PAPER II

Topography drives patterns of tundra plant diversity – there is no difference, even 60 years after cessation of sheep grazing

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- Conceived of or designed study: MAM, VTR, NGY, TET, ISJ
- Performed fieldwork: MAM, ISJ
- Performed laboratory work: MAM
- Analyzed data: MAM, VTR, NGY
- Wrote the paper: MAM, VTR, NGY, TET, ISJ

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Abstract

Plant communities in arctic tundra are strongly shaped by topography. Contrasting wind exposures, slopes of different inclination and landforms of different curvature affect growing conditions and ultimately shape plant diversity patterns. Although the great majority of tundra ecosystems are grazed to some degree, the potential of ungulates to outweigh the diversity patterns that are defined by topography is poorly investigated.

Here we investigate if topographically driven within (*alpha*) and between (*beta*) community diversity can be modified by grazing ungulates. We compared presently grazed *versus* un-grazed valleys in Iceland to address effects of sheep grazing cessation on *alpha* and *beta* diversity. Both diversity components were assessed on different spatial scales, which were determined by topography.

Landforms of contrasting curvature, and contrasting elevations representing different slope angles, were the main drivers of *alpha* and *beta* diversity in our study system, affecting mainly species richness. Those topographical units were characterized by contrasting abiotic growing conditions, which are determined by a combination of different moisture regimes and differences in plant growth form abundances. Although we assessed the strongest existing grazing contrasts in Icelandic tundra ecosystems, we found no difference of diversity patterns between grazed valleys and those expected to have recovered from grazing. Our results suggest slow recovery within our valleys, with grazed vegetation states dominating across topographical units and persisting to the present day, decades after cessation of sheep grazing. Slow recovery from grazing can therefore have major implications for management and conservation efforts of plant diversity in tundra ecosystems.

Keywords: site fertility, disturbance, homogenization, land-use history, spatial scale, grain size, *alpha* diversity, *beta* diversity

Introduction

Topographical structuring of different vegetation types is particularly strong in alpine and arctic tundra ecosystems (Daubenmire 1980; Evans et al. 1989; Ostendorf & Reynolds 1989; Matsuura & Suzuki 2012) and determines patterns of plant diversity (Jónsdóttir 1984; Körner 1995; Austrheim & Eriksson 2001). Leeward exposures to the general wind direction and concave depressions have increased snow accumulation compared to windward exposures and convex topography (Evans et al. 1989; Matsuraa & Suzuki 2012). In addition, habitats in gentle slopes are characterized by higher water and nutrient influx compared to steep slopes (Ostendorf & Reynolds 1984). Consequently, wind exposure, slope steepness and landform curvature determine habitat conditions within tundra (Fisk et al. 1998). Biotic interactions, such as vertebrate grazing, may further modulate species diversity, but the role of grazing in shaping diversity in tundra ecosystems is poorly understood.

In general, ungulate grazing influences species richness (Olff & Ritchie 1998; Bakker et al. 2006; Kohyani et al. 2008; Bouahim et al. 2010) and relative abundance of plant species within communities (Augustine & McNaughton 1998; Bråthen et al. 2007; Lezama et al. 2014) (further referred to as *alpha* diversity). The direction of this influence depends on grazing intensity (Huston 1979; Olff & Ritchie 1998; Austrheim et al. 2008) and on the environmental growing conditions (Huston 1979; Proulx & Mazumder 1998; Bakker et al. 2006; Lezama et al. 2014). Grazing can reduce competitive exclusion of species under fertile growing conditions, promoting higher diversity within plant communities. In contrast, even moderate grazing can lead to reduced plant diversity within communities under nutrient poor conditions (Proulx & Mazumder 1998). While grazing effects on *alpha* plant diversity are relatively well studied, less focus has been on how free ranging ungulates modify the species diversity difference between plant communities within a landscape (further referred to as *beta* diversity).

Grazing may alter abundance ranking of graminoids and dicotyledonous forbs or woody plant species (Olofsson 2006; Austrheim et al. 2008; Ravolainen et al. 2014) resulting in a less heterogeneous vegetation structure across habitats within a landscape (Bråthen et al. 2007; Lezama et al. 2014). Thereby, grazing reduces also species *beta* diversity between communities (Chaneton & Facelli 1991; Olff & Ritchie 1998; Ravolainen et al. 2010; Speed et al. 2013; Lezama et al. 2014). However, a reduction of *beta* diversity due to grazing is not always found (e.g. Golodets et al. 2011), which is presumably due to dependencies on the spatial scales of assessments. In general, patterns of plant community *alpha* and *beta* diversity are ultimately the product of the present growing conditions in relation to grazing intensity patterns within a landscape (Senft et al. 1987; Adler et al. 2001; Austrheim & Eriksson 2001). Grazing ungulates are present in almost all tundra areas throughout the northern hemisphere (Mulder 1999; van der Wal 2006) and they are often managed as livestock or semi-domesticated herds. We do not fully understand, however, if and how grazing impacts plant *alpha* and *beta* diversity patterns in tundra landscapes where topography strongly shapes habitat conditions.

Iceland is at the southern limits of the arctic bioclimatic zone and should be well suited for addressing the impact of ungulate grazing on *alpha* and *beta* diversity in tundra landscapes. Land use, including livestock grazing by sheep (*Ovis aries* L.), has strongly altered the natural vegetation since the island was settled eleven hundred years ago (Lawson et al. 2007; Vickers et al. 2011; Brown et al. 2012). Heavy grazing was the main driver of

vegetation change in grazing commons in the tundra areas (at or above the *Betula pubescens* Ehrh. tree line) while in the subarctic lowlands, deforestation and various agricultural activities were additional drivers. There is evidence that the grazing commons that are today strongly dominated by graminoids (grasses, sedges and rushes) were previously dominated by deciduous shrub (mainly *Betula pubescens*, *Betula nana* L. and thicket forming *Salix* species) and forb rich vegetation (Erlendsson et al. 2009; Streeter & Dugmore 2014; Arnalds 2015). Sheep grazing has maintained graminoid dominated vegetation and the relatively homogeneous appearance of most Icelandic landscapes today (Kristinsson 1995; Thórhallsdóttir 1996). Only small areas, inaccessible to sheep, witness vegetation development without livestock grazing. A study of one of these areas in the highland tundra revealed that un-grazed areas had lower species richness within each community (*alpha*, including bryophytes and lichens), but a stronger differentiation of plant communities across topographic gradients compared to adjacent grazed areas (Jónsdóttir 1984). Also, un-grazed vegetation was more strongly dominated by shrubs (mostly *Salix phylicifolia* L.) and broad leaved dicotyledonous herbs (forbs), i.e. species that were largely absent in the surrounding grazed areas. However, the spatial coverage of this study is too small to generalize grazing impacts on plant diversity patterns of Icelandic tundra. After agricultural modernization began in Iceland in the 1940's, many farms in remote regions were abandoned, creating the opportunity of vegetation recovery to un-grazed vegetation states. Those abandoned farming areas provide opportunities to address the effect of grazing on vegetation and species diversity in Icelandic tundra landscapes across various spatial scales.

For the present study, we assessed plant diversity patterns of the strongest possible grazing contrasts in Iceland. We selected three valleys in Northwest and North Iceland that had been abandoned and not grazed by sheep for up to 60 years (Table 1, Figure 1A) and compared them to similar valleys in close proximity that were still grazed. Within each valley, topography creates distinct growing conditions via contrasting slope exposures, elevations of differently inclined slopes and convex *versus* concave landforms, units that can be regarded as spatially nested (see Figure 1B, C) (Wiens 1989; Levin 1992). We first evaluated our assumptions of contrasting growing conditions within each valley by testing differences in soil properties between different slope exposures, elevations and landforms. We predicted *alpha* diversity to differ between those topographical units, assuming lower diversity within relatively productive compared to less productive topographical units (i.e. within concave landforms, low elevations and west facing slopes) due to the exclusion of less competitive plant species. We also expected *alpha* diversity to be generally higher in grazed than un-grazed valleys and that the grazing effects would depend on growing conditions. In addition, we expected *beta* diversity among plant communities of contrasting habitat conditions to be higher in un-grazed compared to grazed valleys across all topographical units. Because diversity indices provide no information on the identity of the plants behind the index value, we additionally tested the difference in abundance of several plant groups. As grazing in Iceland is assumed to have increased graminoid dominated vegetation and suppressed deciduous woody (especially thicket forming) and forb species, we expected differences in abundance of these plant groups between grazed and un-grazed valleys.

Table 1. Contrasting grazing regimes of selected tundra valleys in Iceland

Valley	land use history	presently grazed	number of winterfed sheep	avrg. slaughter weight of lambs	total feces counts 2012
Adalvík	abandoned 1952	no	0	-	0
Grunnavík	abandoned 1962	no	0	-	0
Nesdalur	abandoned ~ 1990	no	0	-	0
Ingjaldssandur	inhabited and still grazed	yes	~ 200	18 - 19 kg	6
Skálavík	abandoned but still grazed	yes	~ 500	20 kg	8
Thorgeirsfjördur	abandoned but still grazed	yes	~ 2500*	17 kg	20

 * The whole surrounding of Thorgeirsfjördur has approx. 2500 winter fed sheep. It is assumed that approx. 1000 sheep are using this valley during summer time

Materials and Methods

SELECTION OF STUDY SITES

Six valleys of similar size, shape, orientation and growing conditions in the Northwest and in the North of Iceland were selected for the study (Figure 1A). They were all situated north of 66° N and within the low arctic subzone E of the arctic bioclimatic zonation (CAVM team 2003). Long term (1949 to 2014) average monthly temperatures during the growing season (June to August) were 9.4 °C (min 7.7 °C; max 10.8 °C) in Northwest Iceland (weather station Bolungarvík), and 10.1°C (min 8.2 °C; max 11.9 °C) in North Iceland (weather station Akureyri) (Icelandic Meteorological Office, http://en.vedur.is/Medaltalstoflur-txt/Manadargildi.html). The available data for the same period showed average annual precipitation of 841 mm (min 590 mm; max 1181 mm) in Northwest Iceland and 515 mm (min 320 mm; min 744 mm) in North Iceland (Icelandic Meteorological Office, http://en.vedur.is/Medaltalstoflur-txt/Arsgildi.html). Snow plays an important role in our sites, with a continuous snow cover from October to Mid-June. All field sites were well outside the Icelandic zones of active rift and volcanism, on bedrock of Tertiary basalts with more than 3.3 million years of age (Jóhannesson & Sæmundsson 2009). Therefore, in contrast with the volcanically active regions, the study sites were not heavily influenced by frequent deposits of volcanic ash or tephra, and typical soil types are classified as Brown Andosols with a soil pH that typically ranges between 4.5 and 6.5 (Arnalds 2015, pp 91-93). The area was glaciated during the last glacial maximum and became de-glaciated about 11 000 years ago (Norðdahl et al. 2008). The valley morphology is shaped by glacial erosion resulting in a typical U-shape. The steep valley

slopes are covered in scree and solifluction lobes, which are important in shaping the smaller-scale topography.
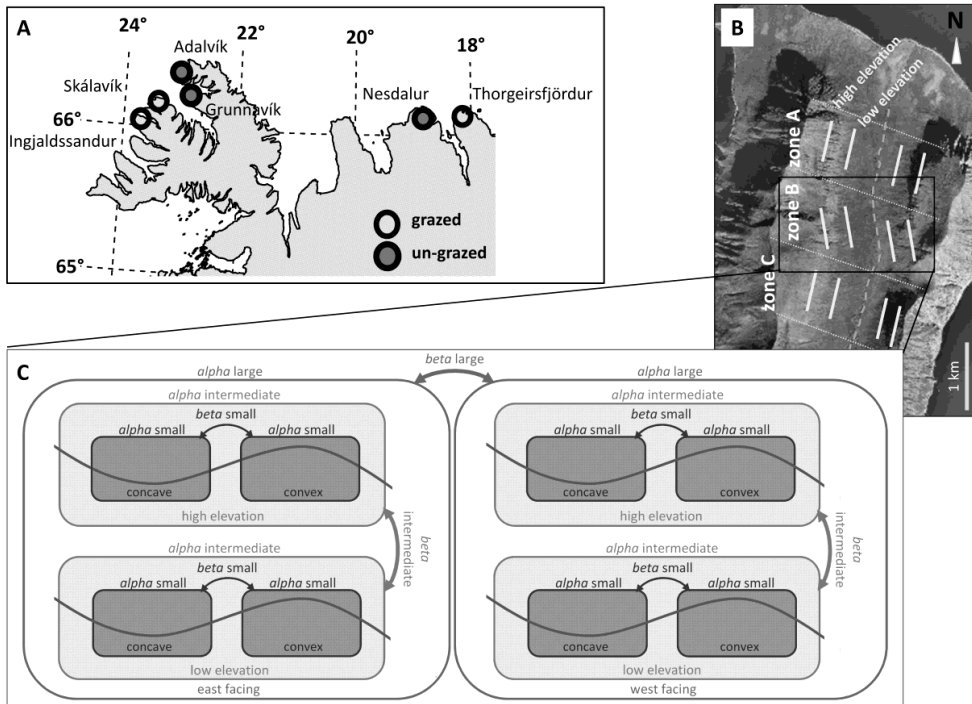

Figure 1. (A) Location of sampling sites in grazed and un-grazed valleys in Iceland. (B) Each valley was split up into three zones (zone A, zone B, zone C) to spread sampling throughout the valley. (C) Within each zone, we covered the major topographical contrasts; landform curvature (small grain size), elevation (intermediate grain size) and slope exposure (large grain size). We sampled vegetation in landforms with concave and convex curvature, which were located within high and low elevations. High and low elevations in turn were located within east and west facing slopes. Alpha small, alpha intermediate and alpha large represent within community diversity on a small, intermediate and large spatial grain size. Beta small, beta intermediate and beta large represent between community diversity on a small, intermediate and large spatial grain size.

The vegetation is generally described as "low shrub tundra" (CAVM team 2003; Walker et al. 2005). The prevailing wind direction is from east and north east (Einarsson 1976) leading to greater snow deposition on west facing than on east facing slopes (Evans et al. 1989). The slopes of the valleys are generally concave (Figure 1B) which leads to a vertical topo-sequence from xeric to mesic and moist conditions towards the valley bottom. However, small streams and alluvial fans running down the valley slopes cause a

horizontally altering pattern of convex and concave landforms within this vertical sequence, leading to differences in growing conditions at even smaller scale.

Besides occasional flocks of migratory geese and resident ptarmigans (*Lagopus muta* Montin, own observations of droppings) and rare occurrence of wood mice (*Apodemus sylvaticus* L.) (Unnsteinsdóttir & Hersteinsson 2009), domesticated sheep (*Ovis aries* L.) are the main vertebrate herbivores in our valleys. The six valleys had contrasting sheep grazing regime (Table 1, Figure 1A).

SAMPLING DESIGN

We aimed for a design that enabled us to capture the vegetation differentiation according to the three spatially nested topographical units, i.e. differentiation according to i) the slope aspect (largest spatial scale), ii) high and low elevations within slopes (intermediate spatial scale) and iii) concave and convex landforms within different elevations (smallest spatial scale).

There were no vegetation maps available for our valleys and available digital data were too coarse to allow stratification by small scale landform differences. We therefore emphasized that all steps of the sampling design were as transparent as possible and based on clearly defined criteria (Mörsdorf et al. 2015). Using topographical maps within a geographical information system (esri ArcGIS 10.1), we drew a cross section along rivers that run through the bottom and the long-axis of the valleys (Figure 1B). To ensure a spread of sampling units throughout the valley, we further stratified the sampling to include three distance zones from the sea: zone A (1-2 km from the coast), B (2-3 km) and C (3-4 km inland) (Figure 1B). Within each zone, and perpendicular to the long axis of each valley, two transects, each running at opposite slopes of the valley, were defined from the river at the valley bottom and up the valley slopes. These transects were spaced at 100 m intervals and both had to traverse a concave valley slope. Transects that crossed transitions to convex topography were discarded. We also used aerial photographs to discard transects that crossed boulder fields, most of which had very low vascular plant cover. To restrict sampling to the foot of the slopes (mild snowbed conditions) and the more inclined parts of the slope (mesic conditions), we noted the GPS coordinates of all remaining transects that intersected with a contour line of 40 m, 60 m and 80 m elevation for zone A, B and C, respectively. The difference in elevations for each zone was due to a general uplift of the valley bottom from the coastline to the inner parts of the valleys. The GPS coordinates built the sampling frame for the present study.

Two GPS coordinates were selected randomly from the sampling frame of each zone, one from either side of the valley. In the field we visited these coordinates and used a priori defined rules to guide us to sampling units of interest that are shaped on smaller spatial scales, i.e. convex and concave landforms: Arriving at the GPS location, we moved horizontally towards the sea until we reached the transition zone of a convex and a concave small-scale landform that spanned at least 15 m horizontally. The center of a 30 m long measuring tape was placed at the transition zone and each end was stretched into the convex and concave landform respectively. We sampled the vegetation systematically along the measuring tape (see next section). We repeated the same procedure at an elevation 60 m above the selected GPS coordinates to sample vegetation data at steeper (mesic) parts of the valley slopes.

DATA COLLECTION

The vegetation was analyzed across the concave and convex landforms along the 30 m measuring tape in 40 x 40 cm plots. Beginning at both ends of the measuring tape, we sampled four plots within each landform at intervals of 3 m. To measure plant species abundance, we applied a refined version of the point intercept method (Jonasson 1988) which is designed to sample vegetation over extensive spatial scales (Bråthen & Hagberg 2004). We used a 40 x 40 cm metal frame with 5 metal pins of 2 mm diameter, one in each corner of the frame and one in its center. The frame was placed at the uphill side of the measuring tape and at each pin all hits through the vascular plant canopy were recorded and identified to species. To measure species richness, we recorded all additional plant species within the plot which were not hit by the pins. In total 576 plots were analyzed.

We used the soil pH, total carbon (C) and total nitrogen (N), as well as C:N ratio as a rough indicator of site fertility (Soil Survey Staff 2011, pp. 247-248). Soil moisture is also an important aspect of soil fertility but *in situ* measurements during the field campaign were expected to be very sensitive to weather fluctuations and therefore difficult to relate to general differences in moisture conditions. Instead we subjectively evaluated the moisture conditions during sampling by assigning each plot to one out of four moisture categories (dry – mesic – moist – wet). This approach improved evaluation of the topographical units with respect to different moisture conditions. Soil samples were taken next to each vegetation plot. Approximately 50 g of fresh soil were excavated from the soil surface to about five cm soil depth, which corresponded to the rooting zone in our study sites. The four soil samples of convex and concave landforms, respectively, were pooled and stored in cooled conditions until arrival in the lab (max. four days). In the lab, soil samples were air dried at ambient temperature, sieved using a two millimeter mesh width and homogenized with a mortar. We measured the soil pH after extraction in distilled water, using a soil to water ratio of 1:5 (method adapted for dried soil samples from Blakemore et al. 1987). In addition, we analyzed total C and total N concentration of the samples using a vario MAX cube CN analyzer (http://www.elementar.de/en/products/vario-serie/vario-max-cube.html).

As an estimate of the current grazing pressure, we counted the number of herbivore droppings within a one meter zone along the 30 m measuring tape (Table 1).

SELECTION OF DIVERSITY METRICS AND PLANT GROUP CLASSIFICATION

For species diversity, we selected *alpha* as well as *beta* diversity metrics that reflect both the occurrence and the abundance of plant species within and between communities. We used species richness to measure properties of *alpha* diversity in terms of species occurrences and Gini-Simpson index to detect differences in relative species abundance (Table 2). In terms of *beta* diversity, we used dissimilarity indices that excluded information on joint species absences. We chose Jaccard dissimilarity to reflect community differentiation based on species occurrences. For differentiation based on relative species abundances, we used a modified version of Gower´s distance (Anderson et al. 2006). This "Modified Gower" distance (*sensu* Anderson et al. 2006) enabled us to weigh the change in abundance over orders of magnitude. By applying a prior logarithmic transformation on the raw abundances, where weighing is done according to the base of the logarithm (Anderson et al. 2006), the distance can be interpreted as an average change in orders of magnitude

per species between two different plant communities. We chose to use a log base of two for this study (and further termed the distance "MG2" throughout this article), as this gives most weight to a change in relative species abundance. Using a log base of two gives a doubling in abundance of one species the same weight as a plant community compositional change of one species. We used the R environment for all our data evaluations (R Core Team 2013) and applied vegdist and decostand function of the vegan package to calculate Jaccard dissimilarities and MG2 distances (Oksanen et al. 2013). All indices are presented in Table 2.

To evaluate whether differences in the various diversity measures could be related to differences in the abundance of those plant groups expected to respond to grazing, the species data were classified according to Table 3. The estimated effects of topography and grazing on the abundance of those plant groups was analysed.

STATISTICAL ANALYSES

We first assessed whether contrasts in topography were characterized by differences in soil conditions in our study. We fitted linear mixed effects models, using the nlme package in R (Pinheiro et al. 2004). The soil variable (soil pH or soil C, N, C:N ratio) was set as response variable and we included the topographical unit of interest, the grazing regime and their interaction as fixed effects. Neither the interaction, nor the grazing regime as an additive factor, had statistically significant effects (based on a 5% significance level) on those response variables, which is why we reduced the models to only include the topographical unit as a fixed factor. This procedure was followed to separately test the effects of landform curvature, elevation and general slope aspect on our soil variables. The random structure of the model reflected the spatial nestedness of our design. Depending on the topographical unit of interest, we had to include different design variables in our models (Table S1 Supplementary material).

For diversity analyses, we regarded the spatial nestedness of our topographical units and the data recordings within those units as different grain sizes (Figure 1C) (Wiens 1989). For analyses of the smallest grain size we aggregated all plant hits (or species number for species richness) of the four plots within each concave and convex landform. Accordingly, we aggregated all the plant data within each high and low elevation transect, representing an intermediate grain size. Finally, we aggregated all the plant data within east and west facing slopes within one zone, which was the largest grain size in our study. Next, all the plant hits were converted into biomass (grams $* m^{-2}$) using weighted linear regression methods (Bråthen & Hagberg 2004). The conversion was based on Ravolainen et al. (2010). For the species found in our Icelandic data that did not exist in their study, we assigned the conversion factor of the most similar species (Table S2 Supplementary material).

Alpha diversity was assessed by setting species richness or Gini-Simpson index as response variable in our models. We tested the effects of the topographical unit and grazing regime plus their interaction by including them as fixed factors in our models. As none of the interactions were statistically significant, we reduced all models to include the topographical unit and grazing as additive fixed factors. Depending on the spatial grain size of analyses, models either included the landform and grazing, elevation and grazing or slope aspect and grazing as additive fixed effects (Table S3 Supplementary material). *Beta*

diversity was calculated as the dissimilarity (Jaccard, MG2) between topographical units for the respective grain sizes of assessment (Figure 1C). Models for *beta* diversity had therefore either Jaccard dissimilarity or MG2 distance as response variables and the grazing regime as a fixed effect. The random structure of all our models reflected the spatial hierarchy of our design on the respective spatial scale (Table S3 of Supplementary material).

For analyses showing statistically significant effects of either topography or grazing on plant diversity, we assessed the biomass of plant groups (Table 3) using the same model structure. The biomass of each respective plant group was used as response variable, but all response variables had to be $\log_e (x+v)$ transformed to fulfill model assumptions, with v being the smallest biomass value of the data set.

We assessed the models' assumptions in terms of constant and normal residual variance and checked for outliers, using diagnostic plots. Within the results section, we report statistically significant effect sizes based on a 5% significance level. Based on a 10% significance level, we annotate effects as "marginal".

Table 2. Mathematical equations of all diversity metrics in this study

Diversity component	Index	Equation
alpha	species richness	$= \text{sum}(n_k)$ n_k: the occurrence of species k in a community
alpha	Gini-Simpson index	$= 1 - \text{sum}(p_k^2)$ p_k: the relative abundance of species k in a community
beta	Jaccard dissimilarity	$= (b+c)/(a+b+c)$ a: the number of species shared b: the number of species occurring in community 1 but not in community 2 c: the number of species occurring in community 2 but not in community 1
beta	Modified Gower distance, using a log base of 2	$= \text{sum}(w_k (\text{abs}(x'_{1k} - x'_{2k}))$ $/\text{sum}(w_k)$ x': $\log_2(x) + 1$ x_{1k}: abundance of species k in community 1 x_{2k}: abundance of species k in community 2 $w_k = 0$ when $x_{1k} = x_{1k} = 0$, otherwise $w_k = 1$

Table 3. Plant species grouping into growth forms. Nomenclature follows the pan arctic flora: http://nhm2.uio.no/paf/

forbs		Grasses		thicket forming shrubs
Alchemilla alpina	*Listera cordata*	*Agrostis capillaris*	*Eriophorum angustifolium*	*Betula pubescens*
Alchemilla filicaulis	*Menyanthes trifoliata*	*Agrostis vinealis*	*Eriophorum scheuchzeri*	*Salix arctica*
Alchemilla glomerulans	*Micranthes nivalis*	*Avenella flexuosa*	*Juncus filiformis*	*Salix lanata*
Alchemilla wichurae	*Omalotheca norwegica*	*Anthoxanthum odoratum*	*Juncus trifidus*	*Salix phylicifolia*
Angelica archangelica agg.	*Oxyria digyna*	*Calamagrostis neglecta*	*Kobresia myosuroides*	
Armeria maritima	*Parnassia palustris*	*Deschampsia alpina*	*Luzula multiflora*	
Bartsia alpina	*Pinguicula vulgaris*	*Deschampsia cespitosa*	*Luzula spicata*	
Bistorta vivipara	*Plantago maritima*	*Festuca rubra ssp. richardsonii*	*Trichophorum cespitosum*	
Caltha palustris	*Limnorchis dilatata*	*Festuca vivipara*		
Cardaminae pratensis agg.	*Potentilla cranztii*	*Hierochloë odorata*	**deciduous woody plants**	
Cerastium alpinum	*Pyrola minor*	*Nardus stricta*	*Betula nana*	
Cerastium cerastoides	*Ranunculus acris*	*Phleum alpinum*	*Betula pubescens*	
Cerastium fontanum	*Rhinanthus minor*	*Poa glauca*	*Comarum palustre*	
Chamaepericlymenum suecicum	*Rumex acetosa*	*Poa pratensis*	*Rubus saxatilis*	
Coeloglossum viridae	*Saxifraga rosacea*	*Trisetum spicatum*	*Salix arctica*	
Epilobium alsinifolium	*Scorzoneroides autumnalis*		*Salix herbacea*	
Epilobium palustre	*Sibbaldia procumbens*	**sedges and rushes**	*Salix lanata*	
Erigeron borealis	*Silene acaulis*	*Carex atrata*	*Salix phylicifolia*	
Gentianopsis detonsa	*Taraxacum officinale*	*Carex bigelowii*	*Vaccinium myrtillus*	
Geranium sylvaticum	*Thalictrum alpinum*	*Carex canescens*	*Vaccinium uliginosum*	
Galium boreale	*Triglochin palustris*	*Carex capillaris*		
Galium normanii	*Veronica alpina*	*Carex chordorrhizza*	**evergreen woody plants**	
Hieracium alpinum agg.	*Viola canina*	*Carex echinata*	*Calluna vulgaris*	
Hieracium thaectolepium	*Viola palustris*	*Carex limosa*	*Dryas octopetala*	
	Viola riviniana	*Carex lyngbyei*	*Empetrum nigrum*	
		Carex nigra	*Kalmia procumbens*	
		Carex rariflora	*Thymus praecox*	
		Carex rostrata		
		Carex vaginata		

Results

ASSUMPTION OF CONTRASTING HABITAT CONDITIONS WITHIN VALLEYS

Soil pH within the field sites ranged between 4.3 and 6.7. Soil pH was significantly higher in convex than in concave landforms and lower in low compared to high elevation (Table 4). The slope aspect had no significant influence on soil pH (Table 4). Soil total C concentrations generally ranged between 1.01 and 38.47%. We found lower soil C concentrations in convex than in concave landforms and higher concentrations in low compared to high elevations, whereas slope aspect had no significant effects (Table 4). Similar patterns were found for total soil N concentrations which ranged between 0.04 and 2.35 %. Total N concentrations were significantly lower in convex than in concave landforms and significantly higher in low compared to high elevations (Table 4), while slope aspect had no significant effects on soil N concentrations (Table 4). Soil C:N ratios were not influenced by landform curvature, elevation or slope aspect (Table 4).

Our subjective evaluation of moisture conditions showed differences between convex and concave, as well as between high and low topographical units (Figure S1 Supplementary material). Concave landforms and low elevations were more often assigned as "moist" and "wet" compared to convex landforms and high elevations. Convex landforms and high elevations had higher frequency in the "dry" category instead. There was no indication for moisture differences between east and west facing slopes.

These results support the assumption that concave landforms and low elevations represent more productive habitats than convex landforms and higher elevations, respectively.

ALPHA AND *BETA* DIVERSITY RELATED TO TOPOGRAPHY AND CESSATION OF GRAZING

The species richness in convex landforms was marginally lower than in concave landforms while grazing did not have an effect on species richness estimates (Table 5, Figure 2A). For Gini-Simpson index, we found no indication of landform or grazing effects (Table 5, Figure 2B). We found no statistically significant grazing effects on *beta* diversity between concave and convex landforms (Table 5). Both, Jaccard dissimilarities (Figure 2C) and MG2 distances (Figure 2D) were similar in grazed and un-grazed valleys.

Species richness was lower at low compared to high elevations but there was no grazing effect on species richness (Table 5, Figure 3A). For Gini-Simpson index, there was no indication of either elevation or grazing effects (Table 5, Figure 3B). *Beta* diversity between high and low elevations was not affected by grazing (Table 5). Both, Jaccard dissimilarities (Figure 3C) and MG2 distances (Figure 3D) were similar in grazed and un-grazed conditions.

Table 4. Soil conditions and effects of topography

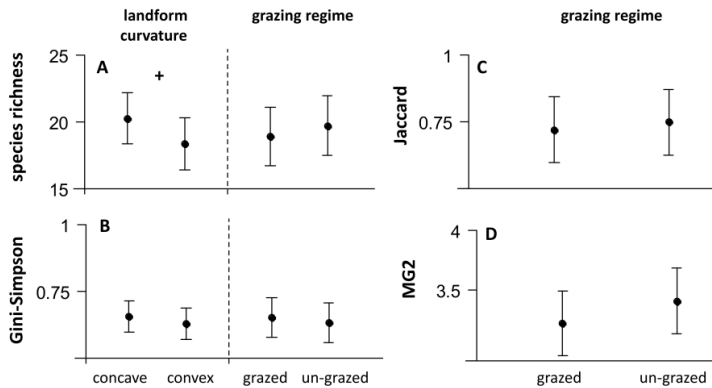| grain size	productivity parameter	effects	effect size	std. error	df	t-value	p-value
small	soil pH	Intercept	5.38	0.10			
		concave -> convex	0.19	0.09	114	2.22	0.029
	soil C	Intercept	17.69	2.43			
		concave -> convex	-3.47	1.35	114	-2.56	0.012
	soil N	Intercept	0.92	0.12			
		concave -> convex	-0.16	0.07	114	-2.36	0.020
	soil C:N ratio	Intercept	18.94	0.78			
		concave -> convex	-0.05	0.55	114	-0.10	0.922
intermediate	soil pH	Intercept	5.60	0.10			
		high-> low	-0.23	0.08	114	-2.72	0.007
	soil C	Intercept	13.00	2.46			
		high-> low	5.81	1.30	114	4.45	<0.001
	soil N	Intercept	0.67	0.12			
		high-> low	0.33	0.06	114	5.16	<0.001
	soil C:N ratio	Intercept	19.20	0.78			
		high-> low	-0.56	0.55	114	-1.02	0.310
large	soil pH	Intercept	5.49	0.10			
		east facing -> west facing	-0.02	0.09	114	-0.18	0.858
	soil C	Intercept	16.27	2.44			
		east facing -> west facing	-0.65	1.33	114	-0.49	0.624
	soil N	Intercept	0.84	0.12			
		east facing -> west facing	0.00	0.07	114	-0.06	0.949
	soil C:N ratio	Intercept	19.39	0.77			
		east facing -> west facing	-0.92	0.58	114	-1.58	0.117

Figure 2. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using a small spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of landform curvature and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity and Modified Gower distance MG2), which was calculated between the landform curvature units, is presented given the influence of grazing. Alfa and beta diversity values are given as predicted values from linear mixed effects models. "+" indicates marginally significant effects and error bars represent 95% confidence intervals.
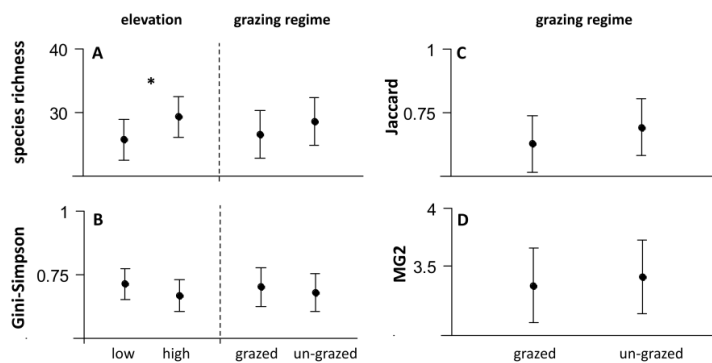

Figure 3. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using an intermediate spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of elevation and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity and Modified Gower distance MG2), which was calculated between different elevations, is presented given the influence of grazing. Alfa and beta diversity values are given as predicted values from linear mixed effects models. "*" indicates statistically significant effects and error bars represent 95% confidence intervals.

Species richness was similar at west and east facing slopes and there was no difference between grazed and un-grazed valleys (Table 5, Figure 4A). We found no effects of the slope aspect or grazing regime on estimates of Gini-Simpson index (Table 5, Figure 4B). For measurements of *beta* diversity between east and west facing slopes, we found no grazing effect (Table 5). Jaccard dissimilarities (Figure 4C) and MG2 distances (Figure 4D) were similar in grazed and un-grazed valleys.
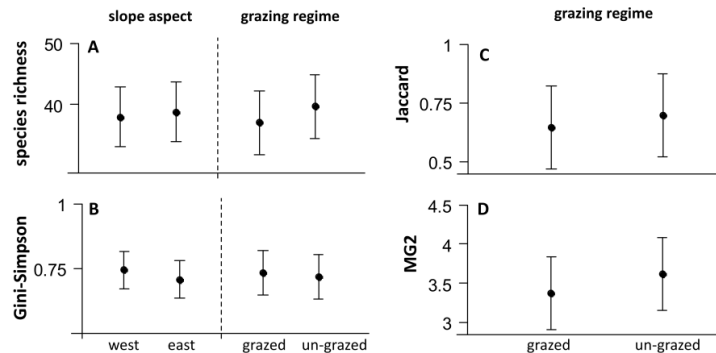

Figure 4. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using a large spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of slope aspect and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity and Modified Gower distance MG2), which was calculated between slopes of different aspect, is presented given the influence of grazing. Alfa and beta diversity values are given as predicted values from linear mixed effects models. Error bars represent 95% confidence intervals

GROWTH FORM ABUNDANCES

Deciduous woody, evergreen woody plants and grasses were the most common growth forms across all topographical units and grazing regimes (Figure 5).

The biomass of forbs was significantly smaller in convex compared to concave landforms (Table S4 Supplementary material, Figure 5A). We also found strong differentiation at both elevations in terms of growth form biomass. The biomass of forbs and of deciduous woody plant species was significantly smaller in low compared to high elevations (Table S5 Supplementary material, Figure 5B). The opposite was the case for grasses and sedges/rushes (Table S5 Supplementary material, Figure 5B). We also found marginal grazing effects on the biomass of *Betula pubescens* and *Salix* shrubs which were less abundant in grazed compared to un-grazed valleys (Table S5 Supplementary material, Figure 5C).

Table 5. Diversity estimates and effects of topography and grazing

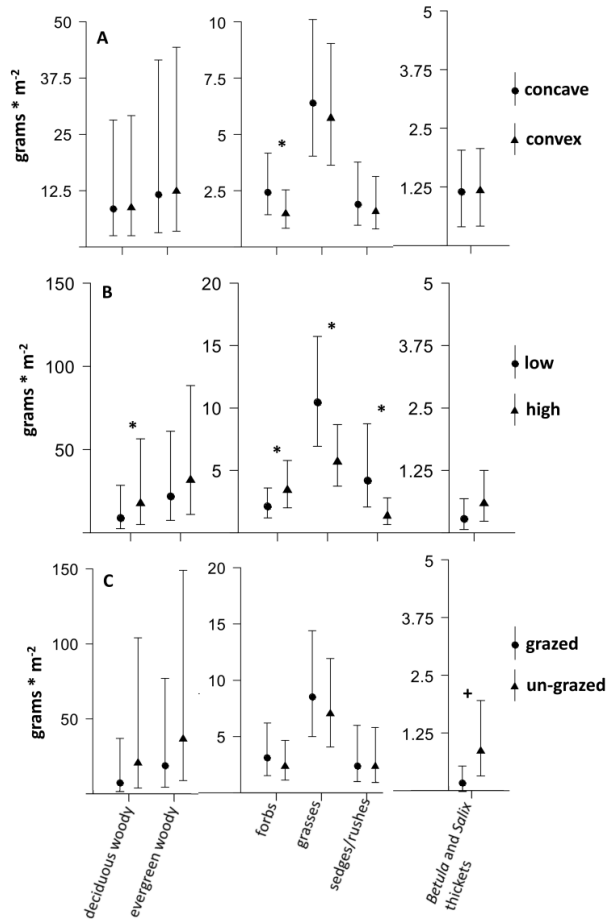| grain size	index	effects	effect size	std. error	df	t-value	p-value
small	species richness	Intercept	20.63	1.26			
		concave -> convex	-1.89	1.14	119	-1.66	0.099
		un-grazed -> grazed	-0.81	1.58	4	-0.51	0.638
	Gini-Simpson	Intercept	0.65	0.04			
		concave -> convex	-0.03	0.02	119	-1.15	0.254
		un-grazed -> grazed	0.02	0.05	4	0.35	0.744
	Jaccard	Intercept	0.75	0.06			
		un-grazed -> grazed	-0.03	0.09	4	-0.33	0.759
	MG2	Intercept	3.41	0.14			
		un-grazed -> grazed	-0.19	0.19	4	-0.99	0.380
intermediate	species richness	Intercept	30.29	2.09			
		high -> low	-3.58	1.79	59	-2.00	0.049
		un-grazed -> grazed	-2.03	2.68	4	-0.76	0.491
	Gini-Simpson	Intercept	0.66	0.04			
		high -> low	0.05	0.03	59	1.52	0.133
		un-grazed -> grazed	0.02	0.05	4	0.40	0.707
	Jaccard	Intercept	0.69	0.05			
		un-grazed -> grazed	-0.06	0.08	4	-0.83	0.452
	MG2	Intercept	3.40	0.16			
		un-grazed -> grazed	-0.08	0.22	4	-0.34	0.751
large	species richness	Intercept	40.11	2.99			
		east facing -> west facing	-0.78	3.13	29	-0.25	0.805
		un-grazed -> grazed	-2.67	3.60	4	-0.74	0.500
	Gini-Simpson	Intercept	0.70	0.05			
		east facing -> west facing	0.04	0.04	29	0.95	0.349
		un-grazed -> grazed	0.02	0.06	4	0.29	0.783
	Jaccard	Intercept	0.70	0.08			
		un-grazed -> grazed	-0.05	0.12	4	-0.45	0.678
	MG2	Intercept	3.62	0.22			
		un-grazed -> grazed	-0.25	0.31	4	-0.80	0.469

*Figure 5. Model estimates of biomass of plant growth forms in contrasting landforms, elevations and grazing regimes. The symbols represent geometric means (g*m2) that were derived via back transforming model estimates. "*" indicates statistically significant effects on a 5% significance level, whereas "+" indicates marginally significant effects based on a 10% level. Error bars represent 95% confidence intervals. Estimates are either based on (A) small or (B, C) intermediate grain size of analyses. Note that y-axes have different dimensions for specific growth forms due to large differences in biomass.*

Discussion

TOPORAPHY – A MAJOR DRIVER OF *ALPHA* AND *BETA* DIVERSITY IN ICELANDIC TUNDRA

We predicted that *alpha* diversity would differ between topographical units and assumed to find lower *alpha* diversity in productive compared to less productive units due to the competitive exclusion of plant species. The plant diversity patterns in our study were clearly related to topography, but only for some of the diversity measures, and hence partly confirming our predictions.

The species richness was clearly related to contrasting landform curvatures and elevations, while the abundance-weighted diversity measure, the Gini-Simpson index, was not. There are several possible explanations behind the higher species richness in concave as compared to convex landforms. Even though soil C and N concentrations, and C:N ratios as measured in this study, do not reveal plant available N, they give a rough estimate of differences in soil properties (Soil Survey Staff 2011). Together with the subjective evaluation of soil moisture, the C and N concentrations indicate more favorable growing conditions in the concave than in the convex landforms. Therefore, opposed to our predictions, species richness patterns between landform curvatures represent a positive relationship between species richness and productivity. In general, soil pH is also a strong determinant of species richness within tundra, with higher pH leading to high numbers of species within communities (Gough et al. 2000), but in our study the pH range was too narrow to base species richness patterns on this variable. At an intermediate scale (low and high elevation), the opposite relationship was found between species richness and productivity estimates than at the small-scale landform contrasts. In general, other factors than the measured soil conditions may come into play, such as differences in the abundance of plant growth forms. The abundance of certain growth forms within plant communities can be as important as abiotic growing conditions in determining *alpha* diversity patterns within tundra (Bråthen & Ravolainen 2015).

Species richness differences between landform curvatures were associated by a higher biomass of forbs in concave compared to convex landforms. Thereby, forb rich communities have usually higher bacterial:fungal ratios than shrub dominated communities (Sundqvist et al. 2011), causing fast rates of nutrient recycling (Eskelinen et al. 2009). Plant communities with relatively high abundance of forbs may thus promote relatively higher inorganic nutrient supply than communities that are dominated by other growth forms, as for instance evergreen shrubs (Bråthen & Ravolainen 2015). Higher biomass of forbs was also found in high compared to low elevation and the same was found for deciduous woody species. The latter plant group can potentially promote species richness via canopy effects that create shelter for other species in tundra (Bråthen & Lortie 2015). Graminoids, which were more abundant in low elevations, may also facilitate nutrient supply, but in contrast to forbs they are generally highly competitive. The graminoid biomass such as found in low elevations here may cause competitive exclusion of plant species due to both nutrient competition and shading (Bråthen & Lortie 2015).

Based on our data it is, however, not possible to disentangle the effects of growth form abundances from general abiotic conditions, as we also found more favorable moisture regimes in concave landforms and low elevations, likely to promote greater soil organic matter content and plant nutrient availability. Hence moisture is likely involved in the

interplay between plant diversity and growing conditions that are modified by growth forms.

PERSISTENCE OF GRAZING EFFECTS ON PLANT DIVERSITY IN ICELANDIC TUNDRA

We predicted that topographically driven patterns in *alpha* diversity would be different under contrasting grazing regimes and that *beta* diversity among topographical units would be lower in grazed, compared to un-grazed valleys. The topographically induced contrasts in *alpha* diversity, which were described above, were not different between grazing regimes though, which is in contrast to what we had predicted. We did not find support for lower *beta* diversity due to grazing at any of the topographic units. It has been shown that ungulates can push vegetation into different stable states (Westoby et al. 1989; Laycock 1991) and the same has been suggested for the arctic tundra (van der Wal 2006). In general, two important characteristics of an ecosystem are relevant to evaluation of its resilience to grazing impacts, which are i) the history of grazing and ii) the availability of resources (Milchunas et al. 1988; Cingolani et al. 2013).

In Iceland, grazing has been extensively practiced since the time of the Norse settlement 1100 years ago (Erlendsson et al. 2009). Sheep grazing is assumed to have maintained graminoid dominated vegetation in many Icelandic landscapes, preventing vegetation shifts back to states which were dominated by shrub and forb species (Kristinsson 1995; Thórhallsdóttir 1996). Grass dominance can also be expected because long grazing history usually selects for a subset of the plant species pool which has high resilience to grazing, and can prevent re-establishment of species that are less resilient (Milchunas et al. 1988; Cingolani et al. 2013). Albeit we sampled the strongest existing grazing contrasts in Icelandic tundra, all of the presently un-grazed valleys had been grazed over hundreds of years before the abandonment. The lack of grazing effects in our study might therefore relate to the persistence of historical grazing effects in presently un-grazed valleys. However, we found that deciduous and evergreen shrubs, which can be reduced under high grazing pressure (Olofsson 2006, Austrheim et al. 2008), were the most abundant plant groups in our valleys. We therefore interpret the state of vegetation in our valleys to be similar to reindeer summer grazing districts in northern Norway (Bråthen et al. 2007, Ravolainen et al. 2010). As woody plant species have a higher density of biomass per unit area than grasses, and because grasses were the third most abundant plant growth form in our study, their abundance can still be regarded as high. The seeming discrepancy to studies that showed graminoid dominated vegetation under grazing (Jónsdóttir 1984, Olofsson 2006, Eskelinen & Oksanen 2006) is presumably because dominance of graminoids occurs only under very high animal densities, including high defecation rates and trampling. The valleys included in the present study may not have experienced this intensive grazing overall, although local patches can be heavily used. This interpretation is further supported by that we only found marginal differences in the abundance of plant groups that have low grazing tolerance, such as thicket forming *Betula pubescens* and *Salix* species. This finding was unexpected, given that the many decades in our un-grazed valleys could be expected to have given sufficient time for an increase in those growth forms, potentially affecting *alpha* or *beta* diversity in our study (Ravolainen et al. 2010, Bråthen & Lortie 2015). Some part of the explanation may lie in the recruitment pulses of woody plants, which are generally temperature dependent, but operate with a time-lag even

after years with good growing conditions within tundra (Büntgen et al. 2015). Whether a future increase of thicket forming woody plants in our sites will affect *alpha* or *beta* diversity in the long term is, however, questionable. Based on present knowledge from Norwegian tundra sites, increasing shrub biomass can facilitate species richness up to a certain threshold after which competitive exclusion takes place (Bråthen & Lortie 2015).

The lack of grazing effects on *alpha* and *beta* diversity which we relate to the persistence of grazed vegetation states can also be explained by low resource availability in our sites. As we worked within an ecosystem of relatively scarce nutrient supply, recovery to un-grazed vegetation states can take long time and appear to be stagnating (Cingolani et al. 2013). Grazing influenced vegetation can thereby persist for decades (Laycock 1991) or even centuries after grazing cessation (Ransijn et al. 2015). In Icelandic grazing commons, centuries of heavy summer grazing by livestock where nutrients were constantly removed out of the system in form of animal biomass, could have deteriorated nutrient stocks to even lower levels than in tundra without livestock grazing. Detailed vegetation analyses inside and outside an exclosure in grazing commons in the Icelandic highlands also indicated that recovery from continuous grazing is slow: no difference was detected after 4 years without grazing (Jónsdóttir et al. 2005). Our data provides evidence that recovery from grazing is slow because even more than to 60 years after cessation did not lead to considerable vegetation changes in our valleys.

Conclusions

Our study showed that present patterns of *alpha* and *beta* diversity in Icelandic tundra are shaped by topography at two different spatial scales, which are defined by contrasting landform curvatures and elevations. Topographically induced species richness patterns are caused by abiotic growing conditions that are shaped by a combination of contrasting moisture regimes and different relative growth form abundances within topographical units. Contrary to our predictions, there were no detectable differences in *alpha* or *beta* diversity patterns between grazed and un-grazed valleys, which are most likely explained by the slow recovery of tundra plant communities after centuries of intensive livestock grazing.

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Supplementary material

Table S1. Structure of models for estimating soil variables in different topographical units

response variables	estimated effects (fixed)	design variables (random)
soil pH, soil C, soil N, soil C:N ratio	landform (concave -> convex)	valley/slope aspect/elevation
soil pH, soil C, soil N, soil C:N ratio	elevation (high -> low)	valley/slope aspect/landform
soil pH, soil C, soil N, soil C:N ratio	slope aspect (east facing -> west facing)	valley/elevation/ landform

Table S2. Plant species and their corresponding factors to convert plant hits into biomass based on the "five point intercept method" (Bråthen & Hagberg 2004). Conversion factors of species were taken from Ravolainen et al. (2010). Species that were not existent in their study were given conversion factor based on similar morphology to other species and are marked with "".*

Forbs	*Coeloglossum viridae* - **6.94***	*Omalotheca norwegica* - **13.52**	*Taraxacum officinale* - **13.52**	*Festuca rubra ssp. richardsonii* - **6.29**
Alchemilla alpina - **13.52**	*Epilobium alsinifolium* - **6.94**	*Oxyria digyna* - **6.94**	*Thalictrum alpinum* - **6.94**	*Festuca vivipara* - **6.29**
Alchemilla filicaulis - **13.52***	*Epilobium palustre* - **6.94**	*Parnassia palustris* - **13.52**	*Triglochin palustris* - **6.94**	*Hierochloë odorata* - **9.91**
Alchemilla glomerulan - **13.52***	*Erigeron borealis* - **6.94**	*Pinguicula vulgaris* - **6.94**	*Veronica alpina* - **6.94**	*Nardus stricta* - **6.29**
Alchemilla wichurae - **13.52***	*Euphrasia frigida* - **6.94**	*Plantago maritima* - **6.94**	*Viola canina* - **6.94**	*Phleum alpinum* - **9.91**
Angelica archangelica agg. - **15.34***	*Gentianopsis detonsa* - **6.94***	*Limnorchis dilatata* - **6.94***	*Viola palustris* - **6.94**	*Poa glauca* - **9.91**
Armeria maritima - **6.94***	*Geranium sylvaticum* - **15.34**	*Potentilla cranztii* - **13.52**	*Viola riviniana* - **6.94**	*Poa pratensis* - **9.91**
Bartsia alpina - **13.52**	*Galium boreale* - **6.94**	*Pyrola minor* - **13.52**	**Grasses**	*Trisetum spicatum* - **9.91**
Bistorta vivipara - **13.52**	*Galium normanii* - **6.94**	*Ranunculus acris* - **15.34**	*Agrostis capillaris* - **9.91**	**sedges and rushes**
Caltha palustris - **13.52**	*Galium verum* - **6.94**	*Rhinanthus minor* - **13.52**	*Agrostis vinealis* - **9.91**	*Carex atrata* - **11.62**
Cardaminae pratensis agg. - **13.52***	*Hieracium alpinum* agg. - **13.52***	*Rumex acetosa* - **13.52**	*Anthoxanthum odoratum* - **9.91**	*Carex bigelowii* - **11.62**
Cerastium alpinum - **6.94***	*Hieracium thaectolepiun* - **13.52***	*Saxifraga rosacea* - **6.94**	*Avenella flexuosa* - **6.29**	*Carex canescens* - **11.62**
Cerastium cerastoides - **6.94**	*Listera cordata* - **6.94**	*Scorzoneroides autumnalis* - **13.52**	*Calamagrostis neglecta* - **9.91**	*Carex capillaris* - **11.62**
Cerastium fontanum - **6.94**	*Menyanthes trifoliate* - **13.52***	*Sibbaldia procumbens* - **13.52**	*Deschampsia alpina* - **9.91**	*Carex chordorrhiza* - **11.62**
Chamaepericlymenum suecicum - **6.94***	*Micranthes nivalis* - **6.94**	*Silene acaulis* - **13.52**	*Deschampsia cespitosa* - **9.91**	*Carex echinata* - **11.62**

Carex limosa - **11.62**	**deciduous woody plants**	**Pteridophytes**
Carex lyngbyei - **11.62**	*Betula nana* -**73.53**	*Athyrium distentifolium* - **15.35**
Carex nigra - **11.62**	*Betula pubescens* - **73.53***	*Athyrium filix-femina* - **15.35**
Carex rariflora - **11.62**	*Comarum palustre* - **13.52***	*Botrychium lunaria* - **13.52**
Carex rostrata - **11.62**	*Rubus saxatilis* - **13.52***	*Diphasiastrum alpinum* - **13.52**
Carex vaginata - **11.62**	*Salix arctica* - **73.53***	*Equisetum arvense* - **6.94**
Eriophorum angustifolium - **11.62**	*Salix herbacea* - **35.46**	*Equisetum fluviatile* - **6.94**
Eriophorum scheuchzeri - **11.62**	*Salix lanata* - **73.53**	*Equisetum hyemale* - **6.94**
Juncus filiformis - **6.29**	*Salix phylicifolia* - **73.53**	*Equisetum palustre* - **6.94**
Juncus trifidus - **6.29**	*Vaccinium myrtillus* - **35.46**	*Equisetum pratense* - **6.94**
Kobresia myosuroides - **6.29**	*Vaccinium uliginosum* - **35.46**	*Equisetum variegatum* - **6.94**
Luzula multiflora - **11.62**	**evergreen woody plants**	*Gymnocarpium dryopteris* - **13.52**
Luzula spicata - **11.62**	*Calluna vulgaris* - **79.02***	*Huperzia selago* - **13.52**
Trichophorum cespitosum - **6.29**	*Dryas octopetala* - **13.52**	*Lycopodium annotinum* - **13.52**
	Empetrum nigrum - **79.02**	*Selaginella selaginoides* - **13.52**
	Kalmia procumbens - **79.02**	
	Thymus praecox - **6.94**	

Table S3. Structure of models for estimating alpha and beta diversity on three spatial grain sizes

grain size	response variables	estimated effects (fixed)	design variables (random)
small	*alpha* diversity (species richness; Gini-Simpson)	landform unit (concave -> convex) grazing regime (un-grazed -> grazed)	valley/slope aspect/elevation
	beta diversity (Jaccard; MG2)	grazing regime (un-grazed -> grazed)	valley/slope aspect/elevation
inter-mediate	*alpha* diversity (species richness; Gini-Simpson)	elevation (high -> low) grazing regime (un-grazed -> grazed)	valley/slope aspect
	beta diversity (Jaccard; MG2)	grazing regime (un-grazed -> grazed)	valley/slope aspect
large	*alpha* diversity (species richness; Gini-Simpson)	slope aspect (east facing -> west facing) grazing regime (un-grazed -> grazed)	valley
	beta diversity (Jaccard; MG2)	grazing regime (un-grazed -> grazed)	valley

Table S4. Model estimates and effects of landform and grazing on the biomass of selected plant growth forms

plant group	effects	effect size	std. error	df	t-value	p-value
forbs	Intercept	0.78	0.36			
	concave -> convex	-0.49	0.22	119	-2.24	0.027
	un-grazed -> grazed	0.29	0.48	4	0.59	0.587
grasses	Intercept	1.74	0.31			
	concave -> convex	-0.11	0.18	119	-0.62	0.537
	un-grazed -> grazed	0.25	0.42	4	0.59	0.589
sedges/rushes	Intercept	0.69	0.46			
	concave -> convex	-0.19	0.28	119	-0.67	0.502
	un-grazed -> grazed	-0.04	0.62	4	-0.06	0.956
deciduous woody	Intercept	2.59	0.84			
	concave -> convex	0.04	0.26	119	0.14	0.891
	un-grazed -> grazed	-0.86	1.17	4	-0.74	0.502
evergreen woody	Intercept	2.78	0.89			
	concave -> convex	0.07	0.36	119	0.18	0.856
	un-grazed -> grazed	-0.65	1.23	4	-0.53	0.625
Betula pubescens and *Salix* shrubs	Intercept	1.70	0.11			
	concave -> convex	0.01	0.10	119	0.06	0.949
	un-grazed -> grazed	-0.26	0.14	4	-1.86	0.136

Table S5. Model estimates and effects of elevation and grazing on the biomass of selected plant growth forms.

plant group	effect	effect size	std. error	df	t-value	p-value
forbs	Intercept	1.12	0.35			
	high -> low	-0.46	0.19	59	-2.40	0.020
	un-grazed -> grazed	0.28	0.47	4	0.60	0.580
grasses	Intercept	1.71	0.27			
	high -> low	0.58	0.17	59	3.47	0.001
	un-grazed -> grazed	0.18	0.36	4	0.51	0.638
sedges/rushes	Intercept	0.30	0.48			
	high -> low	1.13	0.34	59	3.29	0.002
	un-grazed -> grazed	0.03	0.64	4	0.04	0.969
deciduous woody	Intercept	3.37	0.82			
	high -> low	-0.67	0.29	59	-2.28	0.027
	un-grazed -> grazed	-1.02	1.14	4	-0.90	0.420
evergreen woody	Intercept	3.80	0.71			
	high -> low	-0.37	0.26	59	-1.41	0.163
	un-grazed -> grazed	-0.66	0.99	4	-0.66	0.543
Betula pubescens and *Salix* shrubs	Intercept	0.29	0.40			
	high -> low	-0.49	0.35	59	-1.40	0.167
	un-grazed -> grazed	-1.09	0.51	4	-2.14	0.099

Figure S1. Number of plots that were subjectively assigned into different categories of moisture