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Aboveground vertebrate and invertebrate herbivore impact on net N mineralization in subalpine grasslands

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Abstract. Aboveground herbivores have strong effects on grassland nitrogen (N) cycling. They can accelerate or slow down soil net N mineralization depending on ecosystem productivity and grazing intensity. Yet, most studies only consider either ungulates or invertebrate herbivores, but not the combined effect of several functionally different vertebrate and invertebrate herbivore species or guilds. We assessed how a diverse herbivore community affects net N mineralization in subalpine grasslands. By using size-selective fences, we progressively excluded large, medium, and small mammals, as well as invertebrates from two vegetation types, and assessed how the exclosure types (ET) affected net N mineralization. The two vegetation types differed in long-term management (centuries), forage quality, and grazing history and intensity. To gain a more mechanistic understanding of how herbivores affect net N mineralization, we linked mineralization to soil abiotic (temperature; moisture; NO_3^-, NH_4^+, and total inorganic N concentrations/pools; C, N, P concentrations; pH; bulk density), soil biotic (microbial biomass; abundance of collembolans, mites, and nematodes) and plant (shoot and root biomass; consumption; plant C, N, and fiber content; plant N pool) properties.

Net N mineralization differed between ET, but not between vegetation types. Thus, short-term changes in herbivore community composition and, therefore, in grazing intensity had a stronger effect on net N mineralization than long-term management and grazing history. We found highest N mineralization values when only invertebrates were present, suggesting that mammals had a negative effect on net N mineralization. Of the variables included in our analyses, only mite abundance and aboveground plant biomass explained variation in net N mineralization among ET. Abundances of both mites and leaf-sucking invertebrates were positively correlated with aboveground plant biomass, and biomass increased with progressive exclusion. The negative impact of mammals on net N mineralization may be related partially to (1) differences in the amount of plant material (litter) returned to the belowground subsystem, which induced a positive bottom-up effect on mite abundance, and (2) alterations in the amount and/or distribution of dung, urine, and food waste. Thus, our results clearly show that short-term alterations of the aboveground herbivore community can strongly impact nutrient cycling within ecosystems independent of long-term management and grazing history.

Key words: above–belowground interactions; exclosure types; functionally different herbivores; herbivory; nutrient cycling; plant biomass; plant properties; soil arthropods; soil mites; soil properties; subalpine grasslands; Switzerland.

Introduction

Aboveground vertebrate and invertebrate herbivores have strong effects on grassland ecosystem functioning and can consume >50% of the available aboveground biomass (Detling 1988). They alter plant species composition (e.g., Del-Val and Crawley 2005, Bakker et al. 2006) and directly and indirectly affect belowground properties (e.g., Bardgett and Wardle 2003). Direct impacts such as trampling or burrowing can alter soil structure or permeability (e.g., Binkley et al. 2003, Schrama et al. 2013, Barth et al. 2014). The deposition of dung, urine, or food waste can stimulate the activity of roots (Milchunas and Lauenroth 1993, Chaneton et

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al. 1996), microbes (McNaughton et al. 1997, Frank and Groffman 1998), and/or soil arthropods (e.g., Schon et al. 2012), and therefore can alter nitrogen (N) availability within the soil (e.g., Butterbach-Bahl et al. 2011). By consuming aboveground plant biomass, herbivores also affect the amount of litter returned to the soil (e.g., Ruess and Seagle 1994), plant physiological properties (e.g., Bardgett et al. 1998, Frank et al. 2002, Bardgett and Wardle 2003), and the competitive interactions among plant species. These changes can alter litter quality (Frank et al. 2002, Wardle et al. 2002), which can indirectly affect the activity and abundance of soil organisms and therefore soil nutrient cycling (Bardgett and Wardle 2003). Changes in aboveground plant biomass and plant structure can also alter the soil microclimate and, therefore, affect soil organisms and their ability to decompose organic material. Consequently, these herbivore-driven top-down effects can induce bottom-up feedbacks within ecosystems.

Many studies have shown that large herbivores are key drivers of N cycling in grassland ecosystems (e.g., Frank and Groffman 1998, Bardgett and Wardle 2003, Singer and Schoenecker 2003). Depending on the productivity and grazing intensity of an ecosystem, they can accelerate or slow down soil N mineralization (Bardgett and Wardle 2003, Wardle et al. 2004). The outcome of herbivore-induced changes in N mineralization depends on the quantity and quality of resources that are returned to the soil (see e.g., Bakker et al. 2004). An acceleration of N mineralization is expected when herbivory leads to an increase in fast-growing plants of high quality (grazing optimization theory; McNaughton 1979), while a slowdown is expected when forage of low quality is promoted.

Herbivory represents the combined impact of several vertebrate and invertebrate herbivore species or guilds that differ in their functional behavior, feeding habits (Belovsky 1997, Hunter 2001, Pawar et al. 2012), trampling or burrowing impact (Davidson et al. 2012, Barth et al. 2014), and amount, distribution (patchy, evenly), and quality of their waste (Bakker et al. 2004). However, most studies have only assessed how large ungulates alter N cycling within grasslands. Only a handful have excluded all vertebrate herbivores with body mass $>$ 1 kg (e.g., Bakker et al. 2009, Veen et al. 2010), or small mammals only (e.g., Olofsson et al. 2007). To our awareness, only Bakker et al. (2004) deliberately excluded herbivores of different body sizes when assessing N mineralization rates by first removing cattle, then rabbits, and finally voles. Thus far, to our knowledge, no study has excluded the smallest herbivores, invertebrates, in combination with larger herbivores when assessing net N mineralization processes, even though it is known that invertebrates can significantly alter net N mineralization (e.g., Belovsky and Slade 2000).

Our goal was to gain a mechanistic understanding of how different herbivore assemblages affect net N mineralization by their direct and indirect effects on soil abiotic, soil biotic, and plant properties. We used size-selective fences to progressively exclude from subalpine grasslands four groups of functionally different herbivores: large (ungulates), medium (marmots/hares), and small (voles/mice) mammals, and invertebrates. The experimental design allowed us to assess how net N mineralization responded to progressive removal of herbivores, but did not assess how single herbivore types (except for the largest herbivore type) affected net N mineralization.

Eighteen exclosure networks were established in two different vegetation types: (1) short-grass vegetation characterized by both high forage quality and consumption (~60% consumption), and (2) tall-grass vegetation characterized by low forage quality and consumption (<20% consumption; Schütz et al. 2006). We hypothesized that progressively excluding members of the herbivore community will lead to a stronger response in net N mineralization in the short-grass vegetation (high grazing/forage quality; fast cycle) compared to the tall-grass vegetation (lower consumption/forage quality; slow cycle). We also hypothesized that excluding ungulates leads to the strongest response in net N mineralization due to highest biomass consumption (removal of plant material) and their effects on soil microclimate and soil biota. Further, with each herbivore group excluded, we expected a progressive alteration in soil properties, including net N mineralization, because the amount of plant material returned to the system should increase and the distribution of the dung and urine should shift from patchy to a more even distribution.

Materials and Methods

Study area

The study was conducted in the Swiss National Park (SNP), which is located in the southeastern part of Switzerland (1350 to 3170 m above sea level) and covers 170 km^2 of forest and subalpine and alpine grasslands, along with scattered rock outcrops and scree slopes. Annual precipitation and temperature, 2009–2013, were 826 ± 112 mm (mean ± SD) and 0.9° ± 0.5°C, respectively (MeteoSchweiz 2014). Large, fairly homogeneous patches of short- and tall-grass vegetation are characteristic of the subalpine grasslands. Short-grass vegetation, roughly 2–5 cm in height, is dominated by lawn grasses (e.g., *Festuca rubra* L., *Briza media* L., *Agrostis capillaris* L.; Schütz et al. 2006). Tussocks of *Carex sempervirens* Vill. and *Nardus stricta* L. dominate the tall-grass vegetation (~20 cm in height; Schütz et al. 2006). The two vegetation types originate from different historical management and grazing regimes. Briefly, short-grass vegetation developed where cattle and sheep rested (high nutrient input) from the 14th century until 1914; tall-grass vegetation developed during this same time period where cattle and sheep grazed, but did not rest (Schütz et al. 2003, 2006). After 1914, short-grass

TABLE 1. Characteristics of the 18 sites sorted by vegetation (veg. type) and grassland (grassl.). Values are means for each site prior to the start of the study.

Veg. type, site, grassl.	Elev. (m)	NS, EW	Soil characteristics								
			C:N	OM (%)	pH	Sand (%)	Silt (%)	Clay (%)	Type	Rock (%)	Bulk density (g/m^3)
A) Short											
1, Stab	1975	814522, 171877	24.58	9.52	7.70	55.4	39.4	5.2	sandy loam	31.5	1.20
3, Stab	1980	814532, 171889	26.44	9.47	7.69	58.2	36.6	5.2	sandy loam	33.7	1.26
5, Dadaint	2133	814749, 172837	26.67	6.20	7.81	40.4	49.2	10.4	loam	8.5	0.84
7, Margunet	2275	814645, 173128	20.98	7.28	7.10	46.0	31.6	22.4	loam	10.8	0.95
9, Botsch	2091	814671, 173216	30.83	7.15	7.50	82.4	17.6	0.0	loamy sand	30.0	1.03
11, Grimmels	2032	810494, 171939	15.68	12.93	7.74	48.2	38.6	13.2	loam	15.5	0.94
13, Grimmels	2079	810387, 171873	15.29	11.22	7.28	44.6	39.0	16.4	loam	12.0	0.93
15, Mingér	2170	816557, 176744	16.57	28.71	6.59	57.5	37.7	4.8	sandy loam	9.8	0.60
17, Mingér	2181	816540, 176734	26.62	8.43	7.18	60.8	37.0	2.2	sandy loam	21.8	0.97
B) Tall											
2, Stab	1981	814429, 171926	25.28	12.81	7.60	56.0	34.4	9.6	sandy loam	26.3	1.00
4, Stab	1986	814441, 171954	21.63	15.84	7.60	53.4	37.2	9.4	sandy loam	23.8	0.93
6, Dadaint	2140	814805, 172868	33.33	5.72	7.84	60.4	36.2	3.4	sandy loam	38.7	1.42
8, Margunet	2299	814671, 173216	14.29	9.86	6.33	49.8	28.6	21.6	loam	10.0	0.83
10, Botsch	2075	813732, 172958	23.55	13.25	7.60	59.2	37.6	3.2	sandy loam	34.7	1.22
12, Grimmels	2060	810488, 171968	15.51	13.42	7.63	48.2	39.6	12.2	loam	13.4	0.91
14, Grimmels	2112	810376, 171843	14.49	8.67	7.12	39.5	32.7	27.8	clay loam	12.4	1.10
16, Mingér	2176	816580, 176716	20.99	11.70	7.40	49.8	41.0	9.2	loam	12.4	0.67
18, Mingér	2162	816554, 176772	30.83	8.87	7.40	53.6	41.0	5.4	sandy loam	18.2	0.89

Note: Abbreviations are Stab, Alp Stabelchod; Dadaint, Stabelchod da daint; Botsch, Val dal Botsch; Grimmels, Alp Grimmels; Mingér, Alp Mingér; Elev., elevation above sea level; NS, coordinates expressed as northings in the CH1903+ LV95 coordinate system; EW, coordinates expressed as eastings in the CH1903+ LV95 coordinate system; C:N, mineral soil C:N ratios; OM, mineral soil organic matter content; soil rock content, volumetric rock content.

sites became preferred for grazing by red deer (*Cervus elaphus* L.). A very diverse herbivore community inhabits these grasslands and can be divided into four groups based on body size: large (red deer and chamois *Rupicapra rupicapra* L.; 30–150 kg), medium (marmot *Marmota marmota* L. and mountain hare *Lepus timidus* L.; 3–6 kg), and small vertebrate herbivores (small rodents: e.g., *Clethrionomys* spp., *Microtus* spp., *Apodemus* spp.; 30–100 g), and invertebrates (e.g., grasshoppers, caterpillars, leafhoppers, <5 g). Ungulates consume the largest proportion of available biomass, closely followed by invertebrates: medium and small mammals consume the least (Risch et al. 2013).

Experimental design

A detailed description of our experimental setup and fence construction can be found in Risch et al. (2013) and Haynes et al. (2014). Briefly, we selected 18 subalpine grassland sites (nine short-grass, nine tall-grass vegetation) distributed over six subalpine grasslands throughout the park. All exclosure networks were located on dolomite parent material at altitudes of 1975–2300 m (for site characteristics, see Table 1). The exclosures were erected in spring 2009 immediately after snowmelt. Each exclosure network consisted of five plots (2×3 m) that progressively excluded the herbivores just listed (further labeled according to the herbivore guilds that had access: "All," "Marmot, Mice, Invertebrates," "Mice, Invertebrates," "Invertebrates," and "None"). The "All" plot (not fenced) was located at least 5 m away from the 2.1 m tall and 7×9 m main electrical fence that enclosed the other four exclosure types (ET). Within each main fence, we randomly established four plots: (1) the "Marmot, Mice, Invertebrates" plots (unfenced; access for all but ungulates); (2) the "Mice, Invertebrates" plots (electrical fence), which excluded all medium-sized mammals; (3) the "Invertebrates" plots (metal mesh), which excluded all mammals; and (4) the "None" plots (mosquito net covered with a roof), which excluded all herbivores (for details on fence construction, see Risch et al. 2013, Haynes et al. 2014). In addition, we established six "microclimate control" exclosures to assure that the "None" exclosure construction (mesh and roof) did not affect the microclimatic conditions within the plots and therefore the results. We were able to confirm that with the exception of incoming UV light, the construction did not affect any of the parameters measured (e.g., soil microclimate, plant biomass). The fences were dismantled every fall (late October) to protect them from snow pressure and avalanches, and were reconstructed in the following year immediately after spring snowmelt (early May). Human disturbance was minimal at the sites (no hunting, fishing, camping, or off-trail hiking).

Measuring soil N mineralization and soil abiotic parameters

In June 2013, at the beginning of the fifth season of progressive herbivore exclusion, we randomly collected one 5 cm (diameter) $\times$ 10 cm (depth) soil sample within each ET (90 plots) with a slide hammer corer (AMS Samplers, American Falls, Idaho, USA), after clipping

the vegetation. The soil cores (including surface organic and mineral soil) were put in a cool box and transported to the laboratory for weighing and sieving (4-mm mesh). A 20-g subsample was extracted in a 100-mL PE-bottle with 80 mL 1 mol/L KCl for 1.5 h on an end-over-end shaker and filtered through ashless folded filter paper (DF 5895 150, ALBET LabScience, Hahnemühle FineArt GmbH, Dassel, Germany). We measured NO_3^- colorimetrically (Norman and Stucki 1981) and NH_4^+ concentrations (flow injection analysis; FIAS 300, Perkin Elmer, Waltham, Massachusetts, USA) on these filtrates. The remaining soil was dried at 105°C to constant mass, sieved (4-mm mesh), and weighed to determine fine-fraction bulk density. Soil NO_3^-, soil NH_4^+, and total inorganic soil N pools (NO_3^- plus NH_4^+) were calculated using the respective concentrations and fine-fraction bulk density.

We collected a second soil sample within each plot in June 2013. A corer lined with a 5 × 13 cm aluminum cylinder was driven 11.5 cm deep into the soil (after clipping vegetation) so that 1.5 cm on top of the cylinder remained empty. We placed a bag made from polyester mesh into this space on the top of the cylinder to capture incoming N. The bag (mesh 250 μm) was filled with 18.1 ± 0.1 g of a 1:1 mixture of acidic and alkaline exchanger resin (ion-exchanger I KA/ion-exchanger III AA, Merck AG, Darmstadt, Germany). Thereafter, we removed 1.5 cm soil at the bottom of the cylinder and placed another bag (filled with resin), which served to capture N leached from the soil column. To ensure that the exchange resins were saturated with H^+ and Cl^- prior to filling the bags, we stirred the mixture in HCl at 1.2 mol/L for 1 h and rinsed it with demineralized water until the electrical conductivity of the water reached 5 μS/cm. The cylinders (with resin bags on top and bottom) were reinserted into the soil (top flush with the soil surface), incubated for three months, re-collected in September 2013, put in a cool box, and transported to the laboratory. The resin bags and sieved soil (4-mm mesh) from the cylinders were separately extracted with 1 mol/L KCl, and NO_3^- and NH_4^+ concentrations were measured as described previously. Nitrate and NH_4^+ concentrations were converted to a content basis by multiplying their values by the bulk density of the fine fraction. Net N mineralization was calculated as the difference between the inorganic N content of samples collected at the end of the three-month incubation (plus N extracted from the bottom resin bag) and the N content at the beginning of the incubation.

In September 2013 we also randomly collected three 5 cm diameter × 10 cm deep soil samples within each ET from two 10 × 100 cm strips where we previously clipped the vegetation. Here, we distinguished between the two different soil layers. First, we collected top mineral soil rich in organic matter (surface organic layer/rhizosphere; typically 1 to 3 cm in depth). Second, we took a 10-cm mineral soil core beneath this surface layer. The cores for each layer were pooled, dried at 65°C for 48 h, and fine-ground to pass a 0.5-mm screen. All soil material was analyzed for total C and N concentrations (Leco TruSpec Analyzer, Leco, St. Joseph, Michigan, USA). Soil P concentration was determined by the Olsen method (alkaline soil) and was analyzed using the ascorbic acid colorimetric method. Mineral soil pH was measured potentiometrically in 10 mmol/L $CaCl_2$ (soil : solution ratio = 1:2, equilibration time 30 minutes). Soil temperature (with a waterproof digital pocket thermometer; Barnstead International, Dubuque, Iowa, USA) and soil moisture (with time domain reflectometry with a Field-Scout TDR-100; Spectrum Technologies, Plainfield, Illinois, USA) were measured every second week from mid-May to mid-September for the 0–10 cm depth at five random locations per plot throughout the experiment (2009–2013). We used the 2009–2013 averages for our analyses.

Assessing soil microbial biomass carbon, micro-arthropod, and nematode abundance

Mineral soil microbial biomass carbon (MBC) was determined every September (2009–2013) on three separately collected "fresh" cores (as described previously; kept at 4°C after collection) following the substrate-induced respiration procedure of Anderson and Domsch (1978; for details, see Risch et al. 2013). We used the average of these values for our analyses. Details on how we sampled the soil micro-arthropod communities can be found in Vandegehuchte et al. (2015). Briefly, we collected undisturbed soil cores (5 × 10 cm) monthly during the 2011 growing season (June–August) in all plots (a total of 270 samples). Extractions started on the sampling day with a high-gradient Tullgren funnel and lasted for four days. We used the sum of all individuals per plot for the analyses presented. To assess nematode abundances, we randomly collected eight 2.2 cm diameter × 10 cm deep soil core samples (Giddings Machine Company, Windsor, Colorado, USA) on each plot in September 2013 from the two clipped strips in each plot. The samples were composited, put into coolers, transported to the lab, and nematodes were immediately extracted from 100 mL of fresh soil using Oostenbrink elutriators (Oostenbrink 1960). We then counted all nematodes in 1 mL of the 10-mL extract and minimally the first 150 individuals/sample encountered were identified to genus or family level (Bongers 1988). We extrapolated the numbers of all taxa to the entire sample and expressed nematode abundance as the number of nematodes/100 g dry soil.

Measuring vegetation properties

Aboveground plant biomass was estimated nondestructively on a 1 × 1 m subplot every season (2009–2013) in each plot at peak biomass (canopy intercept method; Frank and McNaughton 1992). In September of each season, we collected five soil samples (2.2 × 10 cm) to determine root biomass (for details, see Risch et al. 2013). We clipped two strips of vegetation (10 × 100 cm)

on each plot each July and September, dried, ground (to pass a 0.5-mm sieve) the material, and measured shoot C and N concentration and fiber contents (NDF, neutral detergent fiber; ADF, acid-detergent fiber; ADL, acid-detergent lignin) as described in Vandegehuchte et al. (2015). We used the average (2009–2013) of these variables for our analyses. Aboveground plant N pools were calculated using aboveground plant biomass and peak-season N concentrations.

Assessing the vertebrate and invertebrate herbivore abundances

We used the pellet count technique (Neff 1968) to assess ungulate abundance. Fresh dung pellet groups were counted (and removed) once every two weeks in two 4×25 m areas per exclosure network from May–September 2009–2013. Each area was cleaned in spring. Marmots were counted per grassland in July and August 2009–2011, but it was not possible to assign their home ranges to short- or tall-grass vegetation. We did not quantify marmot numbers within the exclosure networks. We attempted to assess small-mammal populations (trapping) around the exclosure networks, but found this approach to be too labor intensive. Game cameras (Moultrie 6MP Game Spy I-60, Moultrie Feeders, Alabaster, Alabama, USA) confirmed, however, that mice were present. Invertebrate herbivore abundance was assessed monthly from June to September 2013. We placed a $60 \times 60 \times 40$ cm high polyethylene frame (lined with a closable mosquito mesh sleeve) in each plot (reaching in from the outside to avoid disturbance), inserted a suction sampler (Vortis, Burkhard Manufacturing, Rickmansworth, Hetfordshire, UK) through the opening of the mesh sleeve and "vacuumed" the enclosed area for 45 s. The invertebrates were stored in 70% ethanol, sorted, and all individuals were counted and identified. We counted 43 752 invertebrates (herbivores, detrivores, and predators), with 75% of them being assigned to Auchenorrhyncha (7301 individuals), Aphidoidea (8072), and Thysanoptera (17 957). We used the total of these plant-feeding herbivores for further analyses.

Statistical analyses

We used a linear mixed-model approach to investigate how herbivore exclusion affected soil net N mineralization. Mineralization was the dependent variable (no transformation), modeled as a function of the fixed-factors exclosure type (ET), vegetation, and ET × vegetation. Exclosure network was included as a random factor nested within grassland. Pairwise comparisons were made for the main effect ET using Bonferroni confidence interval adjustment. Because vegetation and ET × vegetation did not significantly affect net N mineralization, they were dropped from the model. Differences in soil abiotic, soil biotic, and vegetation variables (transformed where necessary) between ET, vegetation, and ET × vegetation were assessed as described previously. Thereafter we related these variables to net N mineralization using Spearman rank correlations. The significant variables were selected and transformed if necessary. These variables were then included individually as covariates into the mixed model to assess whether they explained the differences in net N mineralization among ET. We first fitted the covariate and then ET using Type I sums of squares. We then assessed the relationship between the covariates and the abundance of herbivores (except small mammals; no counts) using linear regression techniques (transforming count data where needed) to assess which herbivore groups were driving the changes in soil and plant properties. The covariates were considered the dependent and the herbivore counts the independent variables. All statistical analyses were performed with the PASW Statistics 22.0 statistical package (IBM SPSS, Chicago, Illinois, USA).

Results

Changes in net N mineralization as a result of progressive herbivore exclusion

Net N mineralization ranged from 0.65 ± 0.05 to 1.02 ± 0.12 $kg \cdot ha^{-1} \cdot season^{-1}$ (mean ± SE) and significantly differed among our five ET ($F_{4,63} = 2.640$, $P = 0.042$; Fig. 1A), but not between the two vegetation types (vegetation: $F_{1,16} = 1.066$, $P = 0.317$; ET × vegetation: $F_{4,64} = 0.219$, $P = 0.927$). Highest net N mineralization was found in the plots grazed by invertebrates only (all mammals excluded) and was significantly different from the "All" treatment (no exclusion), but not from plots where smaller mammals were present or where all herbivores were excluded (Fig. 1A). NO_3^-, NH_4^+, and total inorganic N concentrations and pools were rather low in our dolomite soils and did not differ between the ET or vegetation types (Table 2, Fig. 1B). However, the ET affected aboveground plant biomass N pools, but again, no differences between vegetation types were found (Table 2, Fig. 1C). Root biomass N pools were not available.

Net N mineralization was unrelated to the initial concentrations of soil nutrients and the amount of N contained in the aboveground vegetation (Table 3). However, we found negative correlations between net N mineralization and soil NO_3^- pools, total inorganic N pools, soil moisture, as well as nematode abundance. Net N mineralization was positively correlated with mite abundance, aboveground plant biomass, and root biomass (Table 3). Of these correlating variables, only aboveground plant biomass and mite abundance explained some of the ET differences in net N mineralization (Table 4). Aboveground plant biomass differed between our ET (Fig. 2A, Table 2), whereas mite abundance did not (Fig. 2B, Table 2). Aboveground plant biomass and mite abundance (ln-transformed; $r = 0.230$, $P = 0.029$, $n = 90$) were positively correlated and we found a linear relationship between the average

aboveground plant biomass and average mite abundance between our ET (Fig. 2C).

Linking herbivore abundance to net N mineralization

Ungulate dung pellet counts representative for the 18 "All" plots varied considerably across our exclosure networks, with a sevenfold difference between the lowest (20 pellet groups per season) and highest (147.8) counts. We counted an average of 6.2 marmots (representative for the 36 "All" and "Marmot/Mice/Invertebrates" plots) on our grasslands over the course of three growing seasons, with a minimum of 2.33 and a maximum of 17.80 marmots per grassland (sevenfold difference). Neither ungulate (biomass, $F_{1,17} = 0.082$, $P = 0.778$; mites, $F_{1,17} = 0.147$, $P = 0.706$) nor marmot (biomass, $F_{1,35} = 1.685$, $P = 0.203$; mites, $F_{1,35} = 0.128$, $P = 0.722$) counts were related to aboveground plant biomass or mite abundance. In contrast, we found a significant positive relationship between invertebrate abundance (1286 individuals/m^2; minimum 103, maximum 6917; 67-fold difference; counted on all but the "None" plots) and aboveground plant biomass ($F_{1,71} = 23.765$, $P < 0.001$), whereas no relationship between invertebrate abundance and mites abundance was detected ($F_{1,71} = 0.120$, $P = 0.741$).

Discussion

Progressive herbivore exclusion led to higher net N mineralization when all mammals were excluded compared to when all herbivores had access, regardless of vegetation types. Thus, all mammals combined slowed down net N mineralization. The variability in N mineralization among our treatments was partially explained by increases in aboveground plant biomass that affected mite abundance. We discuss the potential mechanisms behind these changes, as well as the reason for a lack of vegetation type differences.

Lack of difference in net N mineralization between the two vegetation types

Unexpectedly, there were no differences in net N mineralization between the vegetation types. This was surprising, because the long-term human land use (since the early 14th century) and different grazing patterns by red deer after the park's foundation led to considerably different plant community composition and structure, grazing intensity, plant quality, and soil invertebrate community composition in these vegetation types (Risch et al. 2013, Vandegehuchte et al. 2015). Other studies showed marked differences in grassland net N mineralization with varying grazing intensities and changing plant community composition (e.g., Holland and Detling 1990, Frank and Groffman 1998), which sharply contrasts with our findings. One potential explanation for the differences between studies is that soil temperature and moisture, strong drivers of net N mineralization, did not differ between vegetation types at our sites between 2009 and 2013 (see Table 2). Further, nutrient availability did not differ that much between our vegetation types (see Table 2), as both were located on the same rather poor underlying bedrock (dolomite). In comparison, other studies of herbivore exclusion compared the effects of vegetation composition or grazing intensity across soils derived from differing bedrock material (e.g., Bardgett et al. 1997, Stark et al. 2015).

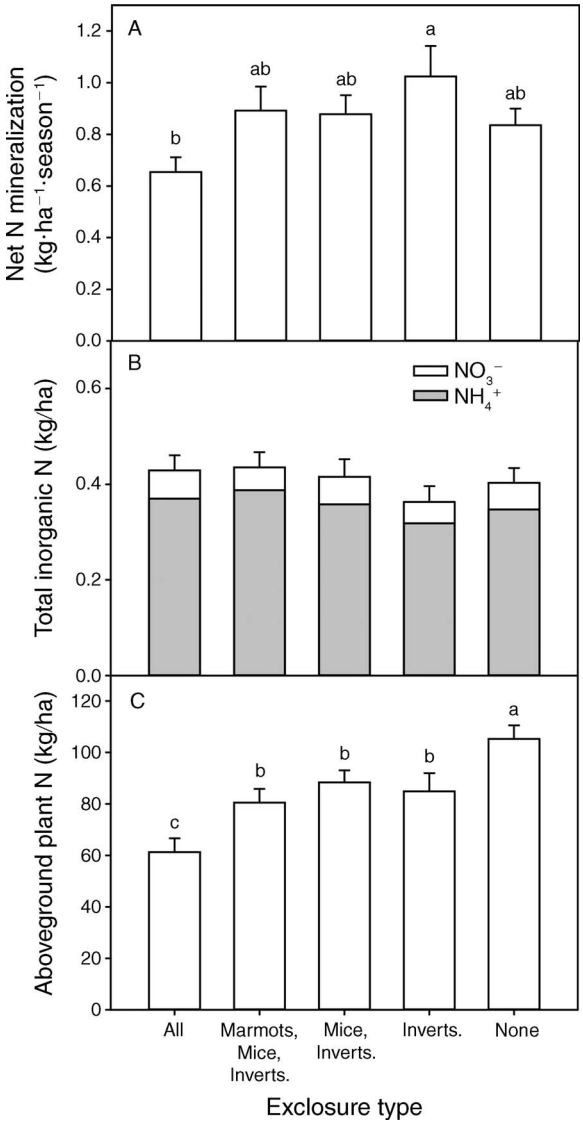

FIG. 1. Exclosure type effects on (A) net N mineralization rates, (B) NO_3^-, NH_4^+, and total inorganic N pools, and (C) aboveground plant biomass N pools. Soil pools are representative for the top 10 cm of soil. Values represent means + SE. Different lowercase letters indicate significant differences between the exclosure types ($\alpha = 0.05$). Exclosure types describe which aboveground herbivores are feeding on the grassland: All, all herbivores; Marmots, Mice, Inverts., medium and small mammals as well as invertebrates; Mice, Inverts., small mammals and invertebrates; Inverts., invertebrates; None, no aboveground herbivores.

TABLE 2. Linear mixed-model results for all parameters.

Parameter	Treatment		Vegetation		Treatment × Vegetation	
	F	*P*	*F*	*P*	*F*	*P*
Soil abiotic properties						
Soil temperature (°C)	**17.46**	**<0.001**	1.326	0.266	1.326	0.394
Soil moisture (%)	**2.749**	**0.036**	0.132	0.721	1.261	0.294
NO_3^- (μmol/g)	1.874	0.126	0.082	0.778	2.464	0.054
NH_4^+ (μmol/g)	1.194	0.322	2.622	0.125	**3.654**	**0.010**
Total inorganic N (μmol/g)	0.872	0.486	1.254	0.279	**3.280**	**0.017**
Surface organic layer soil C (%)	0.065	0.992	0.206	0.656	0.946	0.443
Surface organic layer soil N (%)	0.361	0.835	0.174	0.682	1.512	0.210
Surface organic layer soil C:N ratio	0.409	0.802	0.026	0.874	0.488	0.745
Surface organic layer soil P (μmol/g)	1.540	0.201	1.721	0.208	0.567	0.688
Mineral soil C (%)	0.381	0.822	1.054	0.320	0.213	0.930
Mineral soil N (%)	0.421	0.793	0.580	0.457	1.483	0.218
Mineral soil C:N ratio	0.271	0.896	0.065	0.802	1.084	0.372
Mineral soil P (μg/g)	1.139	0.346	2.736	0.118	0.967	0.432
pH	1.123	0.354	0.918	0.352	0.641	0.635
Bulk density (g/m^3)	0.275	0.893	0.198	0.663	2.176	0.082
NO_3^- pool (kg/ha)†	1.935	0.116	0.017	0.897	0.230	0.920
NH_4^+ pool (kg/ha)†	1.007	0.410	0.880	0.362	0.382	0.821
Total inorganic N pool (kg/ha)†	0.909	0.464	0.721	0.408	0.329	0.858
Soil biotic properties						
Microbial biomass C (mg/kg)	1.888	0.123	0.091	0.767	0.443	0.777
Springtails (individuals/L soil)	0.306	0.873	2.037	0.173	0.671	0.615
Mites (individuals/L soil)	0.992	0.418	2.711	0.119	0.634	0.640
Nematodes (individuals/100 g dry soil)	**5.624**	**0.001**	0.051	0.824	1.260	0.295
Vegetation properties						
Aboveground plant biomass (g/m^2)	**12.61**	**<0.001**	2.070	0.170	**3.419**	**0.014**
Root biomass (g/m^2)	1.570	0.193	**8.145**	**0.011**	**3.649**	**0.010**
Biomass consumption (g/m^2)	**9.209**	**<0.001**	**12.01**	**0.003**	0.966	0.416
Peak biomass C concentration (%)	**10.18**	**<0.001**	**6.209**	**0.024**	0.970	0.430
Peak biomass N concentration (%)	**5.597**	**0.001**	1.156	0.298	**4.570**	**0.003**
Peak biomass C:N ratio	**6.701**	**<0.001**	1.754	0.204	**4.795**	**0.002**
Peak biomass NDF concentration (%)	0.800	0.530	**21.67**	**<0.001**	**8.561**	**<0.001**
Peak biomass ADF concentration (%)	0.575	0.682	**16.21**	**0.001**	**7.859**	**<0.001**
Peak biomass ADL concentration (%)	0.324	0.861	0.093	0.765	0.889	0.476
Late-season C concentration (%)	**6.422**	**<0.001**	**7.612**	**0.014**	0.914	0.461
Late-season N concentration (%)	**2.882**	**0.029**	**10.19**	**0.006**	**4.630**	**0.002**
Late-season C:N ratio	**4.008**	**0.006**	**13.05**	**0.002**	**4.850**	**0.002**
Late-season NDF concentration (%)	0.317	0.866	**16.25**	**0.001**	**7.625**	**<0.001**
Late-season ADF concentration (%)	0.626	0.645	**14.49**	**0.002**	**6.192**	**<0.001**
Late-season ADL concentration (%)	1.393	0.246	0.391	0.541	0.461	0.764
Aboveground plant biomass N pool (kg/ha)	**15.88**	**<0.001**	1.395	0.255	2.069	0.095

Notes: Soil moisture, soil NO_3^-, NH_4^+, total inorganic N concentrations, surface organic layer soil C, N, C:N, P concentrations, mineral soil N, C:N, P concentrations, bulk density, soil NO_3^-, and total inorganic N pools, microbial biomass C, springtails, mites, nematodes were ln-transformed. Mineral soil C concentration, soil NH_4^+ pool, pH, aboveground plant biomass, root biomass, biomass consumption, peak biomass and late-season biomass C, N, C:N, NDF (neutral detergent fiber), ADF (acid-detergent fiber), and ADL (acid-detergent lignin concentrations), and aboveground plant biomass N pool were not transformed. Bold type indicates significance at $\alpha = 0.05$.

† Pools representing top 10 cm soil layer.

Aboveground vertebrate and invertebrate herbivore impact on net N mineralization

Our changes in net N mineralization were partially explained by aboveground plant biomass and total mite abundance, which suggests indirect effects of herbivores through alterations in plant material, a variable that can serve as a proxy of plant litter. The exclusion led to increases in biomass, which in turn may have induced a bottom-up feedback with regard to mite abundance. Several studies showed that mites were highly sensitive to changes in grazing regimes (e.g., Schon et al. 2012). Thus, it is possible that the small, but not significant, increase in mite abundance caused by increases in aboveground plant biomass was sufficient to lead to changes in net N mineralization in our grasslands. It has also been shown that increased "grazing" of fungal mycelium by soil micro-arthropods (including mites) stimulates the release of soil extracellular enzymes (A'Bear et al. 2014) responsible for the depolymerization of N-containing compounds, a critical step in the N mineralization pathway (Schimel and Bennett 2004). Thus, excluding mammals from our grasslands might have affected net N mineralization not only through increased plant material input, but also through alterations of fungal grazing rates by mites.

TABLE 3. Spearman rank correlation coefficients (r) of pairwise correlation between net N mineralization rates and the soil abiotic, soil biotic, and vegetation parameters available.

Parameter	Spearman rho		
	r	P	n
Soil abiotic properties			
Soil temperature (°C)	−0.029	0.790	89
Soil moisture (%)	**−0.247**	**0.020**	**89**
NO_3^- (μg/g)	−0.035	0.747	89
NH_4^+ (μg/g)	−0.065	0.544	89
Total inorganic N (μg/g)	−0.058	0.592	89
Surface organic layer soil C (%)	0.049	0.650	89
Surface organic layer soil N (%)	0.068	0.530	87
Surface organic layer soil C:N ratio	−0.100	0.358	87
Surface organic layer soil P (μg/g)	0.060	0.574	89
Mineral soil C (%)	−0.088	0.412	89
Mineral soil N (%)	−0.037	0.731	89
Mineral soil C:N ratio	−0.063	0.556	89
Mineral soil P (μg/g)	−0.012	0.912	89
pH	−0.063	0.558	89
Bulk density (g/m^3)	−0.185	0.083	89
NO_3^- pool (kg/ha)	**−0.296**	**0.011**	**89**
NH_4^+ pool (kg/ha)	−0.196	0.065	89
Total inorganic N pool (kg/ha)	**−0.244**	**0.035**	**89**
Soil biotic properties			
Microbial biomass C (mg/kg)	0.141	0.187	89
Collembola (individuals/L soil)	0.158	0.140	89
Mites (individuals/L soil)	**0.370**	**<0.001**	**89**
Nematodes (individuals/100 g dry soil)	**−0.217**	**0.042**	**88**
Vegetation properties			
Aboveground plant biomass (g/m^2)	**0.228**	**0.031**	**89**
Root biomass (g/m^2)	**0.269**	**0.011**	**89**
Biomass consumption (g/m^2)	−0.115	0.341	89
Peak biomass C concentration (%)	−0.007	0.949	89
Peak biomass N concentration (%)	−0.113	0.138	89
Peak biomass C:N ratio	0.120	0.264	89
Peak biomass NDF concentration (%)	0.145	0.175	89
Peak biomass ADF concentration (%)	0.200	0.060	89
Peak biomass ADL concentration (%)	0.173	0.105	89
Late-season C concentration (%)	0.138	0.197	89
Late-season N concentration (%)	−0.162	0.129	89
Late-season C:N ratio	0.183	0.087	89
Late-season NDF concentration (%)	0.083	0.442	89
Late-season ADF concentration (%)	0.091	0.397	89
Late-season ADL concentration (%)	−0.060	0.575	89
Aboveground plant biomass N pool (kg/ha)	0.179	0.093	89

Note: Bold type indicates significance at $\alpha = 0.05$.

TABLE 4. Statistical results of the linear mixed-model approach where exclosure type and the respective soil or vegetation variable were introduced as fixed factors.

Parameter	Covariate			Exclosure type		
	df	F	P	df	F	P
Soil moisture (%)	1, 32	4.039	0.053	4, 67	3.017	0.024
NO_3^- pool (kg/ha)	1, 52	0.363	0.550	4, 68	2.621	0.042
Total inorganic N pool (kg/ha)	1, 81	9.142	0.003	4, 66	2.593	0.044
Mites (individuals/L)	*1, 53*	*10.22*	*0.002*	*4, 65*	*2.197*	*0.079*
Nematodes (individuals/100 g dry soil)	1, 38	1.262	0.268	4, 66	2.927	0.027
Aboveground plant biomass (g/m^2)	*1, 78*	*3.290*	*0.074*	*4, 70*	*1.979*	*0.107*
Root biomass (g/m^2)	1, 43	4.790	0.034	4, 68	3.059	0.022

Notes: Italic font indicates the variables that explained part of the variability in net N mineralization between the exclosure types. Soil moisture, NO_3^- pool, total inorganic N pool, mites, and nematodes were ln-transformed. Aboveground plant biomass and root biomass were not transformed.

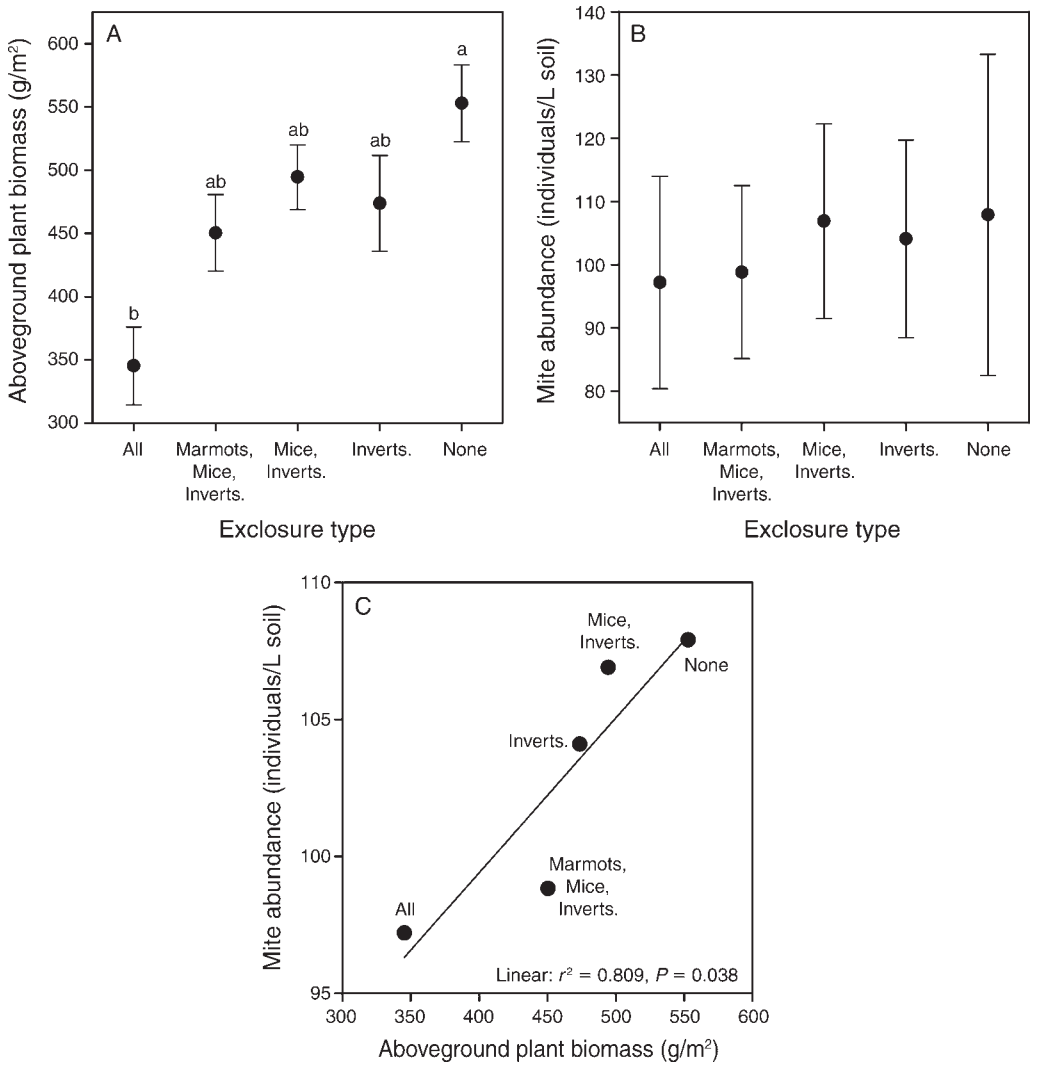

FIG. 2. Exclosure type effects on (A) aboveground plant biomass and (B) mite abundance. Values represent means ± SE. Different lowercase letters indicate significant differences between the exclosure types ($\alpha = 0.05$). (C) Relationship between aboveground plant biomass and mite abundance among the exclosure types. Values represent means. Exclosure types describe which aboveground herbivores are feeding on the grassland: All, all herbivores; Marmots, Mice, Inverts., medium and small mammals as well as invertebrates; Mice, Inverts., small mammals and invertebrates; Inverts., invertebrates; None, no aboveground herbivores.

The lack of net N mineralization increase despite a strong increase in aboveground plant biomass between the "Invertebrate" and "None" plots seems to suggest that the pathways outlined here do not hold as a stand-alone explanation. Based on our results, we propose that direct effects of herbivore exclusion might be responsible for this apparent disconnect. We found increased invertebrate abundance with increasing aboveground plant biomass, which could have led to increased rates of leaf abscission (e.g., Faeth et al. 1981, Hunter 2001) and therefore higher amounts of organic material returned to the soil with progressive herbivore exclusion. Given that we captured, on average, 1286 leaf-sucking invertebrates/m^2, excluding them would result in a decreased input of organic material on the "None" plots, which could be responsible for the "no response" of net N mineralization between the "Invertebrate" and "None" plots, regardless of the increase in aboveground plant biomass. Unfortunately, we do not have any measures of leaf abscission. Similarly to the leaf-sucking invertebrates, changes in grasshopper abundance also could have had an effect on soil net N mineralization rates in our study. It is known that these invertebrates only consume 20–30% of the plant biomass removed (Bailey and Riegert 1973, Ingrisch and Köhler 1998), while the rest is "dropped" to the ground and is directly entering the soil food-web. In addition, Belovsky and Slade (2000) showed that increasing grasshopper densities lead to increases in soil N cycling, and Spalinger et al. (2012) found increased grasshopper abundance with increasing

plant height in the subalpine grasslands of the SNP. Even though we only captured 2.6 grasshoppers/m^2, on average, these insects are much larger than the leaf-sucking invertebrates.

Exclosure type probably also affected the amount and distribution of dung (frass) and urine. We did not measure dung input from medium and small mammals, invertebrate frass, or urine; ungulate feces amounted to between 50 and 370 g dry mass·m^{-2}·$season^{-1}$ (calculated based on Schütz et al. 2006). The "exclusion" of these ungulate dung inputs did, however, not affect net N mineralization, because the rates between "All" and "Marmot, Mice, Invertebrates" did not differ statistically. Yet, Bakker et al. (2004) reported higher dung amounts by voles when cattle and rabbits were excluded. Similarly, we could have had higher amounts of finely distributed invertebrate frass due to higher abundance of invertebrates after excluding the mammals.

Conclusions

Our results showed that large, medium, and small mammals had a negative effect on net N mineralization. These findings may be attributed in part to a reduction in the amount of plant material returned to the soil. This, in turn, resulted in a bottom-up feedback effect through mite abundance, which are considered indirect effects. The findings also might be attributed to changes in the amount and distribution of waste products with progressive herbivore exclusion; these are direct effects. It is difficult to clearly dissect the importance of indirect or direct effects of all the herbivores present in our system. However, our results show that changes in the aboveground herbivore community can strongly influence ecosystems by altering nutrient cycling.

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