Eskelinen et al. 2022). Additionally, our results highlight N as a key driver not only of overall plant species richness (Band et al. 2022) or forb species richness (Nelson et al. 2025) but also of flower species richness. However, it is worth noting that flower species richness and species diversity (measured as inverse Simpson's index) responded differently. While flower species richness declined with increased N, flower species diversity exhibited a three-way interaction among N, P and K, with site-dependent effects of P and K. Therefore, our results illustrate that patterns of flower diversity responses to multi-nutrient additions can strongly depend on the diversity metrics

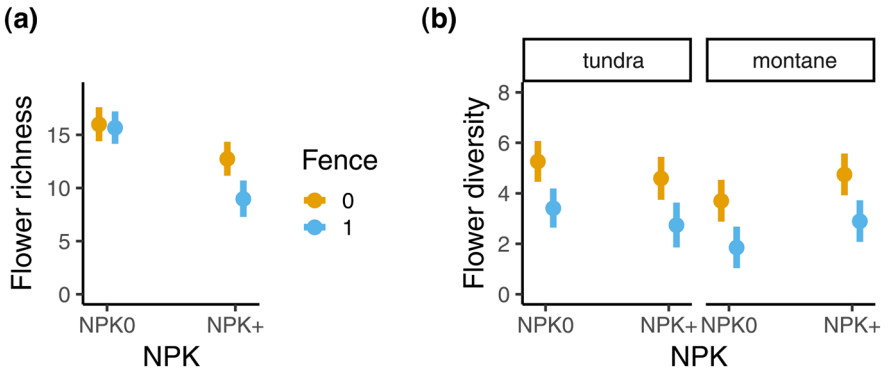


Figure 5. (a) Predicted flower species richness (flower species 25 m^{-2}) in controls, grazing exclusion (Fence), and nutrient addition (NPK addition) treatments. (b) as (a) but predicted flower species diversity (inverse Simpson's index), based on the mixed-effects models (Table 2). Error bars represent 95% confidence intervals.

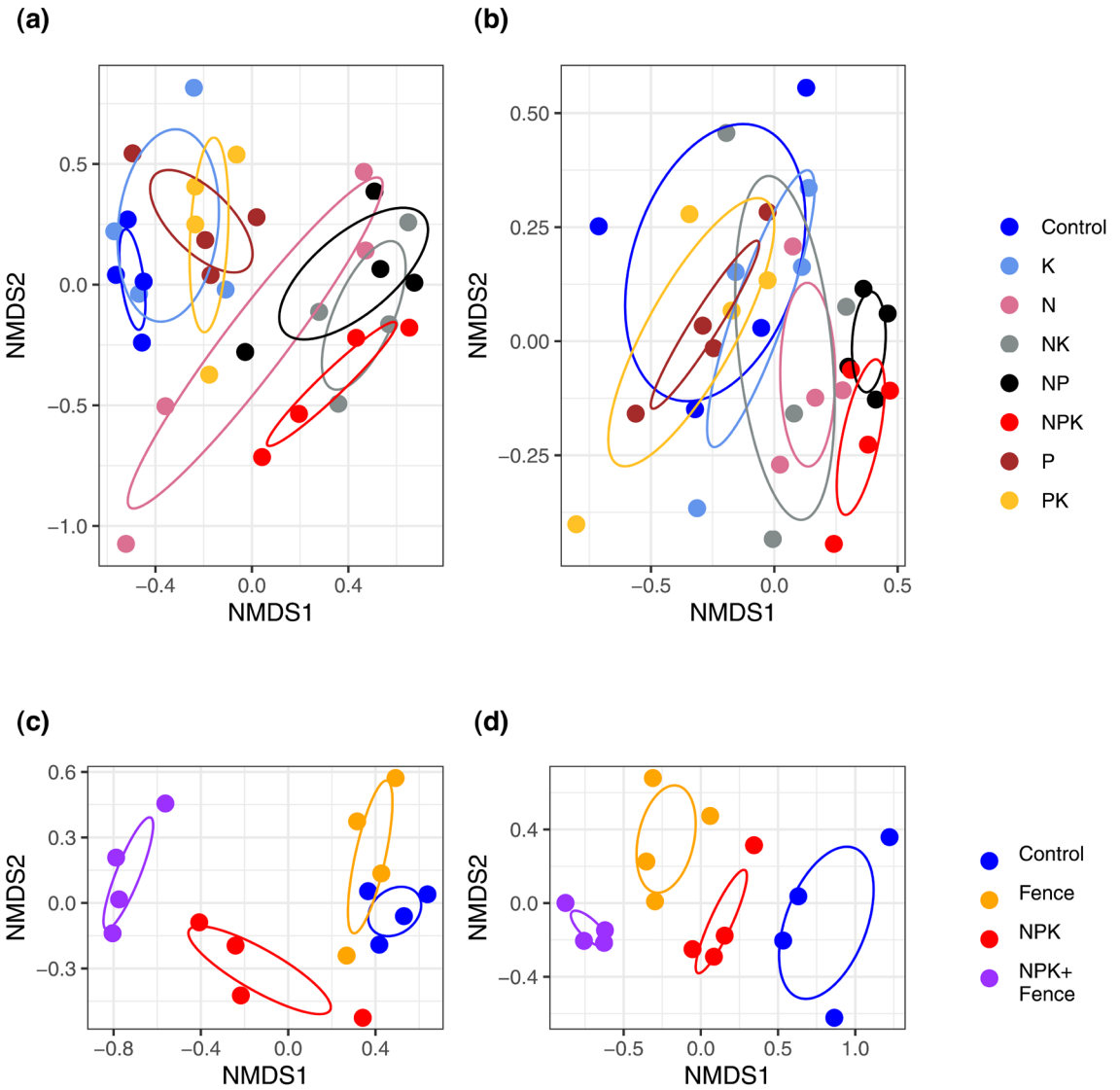


Figure 6. NMDS ordinations for flower assemblage composition in grazed plots receiving N, P and K addition (a) at the tundra grassland (stress 0.22) and (b) at the montane grassland (stress 0.19), and plots with grazing exclusion (Fence) and NPK addition, (c) tundra grassland (stress 0.12) and (d) montane grassland (stress 0.10). The ellipses indicate one standard deviation about the centroid.

Table 3. Summary of permutational analysis of compositional differences (*adonis2*) in flower assemblages across nutrient addition (N, P, K) treatments. p-values less than 0.05 are shown in bold.

			Tundra grassland			Montane grassland			
Term	df	SS	R^2	F	p	SS	R^2	F	p
Block2	1	0.166	0.042	1.848	0.077	0.085	0.023	1.295	0.278
Block3	1	0.177	0.045	1.979	0.057	0.123	0.033	1.877	0.107
Block4	1	0.077	0.020	0.861	0.539	0.234	0.064	3.586	**0.016**
N	1	0.686	0.174	7.650	**0.001**	1.078	0.293	16.522	**0.001**
P	1	0.211	0.054	2.354	**0.029**	0.323	0.088	4.945	**0.004**
K	1	0.311	0.079	3.475	**0.003**	0.035	0.009	0.535	0.723
N × P	1	0.146	0.037	1.628	0.119	0.299	0.081	4.578	**0.006**
N × K	1	0.049	0.012	0.543	0.842	0.032	0.009	0.494	0.804
P × K	1	0.129	0.033	1.443	0.192	0.012	0.003	0.182	0.974
N × P × K	1	0.107	0.027	1.196	0.324	0.095	0.026	1.459	0.215
Residual	21	1.882	0.48			1.371	0.37		
Total	31	3.941	1.0			3.686	1.0		

Table 4. Summary of permutational analysis of compositional differences (*adonis2*) in flower assemblages across NPK addition and grazing exclusion (Fence) treatments. p-values less than 0.05 are shown in bold.

			Tundra grassland			Montane grassland			
Term	df	SS	R^2	F	p	SS	R^2	F	p
Block2	1	0.071	0.034	1.103	0.349	0.022	0.008	0.504	0.695
Block3	1	0.149	0.072	2.309	0.066	0.040	0.015	0.920	0.401
Block4	1	0.115	0.056	1.787	0.137	0.090	0.033	2.071	0.124
NPK	1	0.501	0.242	7.768	**0.001**	0.601	0.217	13.768	**0.001**
Fence	1	0.593	0.286	9.185	**0.001**	1.329	0.480	30.442	**0.001**
NPK × Fence	1	0.059	0.029	0.919	0.461	0.292	0.105	6.687	**0.007**
Residual	9	0.581	0.28			0.393	0.14		
Total	15	2.069	1.0			2.768	1.0		

used, as each captures distinct aspects of community structure. Species richness reflects the number of species present, whereas diversity indices account for species abundance and evenness. Considering multi-diversity metrics rather than relying solely on species richness is important to avoid missing shifts in species dominance or persistence of rare species, factors that can have significant ecological consequences.

Effects of joint nutrient addition and grazing exclusion on flower abundance

Our results did not support the prediction that grazing exclusion and multi-nutrient (NPK) addition would independently increase flower abundance in an additive manner. Instead, the effect of multi-nutrient (NPK) addition alone was minimal, but its combined effect with grazing exclusion resulted in a strong positive interaction effect, yet this synergistic effect depended on site. Grazing exclusion alone increased flower abundance more at the montane grassland (6-fold increase) than at the tundra grassland (2.5-fold increase). Under multi-nutrient (NPK) addition, grazing exclusion increased flower abundance (4.5-fold increase at the tundra grassland and 13-fold increase at the montane grassland). These results are qualitatively consistent with those of Veen et al. (2024) who also observed an interactive effect of NPK addition and grazing exclusion on flower abundance (χ^2-values 16.67, 285.72, and 23.38 for the interaction effect, NPK main effect and grazing exclusion main effect, respectively), suggesting relatively strong effects of multi-nutrient (NPK) addition treatments as compared to the effects observed at our study sites. Therefore, grazing and multi-nutrient effects can vary remarkably not only across sites but also across ecosystems from high latitudes to temperate regions.

Grazing mitigation of nutrient addition-induced diversity loss

Grazing mitigated the negative effects of multi-nutrient (NPK) additions as predicted. Specifically, grazing counteracted declines in flower species richness in NPK fertilized plots, consistent with previous studies showing that grazing buffers the negative effects of nutrient enrichment on plant species richness (Borer et al. 2014a) by preventing light competition from excluding less competitive species (Eskelinen et al. 2016, 2022). However, Veen et al. (2024), using a similar experimental design, found no significant interactive effects between NPK addition and grazing exclusion on flower species richness. This discrepancy may stem from differences in the respective study sites – Veen et al. (2024) studied temperate regions with more fertile soils and a diverse array of natural grazers, while our study focused on arctic-boreal grasslands with lower soil fertility and predominant reindeer grazing.

Unlike flower species richness, grazing exclusion and NPK addition did not show significant interactive effects on flower species diversity (inverse Simpson's index). Based on this diversity metric, our results provide no evidence for grazing mitigation of NPK-driven declines in flower diversity. However, grazing alone promoted flower species diversity, likely by limiting the dominance of taller, competitive plants and allowing smaller species to persist. The differences between flower species richness and diversity (inverse Simpson's index) likely reflect species-specific responses under nutrient-enriched and ungrazed conditions. The decline in flower species richness may result from the disappearance of less competitive small forbs in ungrazed and NPK fertilized plots (a 50% drop in flower species as compared to controls), while flower species diversity responses may be driven by shifts in a few co-dominants.

Floral composition and homogenisation

As predicted, additions of single (N, P and K) and multi-nutrients (NPK), along with grazing exclusion, altered flower assemblage composition. At the tundra grassland, both K and P treatments resulted in moderate compositional changes, whereas K had no significant effect on flower composition at the montane grassland. At both sites, N addition alone and combined N and P additions caused strong shifts in flower assemblages (see also Wang et al. 2022). These results demonstrate that different nutrients, especially N, can substantially alter floral resource production, for instance by changing the relative abundances of graminoids and forbs. Such compositional changes can impact not only floral resources available to insects, but also long-term plant community dynamics through changes in the plant reproductive performance and seed limitation (Turnbull et al. 2000, Côté et al. 2004, Pichon et al. 2023).

Contrary to our prediction, we found no evidence that multi-nutrient additions would lead to homogenisation of flower assemblages. Instead, homogenisation occurred only

at the montane grassland and was caused by grazing exclusion. Therefore, this suggests that grazing may promote variation of flower assemblages in forb-rich communities. While studies explicitly addressing effects of grazing on flower beta diversity remain scarce (but see Rolando et al. 2013), our results indicate that grazing could be regarded as a potentially important driver of beta diversity of floral resources available to flower visitors (Carvalheiro et al. 2013).

Site-specific responses and context dependency

Our results generally aligned with our prediction that treatment effects on flower abundance, diversity or composition are influenced by site-specific conditions. This indicates that initial site factors, such as species composition, can significantly affect how flower assemblages respond to altered environmental conditions. At the tundra grassland, where low-growing forbs dominate, grazing had a relatively small effect on flower abundance. This may reflect lower susceptibility of common forbs in these higher elevation areas to florivory, possibly due to general adaptations to grazing pressure (Oksanen 1990). In contrast, at the montane grassland, reindeer begin grazing early in spring and consume the majority of developing flower stems, particularly those of taller forbs like *Anthriscus sylvestris*, *Geranium sylvaticum* and *Trollius europaeus*. Although lemmings, mountain hares, and microtine rodents may also influence flowering to some extent at our experimental sites (Boulanger-Lapointe et al. 2017), it appears that reindeer grazing is the primary herbivore limiting flower abundance, especially at the montane grassland. Similar susceptibility of taller plant species' inflorescences to large herbivores has been observed in other studies as well (Côté et al. 2004). Florivory and folivory on tall forbs along with their replacement by grazing-tolerant grasses, may also explain the strong effects of grazing on flower assemblage composition in these tall-herb dominated communities.

Our results provided no support for the prediction that nutrient addition would have a stronger impact on flower abundance at the tundra grassland compared to the montane grassland. This contradicts the assumption that plant responses to increased nutrient availability are strongly influenced by initial site conditions and species composition (Chapin et al. 1986). Nevertheless, the effects of nutrient addition varied by site but were limited to individual nutrients and deviated from the expected direction. For instance, N addition had a negative impact on flower abundance in the montane grassland. Additionally, our results revealed that multi-nutrient (NPK) additions led to minimal increases in flower abundance at both sites, likely due to the strong effect of grazing on flowering plant assemblages. The increase in flower abundance in NPK fertilized and fenced areas was relatively strong at the montane grassland, reflecting that plant species adapted to nutrient-rich sites can be inherently more responsive to increased nutrient supply and can readily increase their flowering under nutrient enrichment. However, grazing can eliminate this effect. Consequently, floral resources for flower-visiting insects are regulated not only by nutrient availability but also by grazing pressure, and these effects may vary across sites.

While our study provides insights into how nutrient enrichment and grazing exclusion influence floral resources, it does not measure pollinator communities and visitation rates of plant–pollinator interaction networks directly. Nevertheless, changes in floral resources may have cascading effects on pollinator communities and network stability. Future research that integrates pollinator interaction network analysis and effects on plant reproductive output would allow a deeper understanding of how bottom–up and top–down forces propagate through trophic levels. Finally, exploring the temporal dynamics of flower availability for flower-visiting insects in northern grazing lands could uncover mismatches or resilience in these systems. By linking changes in floral resources to pollinator responses, future studies could help clarify the mechanisms behind global change drivers for plant–pollinator mutualisms and ecosystem functioning.

Concluding remarks

Our study highlights that floral resources in high-latitude grasslands are highly responsive to changes in both nutrient availability and grazing pressure. Notably, floral abundance and species richness often show opposite trends: while abundance increases, richness declines, accompanied by substantial changes in flower species composition. These findings provide new insights into how high-latitude grassland vegetation sustains floral resources for organisms depending on them, and how the production of these resources is regulated by soil nutrients and herbivory.

Although grazing generally reduced flower abundance, it contributed to greater flower species richness and diversity, while also altering flower species composition. Analogous effects of deer species on floral resources (reducing abundance but enhancing diversity) have been observed in other systems (Virtanen et al. 2002, Côté et al. 2004, den Herder et al. 2004, Tamburini et al. 2017, Davidson et al. 2020, Rosenberger and Conforti 2020). Our findings suggest that while reduced grazing pressure might increase floral abundance, it can also lead to a decline in flower species diversity. Moreover, our results highlight the role of reindeer grazing in mitigating the negative effects of nutrient enrichment on flower species richness. Given that greater floral diversity can support a wider range of flower-visiting insects and enhance pollination services (Dorado and Vásquez 2014, Zoller et al. 2023, Redr et al. 2024), we recommend incorporating floral resources into current ecosystem status assessments (Kontula and Raunio 2019).

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Author contributions

Nicolina Johanson: Johanson Funding acquisition (equal); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Harry Olde Venterink**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Luísa G. Carvalheiro**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Anu Eskelinen**: Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Risto Virtanen**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rfj6q57p1 (Johanson et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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