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ORIGINAL ARTICLE

Herbivory-Induced *Nardus stricta* Dominance Enriches Plant Silicon Relative to Phosphorus Enforcing Alternative Ecosystem Stable States in an Alpine Environment

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Abstract

Herbivory can alter plant stoichiometry generating biogeochemical feedbacks that stabilize or drive transitions between ecosystem states. We report results after 23 years from a grazing experiment in Norway comparing five paired exclosures and grazed plots that were complemented with inclusion of five islands serving as a natural control. We tested the hypothesis that herbivory-driven shifts in plant dominance scale to alter elemental stocks and stoichiometry indicative of decelerated ecosystem biogeochemistry. Domestic sheep, *Ovis aries*, grazing was associated with dominance of the herbivory-resistant grass, *Nardus stricta,* rich in silicon (Si), while the ungrazed islands harbored a sheep-preferred grass *Avenella flexuosa* and forbs such as *Solidago virgaurea* relatively richer in phosphorus (P). Inside the exclosures, *N. stricta* had lower abundance than under grazing, but remained dominant at most sites. Its persistence suggests hysteresis on the trajectory to an ungrazed state displayed inside one mainland exclosure and on the islands. *N. stricta* had a high Si:P ratio, and through its dominance, this stoichiometry scaled to aboveground biomass with a more than doubling of the stock of Si (125%) on the mainland compared to the islands and a 46% increase in the concentration of Si. In contrast, the concentration of P in aboveground biomass on the islands was more than double (122%) the mainland. Herbivory appears to stabilize a high-Si ecosystem state compared to a high-P ungrazed state indicated through the plant Si:P ratio in this alpine ecosystem. This enrichment of silicon relative to phosphorus may cascade throughout the ecosystem with far-reaching implications.

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Key words: *Avenella flexuosa*; Dominance; Ecosystem biogeochemistry; Grazing; Norway; *Nardus stricta*; *Ovis aries*; *Solidago virgaurea*; Stoichiometry.

Highlights

- Grazing increased dominance of a grass with a high silicon to phosphorus ratio
- Grazing led to a 125% increase in the stock of silicon in plant biomass
- The Si:P ratio appears indicative of two alternative ecosystem stable states

Introduction

Herbivory is a powerful driver of the stocks and fluxes of elements within ecosystems (Pastor and others 1993, 2006; Loreau 1995; McNaughton and others 1997). The preferential consumption of certain plants over others can have cascading impacts on the import, export and cycling of the essential elements that underpin primary productivity (Bardgett and Wardle 2003; Pastor and others 2006; Sitters and Andriuzzi 2019; Pringle and others 2023). However, the link between plant–herbivore interactions and the ecosystem stocks and stoichiometry of elements is complex, potentially idiosyncratic and uncertain (Pastor and others 2006; Sitters and Andriuzzi 2019; Pringle and others 2023).

The ecosystem consequences of plant–herbivore interactions have been broadly described as an acceleration or deceleration of ecosystem nutrient cycling reflecting regime shifts to alternative ecosystem states (Bardgett and Wardle 2003; Pastor and others 2006; Wal 2006). Herbivores shunt or redirect elemental mass and energy through their digestion, and by preferring certain species over others, generate feedbacks among plant growth, decomposition, and nutrient availability (Loreau 1995; Pastor and others 2006; Harrison and Bardgett 2008; Sitters and Andriuzzi 2019). Herbivores can drive an ecosystem feedback where increased inputs of low quality plant tissue into the soil reduces the supply of elements that herbivores need such as nitrogen (N), phosphorus (P) or sodium (Na) leading to an enrichment in plants of those associated with defense such as silicon (Si) (Bardgett and Wardle 2003; Massey and others 2007; Hartley and DeGabriel 2016; Borer and others 2019; Petit Bon and others 2022; de Tombeur and others 2023). For example, the preferential consumption of N-fixing species reduces N-inputs and favors species with slower decomposing tissue that reduces N-mineralization leading to a deceleration of the N-cycle (Ritchie and others 1998). Drawn from such empirical examples, a general prediction has been that herbivory on low soil fertility leads to a deceleration of ecosystem nutrient cycling while herbivory on high fertility soil leads to its acceleration (Loreau 1995; Wardle and others 2004; Pastor and others 2006; Harrison and Bardgett 2008; Sitters and Andriuzzi 2019). However, we lack a general understanding of when, and why, herbivory accelerates or decelerates ecosystem biogeochemistry. Can herbivory or its absence generate stabilizing or destabilizing feedback to enforce alternative accelerated or decelerated ecosystem states?

The quantification of plant stoichiometry in dominant species and its scaling to ecosystem stocks can help explain how herbivory stabilizes or drives transitions among ecosystem states. As Kaspari and Powers (2016) extol, it is imperative to expand the elemental aperture to less-studied elements such as Si, Ca, Mg, K and Na in order to link ecology and biogeochemistry (Mládková and others 2018; Borer and others 2019; Katz 2019; Hao and others 2020; Kaspari and others 2021; Petit Bon and others 2022; de Tombeur and others 2023). Quantification of plant stoichiometry of less-studied elements such as Si in relation to known elements such as P can inform the ecosystem response to herbivory (de Tombeur and others 2021; Kaspari and others 2021; Petit Bon and others 2022). For example, grazing can benefit grasses which show a phylogenetic signal of being high in Si (Hodson and others 2005) and Si has been associated with defense against herbivory (McNaughton and others 1985; Massey and others 2007; Hartley and DeGabriel 2016). If herbivory promotes the dominance of well-defended, resistant species and decelerates ecosystem nutrient cycling, then the ecosystem state may reflect high Si. For example, Si-based plant defenses have been shown to increase in a 2-million year retrogressive chronosequence with decreasing soil P (de Tombeur and others 2021). If herbivory promotes tolerant species with a faster growth rate and accelerates ecosystem nutrient cycling, then the ecosystem state may reflect high-P along traditional fast-slow axes (Reich 2014). The stoichiometry that is associated with faster growth such as high N, P, and Ca can be related to fast digestion in the rumen

and decomposition in the soil while those associated with structural tissue and defense can slow decomposition and present low digestibility (Cornwell and others 2008; Mládková and others 2018). Examination of the ratio of elements associated with growth and tolerance such as P and those associated with defense and resistance such as Si may serve as a robust proxy to understand herbivory-induced ecosystem stable states.

Using a long-term grazing experiment in the mountains of Norway running for over two-decades (Austrheim and others 2007), our objective was to determine the impact of extensively grazing domestic sheep, *Ovis aries*, on the stocks and ratios of elements within plant biomass and the soil. This region of south-western Norway with a long history of transhumance—the seasonal grazing and movement of animals—on acidic, nutrient poor soil was used to better characterize the ecosystem effects of herbivory in areas of low soil fertility. There is a long-standing phenomenon in the North-Atlantic region that heavy sheep grazing in upland areas promotes the dominance of herbivory-resistant grasses, notably *Nardus stricta,* that is difficult to remediate (Fenton 1936; Welch 1986; Grant and others 1996; Armstrong and others 1997; Holland and others 2008; Ross and others 2016; Marrs and others 2020). We interpret this phenomenon of grazing-induced *N. stricta* dominance through the theory of alternative ecosystem stable states examined through the lens of Si and P stoichiometry (Scheffer and Carpenter 2003). We explored a potential ecological mechanism that herbivory, through promoting dominance of a slow-growing, well-defended species with low litter quality, drives a deceleration of ecosystem nutrient cycling that stabilizes the grazed *N. stricta* state. We tested the hypothesis that herbivory-driven shifts in plant dominance scale to alter elemental stocks and stoichiometry indicative of a decelerated ecosystem state under conditions of low soil fertility combined with seasonal transhumance grazing.

Methods

Site Description

The site is situated in Setesdal Vesthei (59°02′06.2′′N 7°08′37.6′′E), a low-alpine region (840–1050 m a.s.l.) in Norway (Speed and others 2014). The region's climate has an average mean annual temperature of 1.66 °C and mean annual precipitation of 1675 mm from 1989 to 2024 (Lussana and others 2018). The site's granitic parent material gives rise to a nutrient poor soil (Austrheim and others 2007). The soils of the study site vary between Histosols, Gleysols, and Podzols. The mineral soils have an acidic ($pH_{water} \sim 4.4$), deep (mean 13.7; range 4–27 cm) organic (O) horizon (Supplemental Table 1).

Description of the Herbivore Community

The region has a long history of domestic sheep (*Ovis aries*) grazing during summer with densities between 44 and 88 sheep km^{-2} (Speed and others 2014). Given the level of productivity, this area has been classified with grazing above the carrying capacity of around 50 sheep km^{-2} (Rekdal and Angeloff 2007). A small herd of wild reindeer (*Rangifer tarandus*), (0.15–0.25 reindeer km^{-2}) graze in the region year-round. Rodent populations (including lemmings *Lemmus lemmus* and voles *Microtus* spp.) typically show cyclic behavior with frequent signs of grazing at population peaks (Austrheim and others 2007). The invertebrate herbivore community has not been formally assessed.

Experimental Design and Sampling

The experiment was established in 2000 with 10 mainland sites with a paired exclosure design to exclude sheep at each site with two 50 m × 20 m plots: exclosed and grazed (Austrheim and others 2007; Speed and others 2014) (Supplemental Figure 1). The experimental exclosures are active only during the snow-free grazing season and prevent access by large herbivores (that is, sheep and reindeer) but not rodents or invertebrates. The core sampling design consists of repeatedly sampled permanent quadrats surveyed for plant composition (Austrheim and others 2007). In 2012, three non-permanent quadrats (0.25 m^2) were destructively sampled both inside and outside the fences (Speed and others 2014). In addition to the mainland sites, Speed and others (2014) sampled three islands where sheep are not present. At each of these three islands, three non-permanent quadrats on south facing slopes and habitats similar to the mainland sites were selected for sampling. In 2023, these three islands along with an additional two islands were sampled. On some islands, mountain birch stands (*Betula pubescens*) have established in the absence of grazing. For this study, sampling was limited to locations outside of the birch canopy, with quadrat establishment otherwise following the protocol as described in Speed and others (2014). Sampling at five mainland sites and five islands occurred in July (3rd–9th), 2023. Our sampling represents the plant community at the

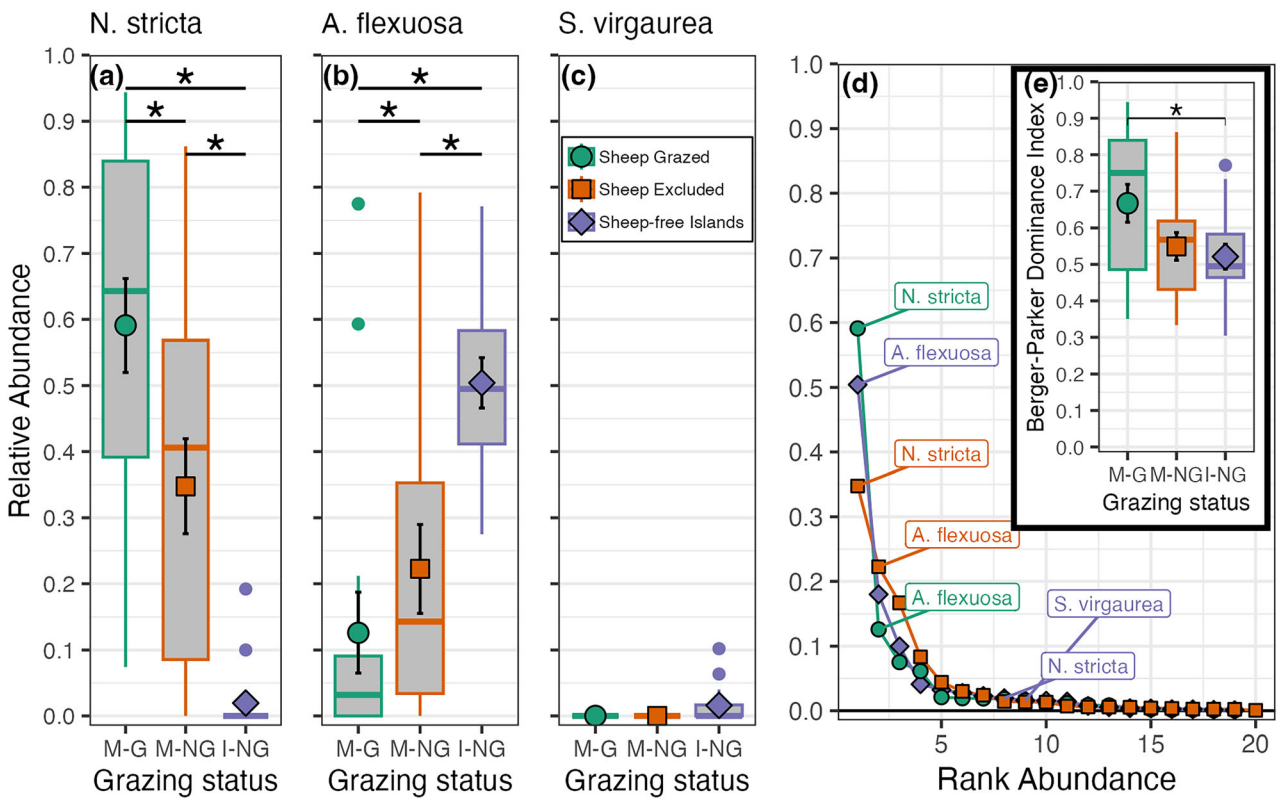


Figure 1. The relative abundance of three plant species **a** *Nardus stricta*, **b** *Avenella flexuosa*, **c** *Solidago virgaurea* across three grazing statuses: Sheep grazed (green circles) (M-G), Sheep excluded (orange squares) (M-NG) and Sheep-free islands (purple diamonds) (I-NG). Each large point represents the mean ± 1 standard error (SE). The boxplots show the min, max, upper and lower quartile, and median of the data. **d** The mean relative abundance sorted by rank for all measured species across the three grazing statuses. **e** The Berger–Parker Dominance Index across the three grazing statuses. Each large point represents the mean ± 1 SE. An Asterix denotes pairwise differences < 0.05.

onset of grazing within approximately two weeks of the snow depth reaching zero. We designate the explanatory variable as ''Grazing status'' denoting three levels: Sheep grazed (M-G, $n = 15$), Sheep excluded (M-NG, $n = 15$) and Sheep-free islands (I-NG, $n = 15$). The sample size was 45 quadrats total with three at each paired mainland plot or island.

Description of the Island versus Mainland Study Design

The experimental exclosures and islands are within an ~ 80 km^2 area (Supplemental Figure 1). The three originally sampled islands are all thought to be natural islands (Speed and others 2014). In the present study, we sampled two additional islands, one in each of the same two waterbodies which were formed during the construction of a hydro-electric dam ~ 43 (I4) and ~ 53 (I5) years ago. Our study therefore includes experimental herbivore exclosures of a 23-year duration, and both human-made and natural islands ranging in age from 50 years to permanent islands. The five islands are all within one kilometer from the lake edge (Supplemental Figure 1). There are several sites along the lake edge with three sampled presently (M2, M3, and M4). A previous analyses found no major differences in elevation, depth of the soil, or soil type including or excluding a lake-edge effect (Speed and others 2014). Furthermore, differences in the plant community from the islands and mainland were robust to including or excluding only sites on the lake edge (Speed and others 2014). However, in-situ microclimate data has not been tested and remains a source of uncertainty. Furthermore, there may be unmeasured island-specific faunal behavior. Based on existing geological maps, the sampling sites are all in areas dominated by gneisses and granodiorite and suggest no differences in mineralogy (Geological Survey of Norway). We additionally report new data showing similar soil texture and phosphorus sorption capacity from the mainland and island plots.

Plant Sampling and Analyses

In each of the 45 quadrats, the abundance of each species was assessed using the point-intercept method with 16 systematically placed pins per quadrat to record intercept frequency with multiple hits per species per pin recorded (Jonasson 1988). Following these counts, the standing stock of aboveground vascular plant biomass was clipped to ground level using an electric hand-clipper (ISIO, BOSCH, USA). *N. stricta* standing litter was included and a noticeable amount of standing litter was observed. The biomass was air-dried for approximately three days and then transported to the lab and dried at 60 C for 72 h and ground to 1 mm. In addition to aboveground biomass at the quadrat scale, leaves were clipped for three species giving one sample per species per main plot or island where present. At the species scale, we focus on three plant species that fall along a spectrum of herbivory resistance: *N. stricta* being a grazing resistant grass that is slow-growing and high in [Si] (Perkins 1968; Massey and others 2007); *Avenella flexuosa* being a grazing preferred grass found on the islands and inside sheep-excluding exclosures (Pakeman 2004; Speed and others 2014); and *Solidago virgaurea*, a forb within *Asteraceae*, that is the most sheep-preferred species (Evju and others 2006) and found on the islands (Speed and others 2014) whose congener *Solidago rigida* has both high litter quality and is herbivore-preferred (Furey and Tilman 2023, 2024). The leaves represent early-season nutrient-rich leaves likely at their relative seasonal peak in quality. The final sample size is then $n = 15$ (5×3) ($n = 5$ for each of M-NG, M-G and I-NG) for the grasses, and $n = 13$ (I-NG = 5, M-NG = 4, M-G = 4) for *S. virgaurea*. The leaves were dried and ground similarly to the other biomass. The samples were analyzed for total C and N by the dry combustion method (LECO CHN628, USA). The samples were acid digested and analyzed using Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES) (5110 VDV, Agilent, USA) for their total elemental composition for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), iron (Fe), copper (Cu), aluminum (Al), manganese (Mn), zinc (Zn), molybdenum (Mo), sodium (Na) and silicon (Si). Further details are provided in the supplement.

Soil Sampling and Analyses

Following the clipping of biomass, in the center of each 0.25m^2 quadrat a soil sample was taken using a 4.8 cm diameter split core sampler to $\sim$ 40 cm. In soils with a mineral fraction, the cores were cut to separate the O-horizon and the remaining mineral soil was cut in 10-cm sections up to 30 cm. In organic soils, three 10 cm cores were cut to 30 cm. The O-horizon in soils with a mineral fraction (33 out of 45) was combined with the top 10 cm of the histosols (12 out of 45) to create a set that we refer to as the O-horizon ($n = 45$). The soils were dried at 40 C, weighed and sieved to a 2 mm fraction to remove the coarse $>$ 2 mm fraction and weighed again.

There were 45 cores split into 138 samples. Three subsets of samples were analyzed using different techniques. The first subset was all 138 samples, both organic and mineral soils. For all samples, plant 'available' P (P_{AL}) was extracted using a solution of ammonium lactate and acetate analyzed using ICP-OES (Egner and others 1960). The concentration in the O-horizon ($n = 45$) and the top 10 cm of mineral soil where present ($n = 32$) are reported. Mass-area stocks for soil P_{AL} were calculated as the total sum per core using soil bulk density and the chemical concentration of each core section with further details in the supplement.

For a second subset, the deepest mineral soil samples were analyzed of those with more than 10 cm of mineral soil with the deepest core per quadrat reported ($n = 22$). An acid ammonium oxalate extraction was used to measure the concentration of active amorphous Fe (Fe_{ox}), Al (Al_{ox}) and oxide associated P (P_{ox}) analyzed using ICP-OES (Schwertmann 1964). P sorption capacity (PSC) was estimated using the sum of Fe_{ox} and Al_{ox} along with the degree of P saturation (DPS) (Kleinman 2017).

For a third subset, one sample per site was selected representing the deepest, longest, mineral core with the smallest coarse fraction ($>$ 2 mm) ($n = 9$). Soil texture was measured using laser diffraction (LS 13 320 XR, Beckman and Coulter, USA). One island had only histosols and therefore was not tested for texture or oxalate extractable elements.

Statistical Analyses

Analyses were conducted using R version 4.4 (R Core Team, 2024). The general statistical framework applied was to treat the paired fencing design on the mainland and the islands as a single categorical variable with three levels (''Grazing status''). Inference was drawn in a two-step process: first an uncorrected test was run based on the exclosure vs. grazed contrast. If there was an exclosure difference ($p < 0.05$), then pairwise

comparisons (Tukey corrected) were conducted among the mainland exclosure plots, the mainland grazed plots and the islands. If there was no significant ($p > 0.05$) difference between grazed and exclosure mainland plots, the mainland plots were pooled, and a contrast was tested between the islands and mainland plots (False-Discovery-Rate corrected). Given the heterogeneity of the soils in this region, for the soil variables we report differences at $p < 0.1$. Model assumptions were tested through residual visualization and assessed using package *Dharma* (Hartig 2022).

A combination of ordinary least squares, linear and generalized mixed effects models were used to test the various response variables based on either the categorical variable Grazing Status or the Island vs. Mainland comparison. At the quadrat scale, models were tested on the relative abundance of *N. stricta* and *A. flexuosa;* the Berger-Parker dominance index; aboveground biomass and the concentration and stock of Si and P in aboveground biomass as well as their mass-based ratio; the concentration of P_{AL} in the O-horizon, the mineral soil and its stock; the concentration of P_{Ox} in mineral soil as well as two P indices PSC and DPS. At the species scale, the concentration of Si and P and their mass-based ratio were each tested with categorical variables for Grazing Status and Species and their two-way interaction. Further details are provided in the SI. For one quadrat per site and islands ($n = 9$), soil texture was used to generate soil texture fractions using the United States Department of Agricultural system with cutoffs for $x < 2$ µm for clay, ≤ 2 µm $x \leq 50$ µm for silt and $50 < x < 2000$ µm for sand using R package *soiltexture* (Moeys 2024). T-tests between the islands and mainland sites were tested with four islands and five mainland sites for % clay, % silt and % sand.

The ratio of Si:P in aboveground biomass, the relative abundance of *N. stricta* and the relative abundance of *A. flexuosa* across the 45 quadrats were analyzed using K-means clustering predefined to two clusters using package *stats*. The Si:P ratio was natural log transformed, and all three variables were standardized. Using the same set of data, a Gaussian mixture model was fit using package *Mclust* (Scrucca and others 2023). The optimal shape and structure of the model was selected using the Bayesian Information Criterion.

Prior to data collection, we hypothesized that the grazed mainland would be high in plant Si reflecting the high abundance of *N. stricta*. After data collection, we discovered that the islands were higher in P than the mainland in both plants and the soil. We focus on P as an indicator of grazing absence for several reasons: the islands ranked highest to the mainland in plant [P] compared to all other elements (Supplemental Figure 2); the soils showed agronomically low available P (Krogstad and others 2008); the region has had high N deposition (Kaste and others 2020), and previous research suggests no evidence of differences in the N-cycle between the mainland exclosures, grazed plots or the islands (Martinsen V., data not shown). We interpret P enrichment reflecting a 'faster' ecosystem biogeochemistry aligning with theory of herbivory accelerating or decelerating ecosystem states. We report results characterizing and exploring these alternative 'fast' and 'slow' ecosystem states and their plant and soil properties indicated through discussion of Si, P and their ratio.

Artificial Intelligence (AI) was not used to independently write any sentences. AI was used in literature search and to help with grammar questions. AI was used for guidance with coding syntax, but not agentially to run the analyses.

Results

Plant Community Abundances

N. stricta had its highest relative abundance on the grazed mainland while *A. flexuosa* had its highest relative abundance on the islands (Figure 1). On the mainland, *N. stricta* had a higher relative abundance under sheep grazing compared to inside the exclosures (Figure 1a) ($p < 0.001$) while there was a higher relative abundance of *A. flexuosa* inside the exclosures (Figure 1b) ($p < 0.001$). However, after 23 years *N. stricta* still had the highest relative abundance of all species inside the exclosures (Figure 1d). Comparing the islands to the mainland, there was less *N. stricta* on the islands than under sheep grazing on the mainland ($p < 0.001$) and inside the exclosures ($p < 0.01$) (Figure 1a). There was more *A. flexuosa* on the islands than under sheep grazing on the mainland ($p < 0.001$), and inside the exclosures but to a lesser degree ($p = 0.0495$) (Figure 1b). In the measured quadrats, *S. virgaurea* was only detected on the islands (Figure 1c). The high relative abundance of *N. stricta* under sheep grazing (Figure 1a, d) resulted in a high dominance as measured using the Berger-Parker Dominance Index (Figure 1e). The highest dominance was detected on the mainland under sheep grazing that was higher than the islands ($p = 0.026$) and marginally greater than the mainland exclosures ($p = 0.0504$). There was no difference in dominance between the mainland exclosures and the islands ($p = 0.88$) (Figure 1e).

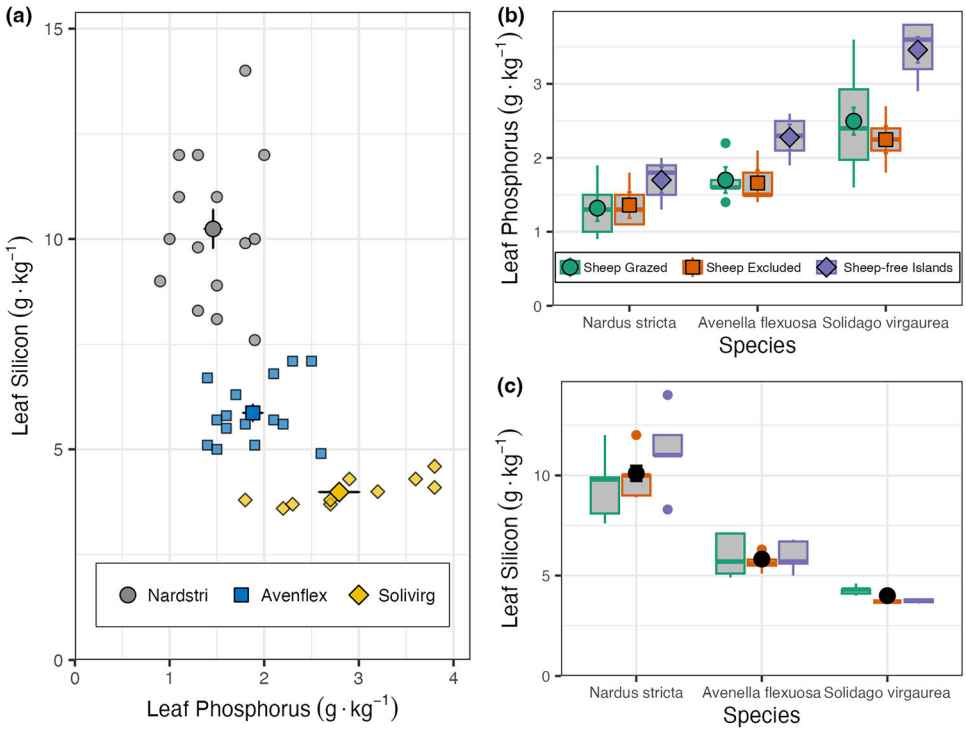


Figure 2. The concentration of silicon (Si) and phosphorus (P) in the leaves of three plant species. **a** Mean ± 1 standard error (SE) of leaf Si and leaf P for *Nardus stricta* (gray circles), *Avenella flexuosa* (blue square), and *Solidago virgaurea* (yellow diamonds). Each small point represents one observation per species. **b** Estimated marginal mean ± 1 SE for each species across three grazing statuses: Sheep grazed (green circles) (M-G), Sheep excluded (orange squares) (M-NG) and Sheep-free islands (purple diamonds) (I-NG). The boxplots show the min, max, upper and lower quartile, and median of the data. **c** Estimated marginal mean ± 1 SE for each species averaged across Grazing status. Boxplots are shown for each species by Grazing status combination.

Species' Leaf Si and P

The concentration of elements in the leaves of *N. stricta*, *A. flexuosa*, and *S. virgaurea* displayed both interspecific and intraspecific differences (Figure 2a). For leaf Si, only a main effect for Species was retained as Si differed only among species ($p < 0.01$). *N. stricta* had the highest Si, followed by *A. flexuosa*, and *S. virgaurea* (Figure 2c). Leaf P had an interaction between Grazing status and Species ($p = 0.0013$) indicative of both interspecific and intraspecific differences (Figure 2b). Only *S. virgaurea* had intraspecific differences among grazing statuses with a higher P concentration on the islands compared to both mainland exclosures ($p < 0.005$) and grazed plots ($p < 0.034$) (Figure 2b). *S. virgaurea* was higher in P than either grass comparing within the three grazing statuses (all $p < 0.05$), but the grasses only differed from each other on the islands with *A. flexuosa* being higher than *N. stricta* ($p = 0.01$) (Figure 2b).

Stocks and Concentration of Si and P in Aboveground Plant Biomass

There was an effect of Grazing status for both the concentration of Si and stock of Si in aboveground biomass ($p < 0.05$). There were no differences comparing the mainland grazed plots to the plots within exclosures in the concentration ($p = 0.84$) or stock of Si ($p = 0.069$) (Figure 3). Rather, contrasting the average of the mainland sites to the islands reveals a 47% higher concentration (Figure 3b) ($p = 0.0032$) and a 125% higher stock on the mainland ($p = 0.001$) (Figure 3c).

There was an effect of Grazing status for the concentration of P in aboveground plant biomass ($p < 0.05$) (Figure 3d), but there were no differences in the stock of P ($p > 0.05$) (Figure 3e). The concentration of P showed no difference between the grazed and exclosure mainland plots (Figure 3d) ($p = 0.14$). Whereas the islands had a 122% higher concentration of P than the average of the mainland (Figure 3d) ($p = 0.0001$).

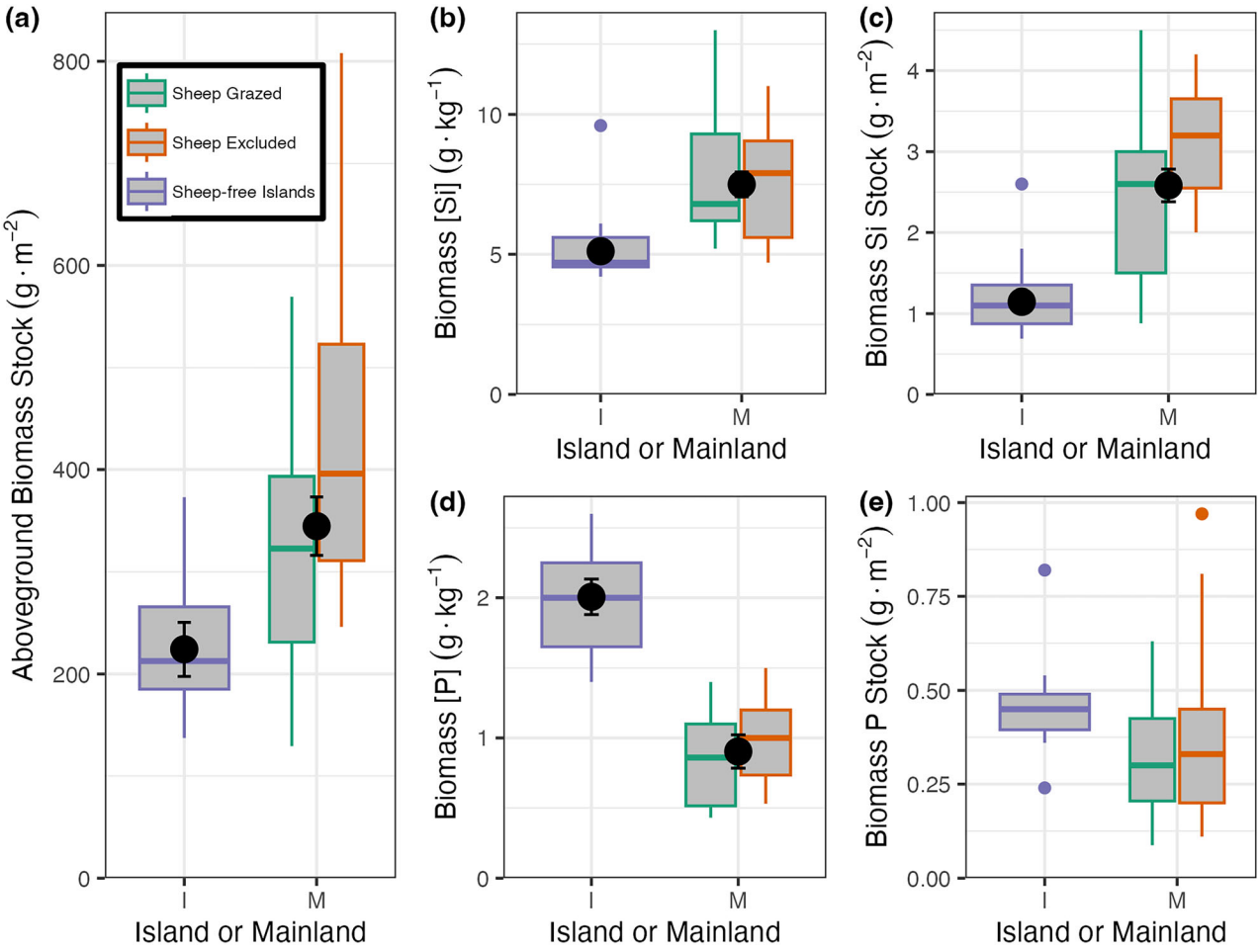


Figure 3. Aboveground plant biomass and the concentration and stocks of silicon (Si) and phosphorus (P) in aboveground plant biomass **a** Aboveground plant biomass across three Grazing statuses: mainland Sheep grazed (green boxplots) (M-G), mainland Sheep excluded (orange boxplot) (M-NG) and Sheep-free islands (purple boxplot) (I-NG) and aggregated as the island plots and mainland plots (black points and error bars representing the estimated marginal mean ± 1 standard error (SE) for island and mainland). The boxplots show the min, max, upper and lower quartile, and median of the data for each grazing status. **b** The concentration of Si in aboveground plant biomass. **c** The stock of Si in aboveground plant biomass. **d** The concentration of P in aboveground plant biomass. **e** The stock of P in aboveground plant biomass. For all panels, the estimated marginal mean ± 1 SE is shown when differences from island to mainland were found at $p < 0.05$ and not shown when no difference was found $p > 0.05$.

There were, similarly to Si and P, no differences between the grazed and exclosure mainland plots in aboveground biomass ($p = 0.10$) (Figure 3a). Rather the mainland plots had 54% higher biomass than the islands ($p = 0.02$) (Figure 3a). As the concentration of Si (Figure 3b) and biomass (Figure 3a) were higher on the mainland, there was a detectable increase in the stock of Si as well (Figure 3c). Whereas the higher concentration of P on the islands (Figure 3d) was not large enough to carry over into a detectably higher stock of P in aboveground biomass (Figure 3e).

Soil P and Edaphic Factors

The soil data has high heterogeneity but provides a signal that the islands trended higher in soil P_{AL} in the O-horizon and the total soil P_{AL} stock. There were not differences for $[P_{AL}]$ in the O-horizon between the mainland grazed and exclosure plots ($p = 0.55$), but there was marginal evidence for a higher $[P_{AL}]$ on the islands compared to the mainland sites (Figure 4a) ($p = 0.082$). $[P_{AL}]$ in the top 10 cm of the mineral soil did not depend on Grazing status ($p = 0.95$) (Figure 4b). There were

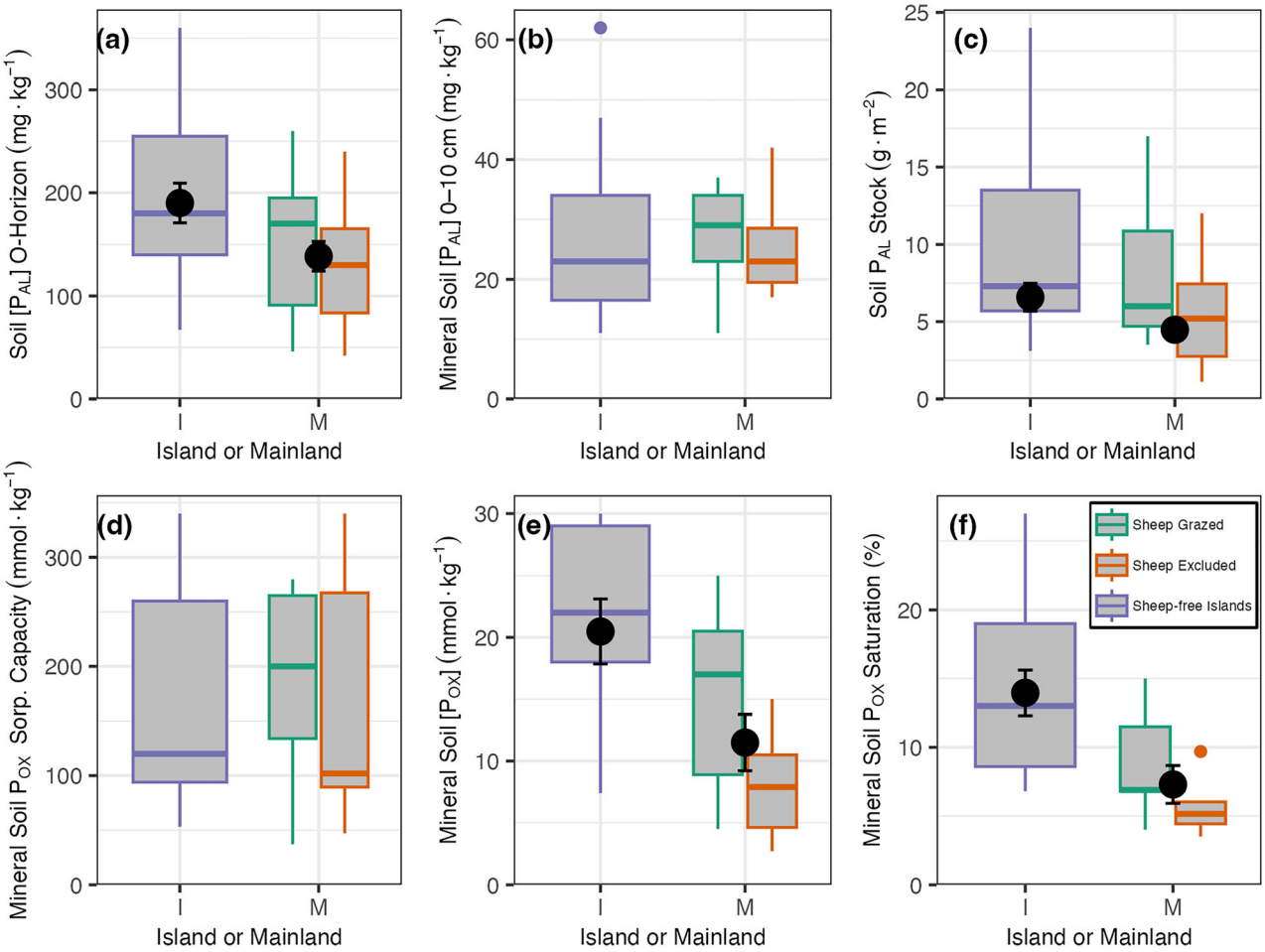


Figure 4. **a** Soil available phosphorus concentration extracted in ammonium lactate ([P_{AL}]) for the soil O-horizon (mean depth = 13.7 cm) across three Grazing statuses: Sheep-free Islands (I-NG) (purple) (n = 15), mainland Sheep grazed (M-G) (green) (n = 15) and mainland Sheep excluded (M-G) (orange) (n = 15), aggregated as the island plots and mainland plots. Each point represents the estimated marginal mean ± 1 standard error (SE) for island and mainland plots, respectively. The boxplots show the min, max, upper and lower quartile, and median of the data for each Grazing status. **b** Soil [P_{AL}] in the top 10 cm of mineral soil where present; I-NG (n = 11), M-G (n = 13) and M-NG (n = 8). **c** The stock of soil P_{AL} to a mean total depth of 31 cm; I-NG (n = 15), M-G (n = 15) and M-NG (n = 15). In the deepest mineral soil fraction per core with a mean midpoint depth of 19.4 cm (I-NG (n = 9), M-G (n = 7) and M-NG (n = 6)): **d** the phosphorus sorption capacity **e** oxalate extractable soil P (P_{ox}) **f** the degree of phosphorus saturation of the soil. For all panels, the estimated marginal mean ± 1 SE is shown when differences from island to mainland were found at $p < 0.1$ and not shown when no difference was found $p > 0.1$.

not differences in the total mass-area stock of P_{AL} between the mainland grazed and exclosure plots (p = 0.28), but there was marginal evidence for a higher P_{AL} stock on the islands compared to the mainland (p = 0.07) (Figure 4c).

The deep mineral soil shows a signal of less sorbed P on the mainland than the islands but not differences in the capacity to sorb P or texture. The capacity of the soil to sorb P (PSC) did not depend on Grazing status (p = 0.94) (Figure 4d). While there were not differences between the mainland grazed and exclosure plots for soil [P_{ox}] (p = 0.16), there was marginally higher [P_{ox}] on the islands compared to the mainland (Figure 4e) (p = 0.055) leading P_{ox} to be closer to saturation (DPS) on the islands as well (Figure 4f) (p = 0.023). The island and mainland sites were similar in texture as sands, sandy loams and loamy sands, and did not differ in their proportion of sand, silt or clay ($p > 0.1$) (Figure 3, Supplemental Figures 3 and 4).

Testing for Alternative Ecosystem States Through Plant Stoichiometry

In both leaves and aboveground biomass, a higher Si:P ratio was indicative of the *N. stricta* dominated mainland whereas a low Si:P ratio was indicative of the islands harboring palatable grasses and forbs such as *A. flexuosa* and *S. virgaurea* (Figure 5). In species' leaves, averaging across species, there was no difference from mainland grazed to mainland exclosure plots ($p = 0.14$), but there was a lower Si:P ratio on the islands ($p = 0.035$). Averaging across Grazing status, *N. stricta* had a higher Si:P ratio than the other species, with *A. flexuosa* in the middle and *S. virgaurea* with the lowest (Figure 5a). In aboveground biomass, there were no differences between mainland grazed and exclosure plots ($p = 0.11$), whereas the islands had a lower Si:P ratio than the mainland (Figure 5b) ($p = 0.0007$).

Combining the information in the relative abundance of *N. stricta*, the relative abundance of *A. flexuosa* and the Si:P ratio in aboveground plant biomass reveals two groups (Figure 5c and d). K-mean clustering with two a priori clusters provided separation with a silhouette width of 0.61 (Figure 5c and d). The plant community alternatively is represented by either grass species, and this contrasting relative abundance scales their leaf stoi-

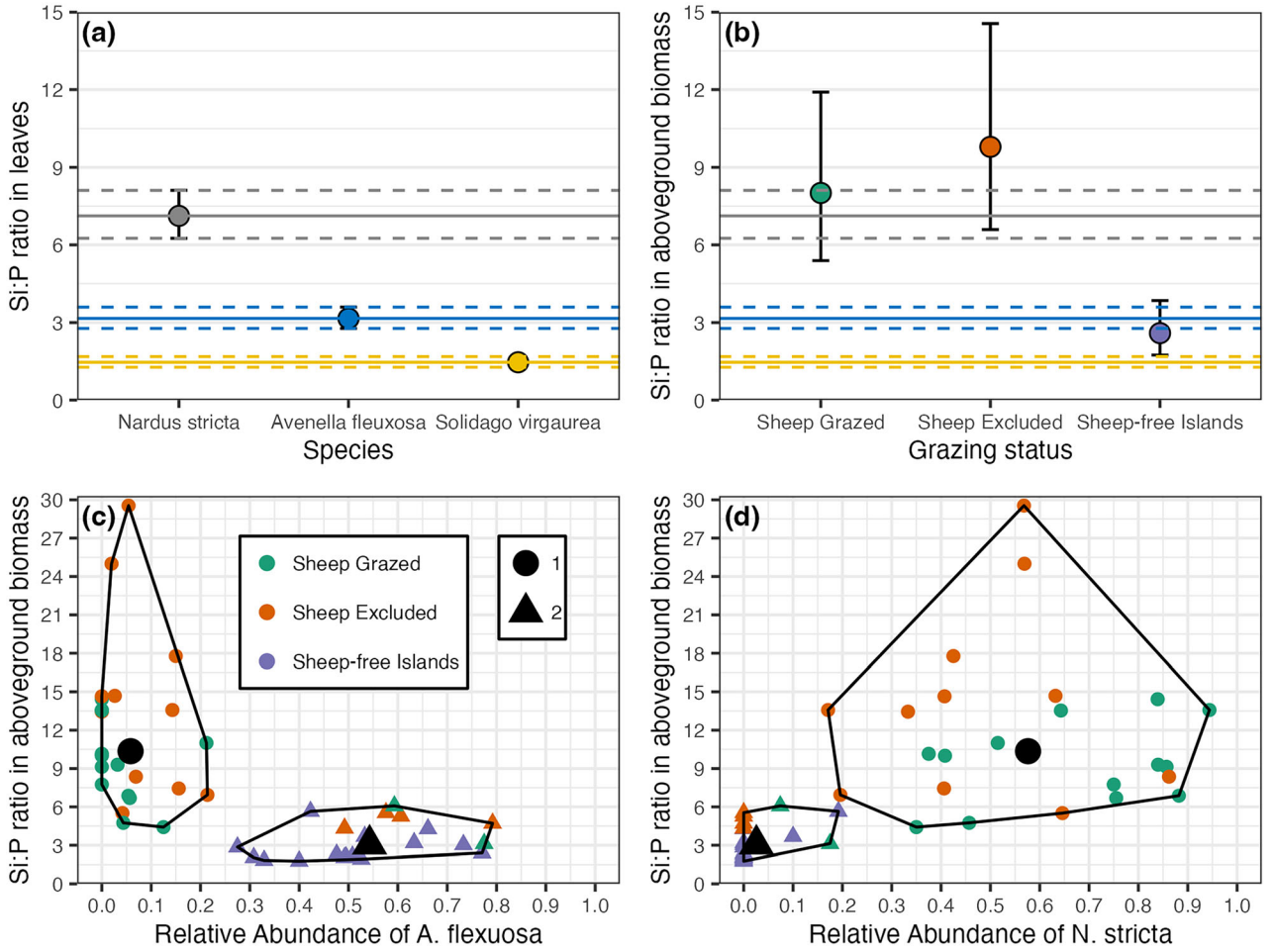


Figure 5. **a** The ratio of silicon (Si) to phosphorus (P) in plant leaves. Each point represents the estimated marginal mean ± 1 standard error (SE) for *Nardus stricta* (gray circles), *Avenella flexuosa* (blue circles), and *Solidago virgaurea* (yellow circles). **b** The ratio of Si to P in aboveground plant biomass for sheep-free islands (I-NG), mainland sheep grazed (M-G) and mainland sheep excluded (M-NG). The gray, blue and yellow lines represent the estimated marginal mean ± 1 SE for the leaves of *N. stricta*, *A. flexuosa*, and *S. virgaurea*, **c** The ratio of Si:P in aboveground biomass compared to the relative abundance of *A. flexuosa*. Each point represents one subplot colored based on Grazing statuses M-G (green), M-NG (orange) and I-NG (purple) where the circles or triangles represent two different groups defined through K-means clustering. The large black circle and triangle represent the K-mean centroid. **d** The ratio of Si:P in aboveground biomass compared to the relative abundance of *N. stricta* similarly defined.

chiometry to the 0.25m^2 quadrat scale as detectable in either high Si:P on the mainland or an enrichment of P relative to Si on the islands (Figure 5c and d). However, for one mainland site, M3, the community has higher *A. flexuosa* abundance inside the exclosure and *N. stricta* was not detected (Figure 5c and d, Supplemental Figure 5). At this site, the Si:P ratio is similar to that detected on the islands and this site was classified within the island cluster (Figure 5c). A Gaussian mixture model fit with the same variables, visualizes the density of the two clusters as a surface (Figure 6). The density, as shown with the surfaces (Figure 6), suggests the basin of attraction of the two theorized ecosystem states.

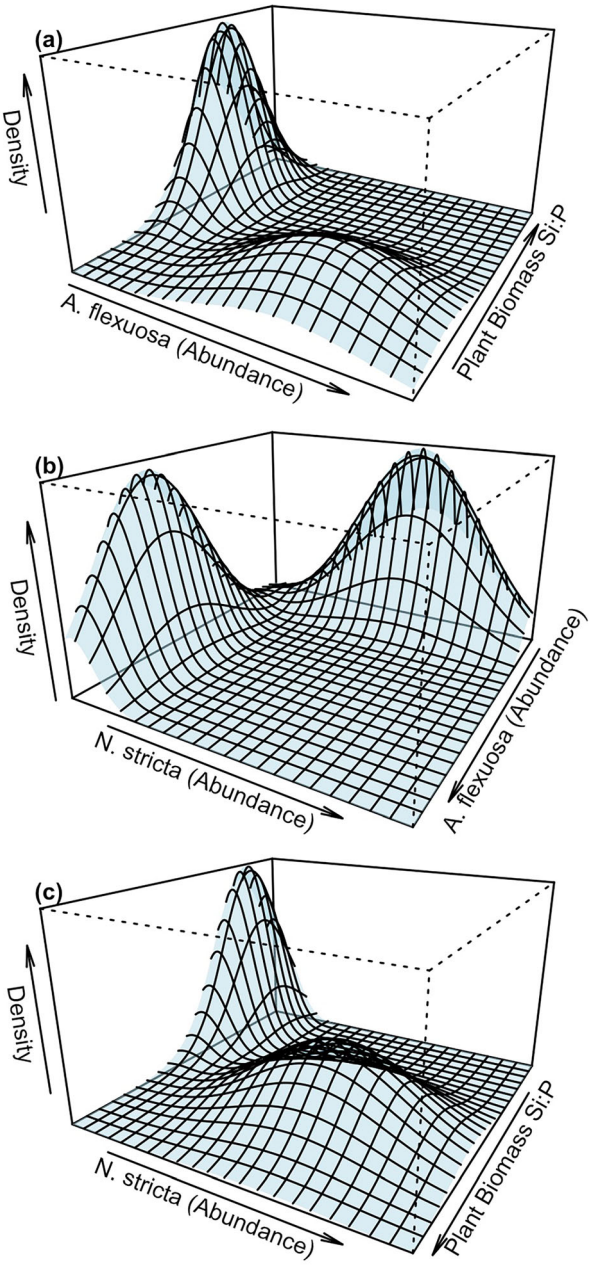


Figure 6. Visualization of the density of a Gaussian mixture model with two clusters. The natural log of the ratio of Si:P in aboveground biomass (SiP) and the relative abundance of N. stricta and A. flexuosa are displayed. **a** A. flexuosa versus the ratio of Si:P in aboveground biomass. **b** N. stricta versus A. flexuosa. **c** N. stricta versus the ratio of Si:P in aboveground biomass. A higher surface on the Z-axis indicates higher density showing the center of the two clusters.

Discussion

We present several concordant lines of evidence that summer-season sheep grazing in a Norwegian mountain area promoted the dominance of *N. stricta*, a grazing-resistant grass, leading to the enrichment of Si relative to P, while sheep-free islands harbored susceptible plant species relatively enriched in P to Si. The experimental exclosures show a signal of change with an increase in the relative abundance of the grazing preferred grass *A. flexuosa*, but *N. stricta* remains dominant inside several exclosures. The preponderance of evidence supports the theory of herbivory-induced deceleration of ecosystem nutrient cycling under conditions of low soil fertility refined to a system where animals seasonally graze and are removed from the ecosystem via transhumance (Ritchie and others 1998; Stark and Grellmann 2002; Bardgett and Wardle 2003; Harrison and Bardgett 2008; Sitters and Andriuzzi 2019). Herbivory increased the dominance of a slow-growing species, low in litter quality with well-defended leaves, and reduced available soil P whereas its absence promoted faster-growing species, higher in litter quality and increased available soil P. We argue that the data supports the existence of two alternative ecosystem stable states driven through herbivory indicated through Si:P stoichiometry: an ungrazed, high-P, accelerated nutrient cycling state and a grazed, high-Si, decelerated nutrient cycling state. Our results reproduce and motivate the importance of Si to understand plant–herbivore interactions (McNaughton and others 1985; Massey and others 2007; Hartley and DeGabriel 2016; Petit Bon and others 2022; de Tombeur and others 2023) and link Si:P stoichiometry to herbivory-induced alternative ecosystem stable states (Olofsson and others 2004; Pastor and others 2006; Wal 2006; Suzuki 2024). The present case thus adds a novel dimension to ecosystem theory by demonstrating the importance of Si:P ratios in a real-world study system with important consequences for management and conservation.

From the perspective of herbivory and plant stoichiometry, our results add to an existing body of empirical evidence demonstrating the ecosystem response to grazing in cold climates with relatively young, acidic, and often-wet soils. Both the increase of *N. stricta* from sheep's selective grazing and the slow change following grazing removal, in some cases to the increase of *A. flexuosa* as we report (Rawes 1981; Hulme and others 1999; Pakeman 2004), has been well-documented in the British Isles (Fenton 1936; Welch 1986; Grant and others 1996; Armstrong and others 1997; Holland and others 2008; Pakeman and others 2019). Our data build on those findings to demonstrate that the herbivory-induced dominance of *N. stricta* scales its high Si:P tissue stoichiometry to bulk aboveground plant biomass. The low P in plant tissue under grazing (Figure 3) and the depletion of available P in the soil O-horizon (Figure 4), all point toward less ecosystem P under grazing. The importance of Si and P have also been shown under reindeer grazing in Norway where high reindeer grazing can induce P limitation (Sitters and others 2017, 2019) and promote the abundance of high [Si] plant species (Petit Bon and others 2022). Si, and the ratio of Si:P in vegetation, stand as important indicators of plant-herbivory interactions, forage preference, and the ecosystem response to herbivory in the North-Atlantic climate region.

Such changes in plant stoichiometry can be linked to herbivory-induced biogeochemical feedbacks that can stabilize or drive the system toward alternative ecosystem states. In the present system, the islands represent a sheep-free state, and the exclosure experiment imposed a system perturbation that changed the mainland to a sheep-free state. However, despite the over two decadal experimental exclosure period, *N. stricta* remains dominant inside many fences suggesting hysteresis on the path to the sheep-free island plant community. A cogent historical account in the 1930 s of Fenton (1936) describes how the legacy of sheep grazing in Scotland promoted *N. stricta* dominance that was resistant to change from fencing and fertilization until the *N. stricta* litter mat decomposed and the fertilizer could favor the other grasses. These results are similar to a litter-driven mechanism where the inhibitory effects of species' litter on its competitors regulate bistability (Meyer and others 2023). Accumulated low nutrient litter from dominant grasses can decelerate nutrient cycling and favor those with low nutrient requirements (Wedin and Tilman 1990). *N. stricta* litter accumulation may promote stabilizing negative feedback until a soil fertility threshold is crossed (Loreau 1995), and the system undergoes a regime shift toward faster-growing species via positive feedback through inputs of higher nutrient quality litter. The islands might serve as a source of propagules of faster-growing species, rare on the grazed mainland, that can increase when rare inside the exclosures and drive a regime shift. One mainland site along a lake edge, M3, has flipped to the *A. flexuosa* fast state and lies with a Si:P ratio akin to the islands (Figure 5, Supplemental Figure 5). Our data suggest that examination of the mineralization of P in the soil O-horizon along with dispersal and germination of faster-growing species can offer insight into the stability of the *N. stricta* state and its transition, or lack thereof, to our theorized fast ecosystem state.

Plant traits along a fast-slow spectrum can be used to link plant community composition to the patterns we observed suggestive of a decelerated ecosystem state. *N. stricta* and *A. flexuosa* are competitors that have been demonstrated to have differing strategies of clonal plants with *N. stricta* of the phalanx strategy of slow-growing tillers forming dense turfs and *A. flexuosa* of the faster-growing, gap-filling guerilla strategy with tillers in loose mats (Herben and others 1993). These strategies are complemented with an analyses showing axes along the leaf economic spectrum where the island community appears faster with higher specific-leaf area and height compared to the slower, shorter-stature, higher leaf dry matter content of the mainland (Reich 2014; Vuorinen and others 2021) that we additionally show is also lower in plant [P]. *N. stricta* and *A. flexuosa* are indicators of varying soil P as shown in a re-survey of a 37-year old P fertilizer addition experiment where *A. flexuosa* benefited to the expense of *N. stricta* (Hejcman and others 2007). *N. stricta* has a suite of characteristics aligning with a decelerated state: high in Si with a slow growth rate (Perkins 1968)—in fact the slowest grower, with the highest [Si], highest leaf toughness and the highest cumulative defense score out of the eighteen species in Massey and others (2007). Its litter is slow to turn over potentially immobilizing nutrients (Güsewell and others 2005), and poorly palatable to herbivores of low quality fodder (Bovolenta and others 2008). *N. stricta* dominance broadly aligns with plant traits and biogeochemical patterns that indicate the herbivory-induced deceleration of ecosystem nutrient cycles.

The high Si:low P in aboveground biomass under *N. stricta* dominance can be linked to theory and empirical evidence on the interactions among herbivory resistance, ecosystem retrogression and

the deceleration of ecosystem nutrient cycling (sensu Bardgett and Wardle 2003; Peltzer and others 2010; de Tombeur and others 2021). For example, in a 2-million year retrogressive chronosequence it was shown that as soil P decreased, Si-based defenses increased (de Tombeur and others 2021). Our study supports the phenomenon that Si-based defenses (Massey and others 2007), are associated with low ecosystem P under soil conditions where P is limiting (de Tombeur and others 2021). While our study does not provide a mechanistic or causal link between plant [Si] and [P], nor between plant [Si] and herbivory, these empirical data can be conceptually mapped to a general model where herbivory promotes dominance and the traits of that dominant species slow ecosystem nutrient cycling (Pastor and others 1993, 2006; Ritchie and others 1998; Bardgett and Wardle 2003; Koerner and others 2018). While other chemical defenses or traits could be at play, the high Si:P tissue of *N. stricta* appears a characteristic indicator of its ability to resist herbivory resulting in its dominance of the plant community under high grazing (Bråthen and others 2007; Petit Bon and others 2022). The set of variables we report matches a case where the defensive resistance to herbivory, in decreasing P and enriching Si, aligns with theory of ecosystem deceleration (Pastor and others 1993; Ritchie and others 1998; Bardgett and Wardle 2003; Harrison and Bardgett 2008; Sitters and Andriuzzi 2019).

Our study system has limitations presenting several caveats on our interpretation of these data. The islands suggest a reference ecosystem state without domestic grazing of sheep to which the mainland exclosures appear to be converging toward. A testable hypothesis is that the plant community inside all the mainland exclosures will converge to the island community along with an enrichment of P relative to Si in plant biomass. However, only grazing sheep on the islands can offer a full experimental control of the island to mainland comparison and our findings may therefore reflect a spurious island effect. Nevertheless, the higher soil P in the O-horizon on the islands likely reflects biological cycling through the higher [P] in aboveground biomass and not differences in background geochemistry. The soils have the same granitic parent material, similar texture, and we find no evidence of a difference in the capacity to sorb phosphorus in the mineral soil. The similarity motivates our use of a space-for-time substitution to infer the long-term dynamics of the system (Pickett 1989). The experiment appears mid-way through transient dynamics (Tilman 1989), for which the reference state on the islands offers insight into a steady-state of the ecosystem in the absence of sheep herbivory.

Our study presents support for herbivory-induced deceleration of ecosystem biogeochemistry reported through the stocks and concentration of two key elements: Si the element associated with grazing resistance and P the element associated with its absence. While not a complete picture, these data paint a pattern of selective herbivory promoting the dominance of a well-defended grass whose traits are strongly aligned to a slow strategy on the trait spectrum. The net consequence is an enrichment of the Si:P ratio that we argue characterizes two distinct ecosystem states of the ungrazed, high-P, accelerated state and the grazed, high-Si decelerated state. There are many regions of the world where animals seasonally graze on low fertility soils where the Si:P ratio may serve as an important indicator of alternative ecosystem states. The ecosystem consequences of a reduction of P in other trophic levels may be profound. While we have only examined a small number of ecosystem pools, there may well be far-reaching consequences cascading throughout the food web resulting from the shifting ratio of Si:P in aboveground plant biomass.

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DATA AND CODE AVAILABILITY

The raw data are stored on dataverse.no (Furey and others, 2025). The code for analyses and derived data is stored on Zenodo (https://doi.org/10.5281/zenodo.18085395). The analyses use a reproducible targets pipeline to generate all figures and derived data from the raw data (Landau 2021).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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