

PAPER III

Species pool size alters the diversity patterns shaped by local forces - an example from the tundra

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- Conceived of or designed study: MAM, KAB, VR, ISJ
- Performed fieldwork: MAM
- Performed laboratory work: MAM
- Analyzed data: MAM
- Wrote the paper: MAM, KAB, VR, ISJ

Species pool size alters the diversity patterns shaped by local forces - an example from the tundra

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Abstract

Regional and local driving forces are known to shape patterns of plant diversity within communities (*alpha* diversity), but how these forces shape patterns of the between diversity component of plant communities (*beta* diversity) has rarely been studied. Here we aim to assess how diversity patterns of tundra plant communities are shaped by regional differences in species pool size and local contrasts in habitat productivity and disturbance regimes.

Comparing regions in Norway (large species pool) and Iceland (small species pool), we found support that species pool size determines *alpha* diversity, but species pool related differences in *beta* diversity were not obvious.

Contrasting landform curvatures (convex *versus* concave), which represented habitats of different productivity, induced similar differences in *alpha* diversity within both regions. Yet, soil parameters indicated that productivity contrasts were stronger in Iceland. We therefore assume that productivity - diversity relationships are stronger expressed in regions with large compared to small species pool size. We found similar effects for analyses on larger spatial scales, where contrasting elevations represented habitats of different productivity. However, analyses on large spatial scales also showed that the effects of species pool size and habitat productivity on *alpha* diversity depend on the diversity measure used.

We did not find effects of grazing on *alpha* or *beta* diversity in our study. We can only speculate to the lack of grazing effects but assume that historical grazing has set valleys throughout our study into similar vegetation states.

Keywords: *alpha* diversity, *beta* diversity, habitat productivity, disturbance, sheep grazing, Jaccard dissimilarity, Modified Gower Distance, spatial scale

Introduction

The question of which processes influence species diversity has been puzzling ecologists for decades (Grime 1973; Huston 1979; Ricklefs 1987). For plant communities, theoretical and experimental approaches have revealed that diversity within communities (*alpha* diversity) is influenced by the combined forces of regional factors such as the species pool size, as well as local factors such as habitat productivity and disturbances (Huston 1999; Loreau et al. 2003; Foster et al. 2004). Similarly, regional (Normand et al. 2006; Lenoir et al. 2010) and local (Chaneton & Facelli 1991; Olf & Ritchie 1998) driving forces have been found to affect the diversity component that characterizes differentiation of plant communities (*beta* diversity). Besides the strong theoretical and experimental knowledge base about how species pool size, habitat productivity and disturbances shape *alpha* and *beta* diversity within landscapes, patterns of both diversity components have rarely been assessed in real landscapes with respect to all of those three drivers.

Views in the field of macro-ecology have emphasized the importance of regionally acting driving forces such as the species pool size, affected by evolutionary development or species colonization, in shaping *alpha* diversity of plant communities (Ricklefs 1987; Ricklefs 2008; Taylor et al. 1990; Cornell & Lawton 1992; Eriksson 1993; Zobel 1997; Zobel 2001). Viewpoints from community ecology have highlighted the importance of local driving forces such as the productivity (Grime 1973; Grime 1979; Tilman 1987) and the intensity of disturbances within communities (Connell 1978; Huston 1979). However, recent evidence suggests that both aspects, regional and local driving forces, need to be taken into account when aiming to understand the shaping of *alpha* diversity patterns within landscapes (Huston 1999; Foster et al. 2004; Zobel & Pärtel 2008; Guo et al. 2014; Michalet et al. 2014). The *Shifting Limitation Hypothesis* (SLH) (Foster 2001; Foster et al. 2004) for instance emphasizes the importance of the plant species pool in connection to locally operating forces, such as site productivity, in the shaping of *alpha* diversity. The relative influence of regional species pool size on *alpha* diversity is strongest in sites of moderate productivity (Zobel & Liira 1997; Pärtel et al. 2000; Foster et al. 2004). When productivity increases the competitive exclusion of plant species causes species pool size to be less important (Pärtel et al. 2000; Foster 2001; Foster et al. 2004). However, when highly productive communities are disturbed, competitive exclusion is reduced and maximum diversity of local communities is shifted towards higher productivity levels (Foster et al. 2004; Dickson & Foster 2008). The SLH model thereby implies that relationships between productivity and *alpha* diversity and between disturbances and *alpha* diversity are stronger pronounced under large compared to small species pool size.

A few case studies independently demonstrated that regional drivers can shape *beta* diversity patterns of several taxa such as plants (Graham et al. 2006; Normand et al. 2006; Lenoir et al. 2010) and beetles (Baselga 2008) as well. Regional drivers have often been attributed to different glacial histories that affected species clades and colonization of habitats (Lenoir et al. 2010), processes that are known to affect species pool size of a region (Taylor et al. 1990). However, via a global scale assessment Qian et al. (2013) showed that regional differences in *beta* diversity are mainly explained by local driving forces that affect local community assembly and species abundance patterns, rather than by the species pool size. Also, locally operating driving forces such as disturbances caused by ungulate grazing have independently been shown to affect *beta* diversity, causing for instance a reduced community differentiation (Chaneton & Facelli 1991; Bråthen et al. 2007; Lezama et al. 2014). In summary, our understanding about the relative importance of

regional species pool size *versus* locally operating drivers such as grazing is far from settled in terms of *beta* diversity of plant communities. Besides, there is also a lack of studies that assess in how far regional and local drivers are in fact reflected in diversity patterns of natural landscapes.

From island systems with small species pool size, there is indication that patterns of *beta* diversity are indeed different compared to neighboring regions with large species pool size (Steindórsson 1964). When describing and classifying vegetation types in Iceland, Steindórsson (1964) observed that species ranges were wider than in neighboring countries, causing difficulties in the delimitation of plant communities. He mentions the small size of the Icelandic flora as one out of several possible reasons (approximately 480 vascular plant species, Kristinsson 2010). Steindórsson's (1964) observations are supported by knowledge about the distribution of many plant species in Iceland. For instance *Calluna vulgaris* is a typical calcifuge species in Northwest Europe (Hultén 1971; Pålsson 1994). In Iceland, it grows in neutral soils together with typical calcicole species such as *Dryas octopetala* and *Silene acaulis* (Kristinsson 2010). A possible explanation is that the few species within the pool cause potential species establishment within a wider range of habitats than within regions of large species pools size, due to the lack of interspecific competition.

Ecological patterns are also spatial scale dependent (Wiens 1989; Levin 1992) and hence the relative importance of regional *versus* local driving forces on patterns of diversity can only be understood when being explicit about the spatial scale on which diversity is assessed (Huston 1999). The importance of this issue has been exemplified in many studies of plant diversity patterns (e.g. Chaneton & Facelli 1991; Normand et al. 2006). For instance, Chaneton & Facelli (1991) found that *alpha* diversity was higher in grazed compared with un-grazed plant communities when analysed at relatively small grain size, while the opposite was found when using an aggregated form of their data, representing a larger grain size. Another example is the study by Normand et al. (2006). They investigated *beta* diversity of palm communities in the north-western Amazon at small and large spatial scales and found that small scale *beta* diversity was mostly driven by environmental heterogeneity whereas large scale *beta* diversity was driven by biogeographical processes such as species dispersal limitations. Both studies exemplify the importance of being explicit about the spatial scales of diversity assessments in order to understand the relative importance of regional and local driving forces.

In the present study, we address whether both regional and local driving forces play a role in shaping patterns of *alpha* and *beta* diversity of plant communities within landscapes. We assessed patterns of both diversity components within regions that represent a large *versus* a small species pool size. Both diversity assessments were conducted with respect to local drivers, i.e. contrasting conditions of habitat productivity and grazing regimes within each region. Furthermore, habitat productivity was considered at two spatial scales of resolution known to be relevant for the shaping of plant communities (Table 1). Using low arctic tundra landscapes in Northern Norway (relative large species pool size) and Iceland (relative small species pool size), we surveyed vegetation within glacially sculptured valleys of comparable climate and topography. The surveys were stratified according to topographical units with the larger scale represented by contrasts in elevation and the smaller scale represented by contrasts in landform curvature. Valleys presently grazed by sheep (*Ovis aries* L.) were compared with un-grazed valleys that had not been used as grazing grounds for several decades.

Table 1. Terminology for driving forces, acting on different spatial scales. Those terms are to be distinguished from assessments that we did in our study, which relate to spatial scaling in terms of different grain sizes.

driving force	acting on spatial scale
species pool size	regional (throughout our study extent)
habitat productivity	local (within valleys)
sheep grazing/disturbance	local (within valleys)
assessments in our study	spatial grain size of analyses
based on high and low elevations within valleys	large
based on concave and convex landforms within valleys	small

Within our study framework, we assumed that we sampled within relatively un-productive tundra habitats where plant communities are not saturated and facilitative effects of plant species may be more important in determining within community diversity than competitive exclusion of plant species (Michalet et al. 2006; Bråthen & Ravolainen 2015). Based on this and the assumption that species pool size is larger in Norway than in Iceland, we had following predictions: 1) *Alpha* and *beta* diversity are generally higher in Norway than in Iceland (Figure 1A, 1B, 1C). 2) Local driving forces related to different habitat productivity modify diversity patterns within regions such that *alpha* diversity is higher in productive compared to un-productive landforms (Figure 1A); 3) Grazing was expected to decrease *alpha* diversity (Figure 1B); 4) *Beta* diversity was predicted to be lower in grazed compared to un-grazed valleys (Figure 1C).

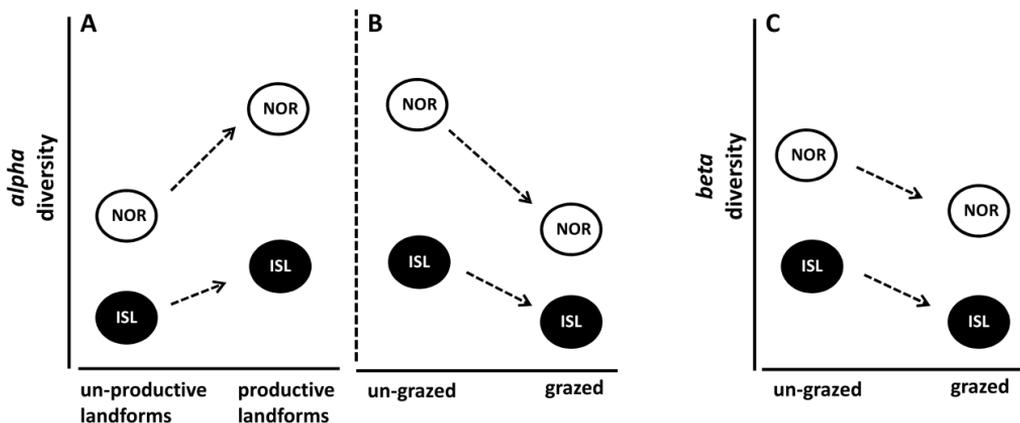


Figure 1. Prior predictions about differences in (A, B) *alpha* and (C) *beta* diversity between regions of different species pool size, topographical units of different habitat productivity and contrasting grazing regimes.

Materials and Methods

SELECTION OF STUDY LOCATIONS

We chose two regions of contrasting species pool size. Most of Iceland's vascular plant flora can also be found in Norway (Ægisdóttir & Thórhallsdóttir 2004), but Iceland harbors a relatively small number of vascular plants of approximately 480 species (Kristinsson 2010). The size of the Norwegian vascular plant flora is approximately 2890 species (Lid & Lid 2005), and although it is not straightforward to compare the size of the two floras due to lack of area standardization, Norway inevitably has a larger vascular plant species pool, which is supported by our data. 179 vascular plant species were found in Norway whereas 116 species were found in Iceland.

In order to reduce confounding effects related to growing conditions, we stratified the survey to geographical regions that were as comparable as possible in terms of geological history, bedrock chemistry and climate. We selected valleys in North Norway and valleys in Northwest- as well as North Iceland (Table 2), which had comparable glacial history (Wohlfarth et al. 2008). All valleys were glacially eroded with a characteristic U-shape. Furthermore, recognizing the contrasting geological history of the two regions, the valleys were chosen based on geological maps for Norway (<http://geo.ngu.no/kart/berggrunn/>) and Iceland (Jóhannesson & Sæmundsson 2009) such that the chemical bedrock composition was as similar as possible (see Table 2). We further used current climate data (1950-2000) from the WorlClim database to stratify to valleys with similar climatic conditions (Hijmans et al. 2005). The spatial resolution of this data is based on a 1x1km raster and we used a GIS (esri ArcGIS version 10.2) to retrieve average temperatures during growing season (June-August) and annual precipitation rates. We randomly selected five pixels in the bottom of the respective valleys to retrieve average values of those parameters for each valley (Table 2).

To assess the effects of grazing on *alpha* and *beta* diversity, we included equal numbers of valleys that were presently used as grazing grounds for sheep (*Ovis aries* L.), and valleys that had not been grazed by sheep for several decades (Table 2). Other ungulates apart from sheep were existent in Norway, such as moose (*Alces alces* L.) and reindeer (*Rangifer tarandus* L.), but sheep was by far the most abundant ungulate. We did not expect any other ungulates in Iceland, but occasionally occurring migratory geese (own observations) and wood mice (*Apodemus sylvaticus* L.; Unnsteinsdóttir & Hersteinsson 2009) as potential herbivores. We used dropping counts to gain information about the relative abundance of all those animals within the valleys by counting all the dropping events (one aggregate of single droplets) within a one meter buffer zone along the measuring tape where vegetation data was collected (further details below). Droppings were mostly from sheep (Table 2). Only one dropping of moose was recorded in Norway (Elsnesdalen), indicating that the present abundance of other vertebrate herbivores within study sites was only minor.

Table 2. Environmental context of the studied valleys in Norway and in Iceland. Presented are geographical location, environmental conditions and grazing regimes. Temperature (temp) data are averages during growing season (June to August) and precipitation (prec) data are annual averages. Both information was based on a 50 year period (1995-2000) and downloaded from the WorldClim database. Grazing information was retrieved from local farmers and dropping counts were conducted during fieldwork.

Geographic context			environmental context				grazing context		
country	valley	lat/ long	main bedrocktype	temp	prec	grazing regime	number winterfed sheep	total feces counts	
Norway	Elsnesdalen	69.32N/ 20.09E	mica-gneiss, mica-schist, metasandstone, amphibolite	7.0	632	un-grazed	0	0	
	Lyngsdalen	69.47N/ 20.05E	greenstone, amphibolite	7.3	648	un-grazed	0	0	
	Horseidet	68.02N/ 12.99E	amphibolite, hornblende-gneiss, mica-gneiss	8.1	1521	un-grazed	0	0	
	Elvevollidalen	69.35N/ 19.89E	mica-gneiss, mica-schist, metasandstone, amphibolite	7.0	647	grazed	~ 150	27	
	Kvalvikdalen	69.52N/ 20.15E	greenstone, amphibolite	7.3	642	grazed	~300	31	
	Stokkvikeidet	68.12N/ 13.12E	amphibolite, hornblende-gneiss, mica-gneiss	8.0	1500	grazed	~ 500	10	
Iceland	Adalvík	66.34N/ 23.08W	basalt	7.7	989	un-grazed	0	0	
	Grunnavík	66.24N/ 22.86W	basalt	7.6	937	un-grazed	0	0	
	Nesdalur	66.17N/ 18.80W	basalt	7.6	667	un-grazed	0	0	
	Ingjaldssandur	66.04N/ 23.69W	basalt	8.1	1202	grazed	~ 200	6	
	Skálavík	66.17N/ 23.46W	basalt	7.8	1132	grazed	~ 500	8	
	Þórgeirsfjörður	66.14N/ 18.16W	basalt	7.6	744	grazed	~ 1000	20	

SAMPLING DESIGN

We first divided each valley into three zones to guarantee a spread of sampling units throughout the valley (Figure 2A). The vegetation was sampled on two spatial grain sizes (Wiens 1989), determined by the topography (Figure 2B). Using GIS, we drew a transect that followed the main river, which flows through the bottom of each valley. We used this line to assess distances of sampling zones from the coastline. The first zone was between 1 and 2 km away from the coastline (zone A). The second zone was between 2 and 3 km (zone B) and the third zone between 3 and 4 km (zone C) away from the coast.

Each zone was divided into 10 equal distances. We therefore drew lines from each 100 m section within each zone, running from the river line vertically uphill in both directions. The GPS coordinates of the intersection of those lines with the contour line 40 m above the valley bottom were noted as potential sampling sites. Those sites were noted for both slopes within valleys that had opposite general aspect (except for the valleys Kvalvikdalen and Lyngsdalen where contrasting grazing regimes were only existent for the south facing slope). Sampling sites that were characterized by boulder fields were *a priori* discarded from sampling, as those sites had a hydrological regime that differs strongly from the one that shapes the vegetation types of interest for our study. In the field, we randomly chose two sites within each zone, one from each valley side. Arriving at the sampling site, we further emphasized that the selection of units in which diversity was assessed was done in a transparent way (Mörsdorf et al. 2015): We moved towards the sea and stopped at the first transition zone between convex and concave landforms (or *vice versa*) that spanned at least 15 m in horizontal distance, in order to conduct the sampling procedure (see below). Vegetation and soil sampling was finally done along 30 m transects (perpendicular to the station line, running across both landforms) at two elevations above the valley bottom, 40 and 60 m (Figure 2A, 2C). We avoided vegetation sampling within valley bottoms because there, the vegetation was frequently influenced by a hayfields. Sampling within those landforms was the basis for vegetation and soil assessments on small spatial grain size (Figure 2B). The same procedure was repeated 60 m above the site in order to sample vegetation data from steep slopes. Sampling within both elevations was the basis for vegetation and soil assessments on large spatial grain size (Figure 2B).

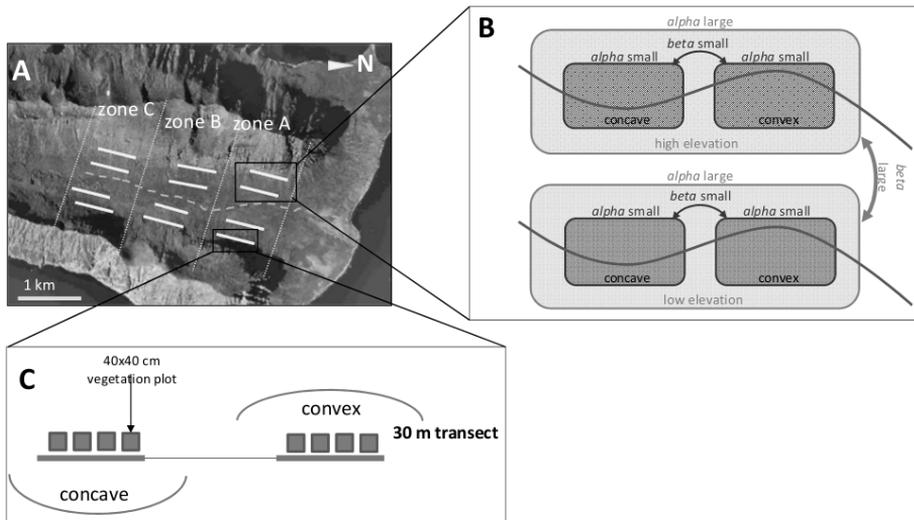


Figure 2. Schematic representation of sampling within each valley and the concept of alpha and beta diversity for the two spatial grain sizes of assessment. (A) Each valley was split into three zones to allow for a spread of sampling units. Within a zone, we sampled vegetation data from each valley side. Sampling was stratified to high and low elevations as well as to convex and concave landforms within those elevations. (B) Alpha diversity assessments on small spatial grain size were based on aggregated vegetation data of each convex and concave landform (alpha small). Alpha diversity assessments on large spatial grain size were based on aggregated vegetation data of each high and low elevation (alpha large). Beta diversity assessments on small spatial grain size were based on the dissimilarity/distance between each adjacent convex and concave landform (beta small). Beta diversity assessments on large spatial grain size were based on the dissimilarity/distance between each adjacent high and low elevation (beta large). (C) We used the Point Intercept Method to record species richness and relative species abundances along transects containing 4 sampling plots for each landform.

VEGETATION AND SOIL SAMPLING

We placed the middle of a 30 m long measuring tape at the transition between all selected convex and concave landforms and stretched both ends of the tape into the contrasting landforms. Vegetation sampling was conducted at constant distances of three meters from both ends of the measuring tape. We sampled four plots within each landform with each plot covering a 40 x 40 cm area. Species richness, including species identities were recorded within plots. We further applied a refined version of the Point Intercept Method (Jonasson 1988) which is especially suitable to record relative species abundances over large spatial extents (Bråthen & Hagberg 2004). Four metal pins of 2 mm diameter were attached to each corner of a frame and one in the centre, and all contacts of each pin throughout the canopy were recorded for each vascular plant species. As hits of different plant species and growth forms relate to different biomass (Jonasson 1988), we later used weighted linear regression to convert plant hits of each species into biomass (grams * m⁻²) (Bråthen & Hagberg 2004). The conversion factors we used in this study were based on the

ones in Ravolainen et al. (2010) and are accessible via the Supplementary material of this article (Table S1 Supplementary material).

We collected soil samples by excavating an approximate amount of 50 g of fresh soil next to each vegetation plot. The soil samples were taken at an approximate depth of five cm which corresponded to the rooting zone in our sites. The four samples from each landform were pooled into a plastic bag and stored in cooled conditions up to arrival in the lab. There, we air dried all the samples at ambient temperature. We then sieved all samples, using a sieve of 2 mm mesh size and homogenized samples using a mortar. Total soil nitrogen (N) and carbon concentration (C) were measured using a vario MAX cube CN analyzer (<http://www.elementar.de/en/products/vario-serie/vario-max-cube.html>). In addition, we measured soil pH in distilled water with a soil to water ratio of 1:5 (Blakemore et al. 1987). To evaluate contrasting moisture regimes between topographical units, we subjectively assigned each vegetation plot to one out of four moisture categories (dry – mesic – moist – wet). More sophisticated electrochemical spot measurements of soil moisture were not applicable due to temporal weather fluctuations over the course of the surveys.

CHOICE OF APPROPRIATE *ALPHA* AND *BETA* DIVERSITY MEASURES

We calculated species richness to reflect the actual number of species within each community in our dataset. In addition, Foster et al. (2004) found Shannon Entropy, reflecting differences in relative abundance of plant species within communities, to be determined by the three driving forces of our interest. As both indices describe properties of the vascular plant diversity within communities, they are categorized and termed as “*alpha*” diversity throughout this article.

To assess community differentiation in terms of species occurrences in our data set, we chose to use Jaccard dissimilarity of adjacent plant communities. We were aware that this index is dependent on the species richness within communities (Chase et al. 2011). Yet, assessments of species richness allowed us to interpret potential effects on Jaccard dissimilarities with respect to this issue. In addition to Jaccard dissimilarity, we calculated a modified version of Gower’s distance (Anderson et al. 2006), to estimate dissimilarity between adjacent communities which is, in addition to differences in species occurrence, caused by differences in relative species abundances. For this study, we chose to use a log base of two for this index (further termed MG2 throughout this article), as this version of “Modified Gower Distance” (*sensu* Anderson et al. 2006) is most sensitive to differences in species abundances between two communities. A doubling in abundance of one species within one community thereby gains the same weight as a compositional change in one species. Both Jaccard dissimilarity and MG2 distance are categorized and termed as *beta* diversity throughout this article.

DATA EVALUATIONS

We used the R environment for our data evaluations (R Core Team 2014). All analyses were separately conducted for Norway and Iceland. We first tested our assumption of contrasting habitat productivity between different topographical units. We used linear mixed effects models applying the `lme` function of the `nlme` package (Pinheiro & Bates 2000). To assess the effects of landform curvature on habitat productivity, we separately set soil pH, total C and total N concentrations and total above ground vascular plant biomass ($\text{g} \cdot \text{m}^{-2}$) as response variables. All response variables were scaled to have a mean of zero and a standard deviation of one (Bråthen & Ravolainen 2015), in order to facilitate comparisons of effects between Norway and Iceland. In separate models, we included either the landform curvature or elevation as fixed effect. Depending on the analyses, we included design variables in the random part of the model, reflecting the spatial nestedness of our study (Table S2 Supplementary material). We additionally inspected relative frequencies of moisture classes for different landforms and elevations for both study regions.

To analyze our plant community data with respect to the two grain sizes of interest, we first averaged the plant species biomass ($\text{grams} \cdot \text{m}^{-2}$) of each plot so that it corresponded to the average biomass per landform (four plots along either concave or convex topography - small grain size), or the average biomass per elevation (eight plots along the measuring tape - large grain size) sampled. We used the information on plant species occurrence and relative biomass of each plant species to calculate *alpha* (species richness and Shannon Entropy) and *beta* diversity (Jaccard dissimilarity and MG2 distance) based on the two grain sizes (see Figure 2B). We plotted average *alpha* and *beta* diversity values from each respective country, separately based on the two spatial grain sizes. We used those figures to visually evaluate our prediction that *alpha* and *beta* diversity are generally higher in Norway than in Iceland due to the larger species pool size.

Next, we tested the effects of topography and grazing on *alpha* and *beta* diversity within each study region in a more detailed way. Separately for each region, we included standardized values of *alpha* and *beta* diversity as response variables in linear mixed effects models. For *alpha* diversity assessments on small grain size, we included the landform, grazing regime and their interaction as fixed factors. *Beta* diversity models on small grain size had only the grazing regime as a fixed factor. For *alpha* diversity assessments on large grain size, we included elevation, grazing regime and their interaction as fixed factors. *Beta* diversity models on large grain size had only the grazing regime as a fixed factor. As none of the interaction effects between topography and grazing were statistically significant, we reduced all model of *alpha* diversity to only include additive fixed effects. The random effects structure was according to the spatial hierarchy of our sampling design and differed with respect to the spatial grain size of our analyses (Table S2 Supplementary material).

Model assumptions in terms of homoscedasticity, normality and outliers were fulfilled for all models.

Results

BACKGROUND INFORMATION ON CONTRASTING HABITAT PRODUCTIVITY

Our soil and biomass data did not indicate any productivity contrasts between convex and concave landforms in Norway (Table 3). Plots in concave landforms were more frequently assigned to be moist or wet compared to plots in convex landforms (Figure S1A Supplementary material). In Iceland soil pH was significantly lower and total soil C and N concentrations were significantly higher in concave compared to convex landforms (Table 3). The total above ground vascular plant biomass was similar in both landforms (Table 3). Plots in concave landforms were more frequently assigned to be moist or wet, whereas plots in convex landforms were more frequently assigned to be dry (Figure S1B Supplementary material).

In Norway, soil total N concentrations were significantly higher in low compared to high elevations (Table 3). None of the other soil variables or above ground vascular plant biomass were distinguished according to elevation (Table 3). Plots in low elevations were more frequently assigned to be moist or wet, whereas plots in high elevations were more frequently assigned to be dry (Figure S1C Supplementary material). In Iceland, soil pH was significantly lower in low compared to high elevations, whereas soil C and N concentrations were significantly higher in low compared to high elevations (Table 3). Total above ground vascular plant biomass was not different between elevations (Table 3). Within low elevations, plots were more frequently assigned to be moist or wet, whereas more plots were assigned into the dry category in high elevations (Figure S1D Supplementary material).

GENERAL PATTERN OF *ALPHA* AND *BETA* DIVERSITY IN NORWAY AND ICELAND

Using a small spatial grain size of analyses, our data showed that *alpha* diversity was higher in Norway than in Iceland, irrespectively of whether we used species richness or Shannon Entropy (Figure 3A, 3B). However *beta* diversity, especially based on Jaccard dissimilarities, was similar in both study regions (Figure 3C, 3D).

Also large spatial grain size of assessments revealed higher *alpha* diversity in Norway than in Iceland (Figure 4A, 4B). Jaccard dissimilarities between both countries were similar but MG2 distances were higher in Norway than in Iceland (Figure 4C, 4D).

Table 3. Effects of landform and elevation on soil variables and total aboveground vascular plant biomass in Norway and Iceland.

topographical contrast	soil variable	country	effects	effect size	std. error	df	t-value	p-value	
between landforms	pH	NOR	convex vs. concave	0.17	0.15	99	1.18	0.240	
		ISL	convex vs. concave	-0.35	0.16	114	-2.22	0.029	
	total C	NOR	convex vs. concave	-0.13	0.14	99	-0.89	0.373	
		ISL	convex vs. concave	0.32	0.14	115	2.32	0.022	
	total N	NOR	convex vs. concave	-0.04	0.14	99	-0.30	0.767	
		ISL	convex vs. concave	0.32	0.14	115	2.38	0.019	
	biomass	NOR	convex vs. concave	-0.20	0.18	99	1.11	0.270	
		ISL	convex vs. concave	-0.05	0.15	119	0.37	0.710	
	between elevations	pH	NOR	high vs. low	0.14	0.14	99	0.97	0.333
			ISL	high vs. low	-0.42	0.15	114	-2.72	0.007
total C		NOR	high vs. low	0.15	0.14	99	1.04	0.302	
		ISL	high vs. low	0.56	0.14	115	4.16	0.000	
total N		NOR	high vs. low	0.30	0.14	99	2.11	0.038	
		ISL	high vs. low	0.68	0.13	115	5.20	0.000	
biomass		NOR	high vs. low	-0.21	0.26	49	-0.82	0.418	
		ISL	high vs. low	0.02	0.18	59	0.11	0.913	

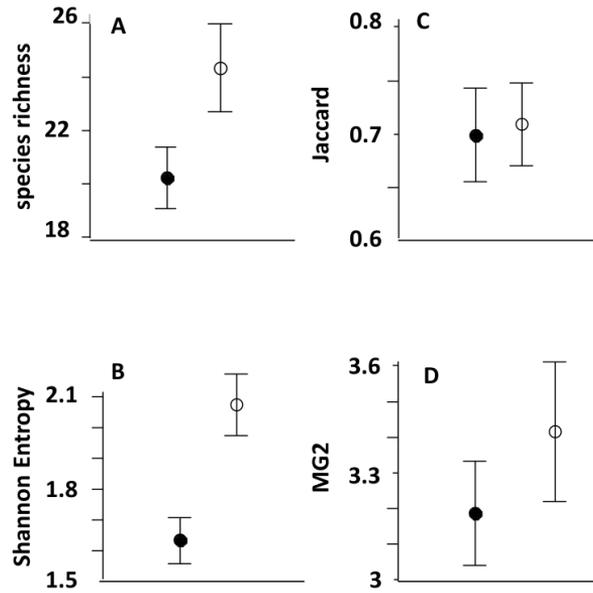


Figure 3. Alpha and beta diversity in both study regions, based on small grain size of analyses. (A) Average species richness and (B) Shannon Entropy within landforms are presented for Norway (open circles) and Iceland (closed circles). (C) Average Jaccard dissimilarity and (D) MG2 distances between convex and concave landforms are given for both study regions. Error bars represent 95% confidence intervals.

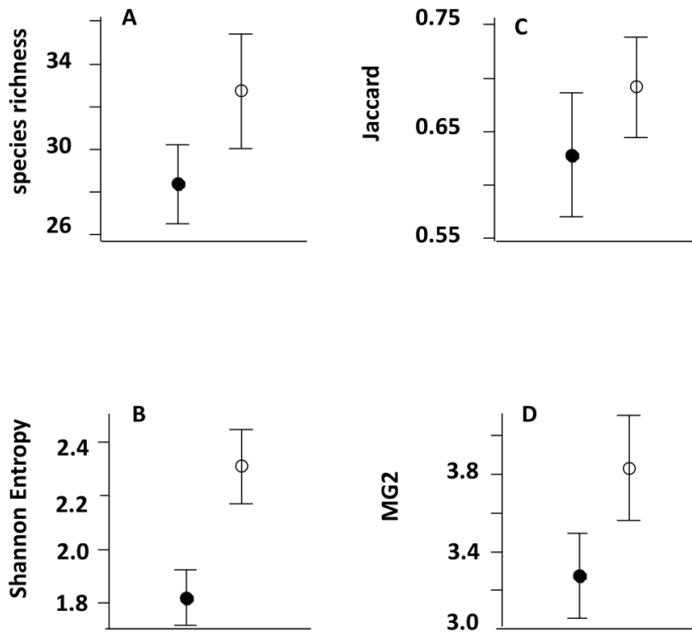


Figure 4. Alpha and beta diversity in both study regions, based on large grain size of analyses. (A) Average species richness and (B) Shannon Entropy within elevations are presented for Norway (open circles) and Iceland (closed circles). (C) Average Jaccard dissimilarity and (D) MG2 distances between high and low elevations are given for both study regions. Error bars represent 95% confidence intervals.

SMALL GRAIN SIZE ANALYSES: EFFECTS OF LANDFORM AND GRAZING ON ALPHA AND BETA DIVERSITY WITHIN STUDY REGIONS

The landform curvature had strong effects on *alpha* diversity within both study regions, with higher species richness (Figure 5A) and Shannon Entropy (Figure 5B) in concave than in convex landforms (Table S3 Supplementary material). Grazing had no effect on *alpha* diversity in Norway or Iceland (Table S3 Supplementary material; Figure 5C, 5D).

In both study regions, there was no grazing effect on the *beta* diversity between convex and concave landforms (Table S3 Supplementary material; Figure 5E, 5F).

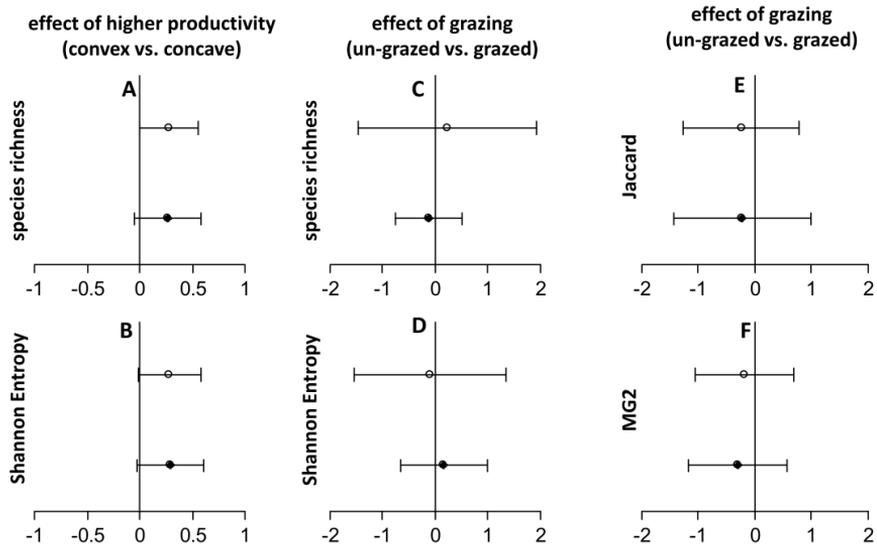


Figure 5. Model estimates representing the effects of landform and grazing on alpha and beta diversity, based on a small grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes. (A, B) effects of landform curvature are given for species richness and Shannon Entropy. (C, D) Effects of grazing are shown for species richness and Shannon Entropy, and (E, F) for Jaccard dissimilarities and MG2 distances.

LARGE GRAIN SIZE ANALYSES: EFFECTS OF ELEVATION AND GRAZING ON *ALPHA* AND *BETA* DIVERSITY WITHIN STUDY REGIONS

Elevation did not affect species richness in Norway, but in Iceland species richness was higher in high compared to low elevations (Figure 6A). On the contrary, in Norway Shannon Entropy was higher in low compared to high elevations, but there was no elevation effect in Iceland (Figure 6B (Table S4 Supplementary material)). Grazing did not have an effect on *alpha* diversity in the two study regions (Figure 6C, 6D) (Table S4 Supplementary material).

Beta diversity between high and low elevations was not affected by grazing in the two study regions (Figure 6E, 6F) (Table S4 Supplementary material).

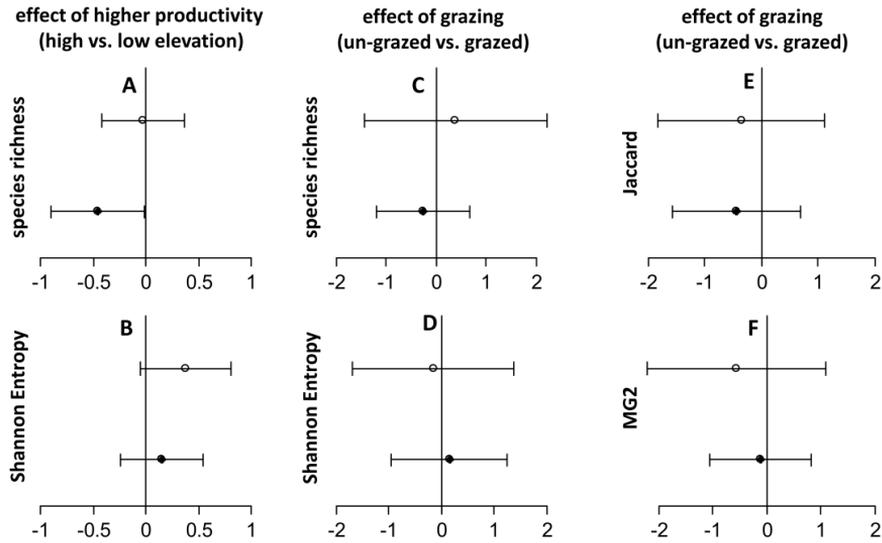


Figure 6. Model estimates representing the effects of elevation and grazing on alpha and beta diversity, based on a large grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes. (A, B) effects of elevation are given for species richness and Shannon Entropy. (C, D) Effects of grazing are shown for species richness and Shannon Entropy, and (E, F) for Jaccard dissimilarities and MG2 distances.

Discussion

SPECIES POOL SIZE DETERMINES AVERAGE *ALPHA* DIVERSITY OF BOTH STUDY REGIONS

According to our prior predictions, *alpha* diversity was on average higher in Norway than in Iceland. As we stratified sampling to similar environmental conditions in both study regions, we relate those differences to the larger species pool size in Norway.

Our assumption that species pool size in Norway was higher than in Iceland was primarily based on the larger number of species that are listed in floras of the former region (Lid & Lid 2005, Kristinsson 2010). We acknowledge that this assumption is lacking any standardization to similar geographical area, but the total number of species in our survey was higher in Norway than Iceland as well. Even on a valley basis we found on average more species in Norway than in Iceland (87 in Norway *versus* 74 in Iceland). Our data therefore shows that not only regional but also actual species pool size was on average higher in Norway than in Iceland, being reflected in a higher *alpha* diversity within plant communities (Zobel 1997).

Unlike our predictions, differences in *beta* diversity were not clearly expressed between Norway and Iceland and seemed to dependent on the spatial grain size of analyses. Very few studies have investigated *beta* diversity with respect to regional effects. Existing

studies indicate that regional contexts such as the abundance of species with high *versus* low dispersal ability determine *beta* diversity, but only at large spatial grain sizes (Normand et al. 2006; Lenoir et al. 2010). Grain sizes in our study were comparably small, and local effects of environmental heterogeneity gain presumably in important in shaping *beta* diversity (Normand et al. 2006).

DIFFERENT EFFECT STRENGTH OF TOPOGRAPHY IN REGIONS OF LARGE *VERSUS* SMALL SPECIES POOL SIZE

According to our predictions, we found strong effects of different landform curvature and elevations on *alpha* diversity within both regions. Small grain size analyses confirmed our predictions of higher diversity within productive, concave landforms in both countries. Although our subjective evaluation of moisture regimes indicated differences between landforms in both countries, analyses of soil variables only revealed landforms differences for Iceland and not Norway. We have to acknowledge that the variables we measured do not accommodate all potential niches in terms of nutrient resources in tundra. Total C and N concentrations for instance do not reflect litter quality or N forms, which might be differently utilized by different plant growth forms (Miller & Bowan 2002, Eskelinen et al. 2009) and therefore create contrasting community assemblies. However, considering the strong effects that landform curvature exerted on soil conditions in Iceland but not in Norway, we suppose that habitat conditions were more differentiated in the former region. Based on this interpretation, our data suggests that contrasting habitat productivity exerts stronger effects on *alpha* diversity in regions of large compared to regions of small species pool size.

Species pool size was shown to affect productivity – diversity relationships (Pärtel et al. 2000; Zobel & Pärtel 2008). Regions with larger species pool size may for instance inherit a larger amount of species that are adapted to productive conditions, leading to increasing diversity under productive conditions, under which diversity may already decrease with a low species pool size (Zobel & Pärtel 2008). A large propagule pool thereby implies that a larger amount of species is available to exploit potential resources (Tilman et al. 1997). Our findings are also in line with SLH (Foster 2001; Foster et al. 2004), even though Foster et al. (2004) did not emphasize that their model implies productivity – diversity relationships to be different depending on species pool size. However, analyses on large spatial grain size revealed different patterns.

We found no elevation effects on species richness in the Norway but in Iceland and accordingly, soil analyses indicated that conditions of habitat productivity were stronger differentiated in the latter region again. The interpretation of this outcome therefore differed from the one used to explain the effects of landform curvature. We found differentiation between elevations in terms of growth form biomass which supported interpretation of our diversity patterns (Figure S2 Supplementary material). In Iceland, graminoids such as grasses and sedges were more abundant in low than in high elevations, which can induce competitive exclusion of other plants and reduce species richness in tundra (Bråthen & Lortie 2015). This mechanism was not expected prior to our study because we assumed unsaturated communities, but considering the biomass of graminoids, competitive exclusion of plants is possible in our sites (Bråthen & Lortie 2015). As opposed to contrast in landform curvature, the elevational contrasts in Iceland therefore

represent a negative relationship between habitat productivity and species richness, in which competitive exclusion limits the amount of species within communities.

Species richness and Shannon-Entropy had similar responses to contrasting landform curvatures in both regions. However, patterns were not consistent for species richness and Shannon-Entropy in contrasting elevations. The potential productivity-diversity mechanisms we described here are based on theoretical models that consider species richness only (e.g. Grime 1973), which is not directly applicable to diversity indices. Svensson et al. (2012) showed that productivity – diversity relationships can be different for either species richness or Shannon-Entropy which may cause inconsistencies within the same dataset.

The same can be postulated for *beta* diversity, where we only found strong differences between Norway and Iceland based on MG2 distance between high and low elevations. Here, MG2 distances were higher in Norway than in Iceland. In Norway, species dominance patterns that create higher community evenness in high compared to low elevations may be connected to this finding but as outline above, those patterns are strongly determined by local topographical differences in our study. Our results thereby contribute to the idea that *beta* diversity within regions is strongly driven by mechanisms of local community assembly which affect species abundance distribution (Qian et al. 2013), but as outlined above, those local effects interact with the effects of species pool size.

LACK OF GRAZING EFFECTS ON *ALPHA* AND *BETA* DIVERSITY

Contrary to our predictions, grazing had no effect on either *alpha* or *beta* diversity in our study. The grazing context is an environmental context which is often difficult to control for in landscape diversity assessments. After stratification to similar climate and geology within Norway and Iceland, we based stratification of grazing entirely on present contrasts of sheep stocks. Yet, many landscapes within Nordic tundra have a history of grazing by ungulates and as such most of the presently un-grazed valleys in our study used to be grazed by sheep in the past. A prior assessment of our Icelandic data showed that historical grazing effects can be persistent for decades due to low nutrient stocks within tundra habitats, where nutrients have also been regularly removed via animal biomass over centuries (Mörsdorf et al. *in prep.*). The mechanisms behind such persistence's might be manifold though (Laycock 1991).

An obvious difference between Norwegian and Icelandic valleys is that the former ones had a stronger prevalence of grasses and forbs for both grazing regimes (Figure S3 Supplementary material). Large scale vegetation assessments within tundra showed that ungulates select for nutrient rich plants such as forbs and grasses (Bråthen et al. 2007), which might indicate that historical or present grazing impacts in Iceland were stronger than in Norway. However, under high animal densities, ungulates can also cause high abundance of especially grasses due to their tolerance to disturbances and effective utilization of grazing induced nutrient cycling (Augustine & McNaughton 1998). Without highly qualitative information on historical animal densities in our valleys, it is not possible to relate the present vegetation states to a history and present intensity of sheep grazing, which is a limitation in our study.

In general, disturbance effects such as induced by ungulates need more attention in connection to the effects of species pool size. Species pool size may exert stronger effects on diversity in low- compared to highly productive communities, because inter-specific competition gains influence in the latter case (Pärtel et al. 2000; Foster et al. 2004), but as grazing reduces competitive interactions between species, the species pool size has stronger effects on diversity in un-grazed compared to grazed conditions (Foster et al. 2004; Dickson & Foster 2008). Historical grazing does additionally affect species prevalence within the propagule pool (Milchunas et al. 1988). Those species left after a long history of grazing may have different properties in terms of dispersal ability and adaption to environmental conditions as opposed to species pools of regions without a grazing history. Both, the dispersal ability and adaption of a species to environmental conditions are character traits that are known to affect productivity diversity relationships as well (Pärtel & Zobel 2007; Zobel & Pärtel 2008; Xiao et al. 2010). However, the importance of those relationships is yet to be explored within tundra.

Conclusions

Our findings support that average species richness of local tundra plant communities is determined by species pool size, whereas species pool size influences on *beta* diversity are not clearly expressed. We found effects of topographical units on *alpha* diversity patterns. Reflecting contrasts in habitat productivity, the effects of topography are different in regions of large *versus* regions of small species pool size, presumably having a stronger influence in the former case. Grazing effects on *alpha* and *beta* diversity were not obvious in our study, but context dependencies that are connected to grazing history of our sites could have potentially masked the impacts of sheep grazing.

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Supplementary material

Table S1. Species list and corresponding grouping into growth forms in our study. Values are calibration factors to convert plant hits into biomass ($g \cdot m^{-2}$). Nomenclature follows the Panarctic Flora (<http://nhm2.uio.no/paf/>)

forbs			
<i>Achillea millefolium</i>	13.52	<i>Galium verum</i>	6.94
<i>Alchemilla alpina</i>	13.52	<i>Gentianopsis detonsa</i>	13.52
<i>Alchemilla ssp</i>	15.34	<i>Geranium sylvaticum</i>	15.34
<i>Angelica archangelica</i> agg.	15.34	<i>Geum rivale</i>	13.52
<i>Angelica sylestris</i>	15.34	<i>Hieracium subsp.</i>	13.52
<i>Anthriscus sylvestris</i>	13.52	<i>Limnorchis hyperborea</i>	13.52
<i>Arctous alpina</i>	35.46	<i>Linnaea borealis</i>	6.94
<i>Armeria maritima</i> subsp. <i>maritima</i>	6.94	<i>Listera cordata</i>	6.94
<i>Bartsia alpina</i>	13.52	<i>Melampyrum pratense</i>	13.52
<i>Bistorta vivipara</i>	13.52	<i>Melampyrum sylvaticum</i>	13.52
<i>Caltha palustris</i>	13.52	<i>Melilotus officinalis</i>	6.94
<i>Campanula rotundifolia</i>	13.52	<i>Menyanthes trifoliata</i>	13.52
<i>Cardamine pratensis</i> agg.	13.52	<i>Micranthes foliolosa</i>	6.94
<i>Cerastium alpinum</i> agg.	6.94	<i>Micranthes nivalis</i>	6.94
<i>Cerastium cerastoides</i>	6.94	<i>Micranthes stellaris</i> subsp. <i>stellaris</i>	6.94
<i>Cerastium fontanum</i>	6.94	<i>Omalotheca norvegica</i>	13.52
<i>Chamaepericlymenum</i> <i>suecicum</i>	13.52	<i>Omalotheca supina</i>	13.52
<i>Chamerion angustifolium</i>	13.52	<i>Orthilia secunda</i>	13.52
<i>Cirsium heterophyllum</i>	15.34	<i>Oxalis acetosella</i>	13.52
<i>Coeloglossum viride</i>	13.52	<i>Oxyria digyna</i>	13.52
<i>Comarum palustre</i>	13.52	<i>Parnassia palustris</i>	13.52
<i>Crepis paludosa</i>	15.34	<i>Paris quadrifolia</i>	13.52
<i>Dactylorhiza maculata</i>	13.52	<i>Pedicularis lapponica</i>	13.52
<i>Draba ssp.</i>	6.94	<i>Phippsia algida</i>	9.91
<i>Epilobium alsinifolium</i>	13.52	<i>Pinguicula alpina</i>	6.94
<i>Epilobium anagallidifolium</i>	6.94	<i>Pinguicula vulgaris</i> subsp. <i>vulgaris</i>	6.94
<i>Epilobium hornemannii</i>	6.94	<i>Plantago maritima</i>	6.94
<i>Epilobium palustre</i>	13.52	<i>Potentilla crantzii</i>	13.52
<i>Erigeron borealis</i>	13.52	<i>Potentilla erecta</i>	13.52
<i>Euphrasia frigida</i>	6.94	<i>Pyrola minor</i>	13.52
<i>Euphrasia stricta</i>	6.94	<i>Pyrola rotundifolia</i> agg.	13.52
<i>Filipendula ulmaria</i>	15.34	<i>Ranunculus acris</i> subsp. <i>acris</i>	15.34
<i>Galium boreale</i>	6.94	<i>Ranunculus auricomus</i>	15.34
<i>Galium normanii</i>	6.94	<i>Ranunculus repens</i>	15.34
<i>Galium palustre</i>	6.94	<i>Rhinanthus minor</i>	13.52
		<i>Rhodiola rosea</i>	15.34

<i>Rumex acetosa</i>	13.52	<i>Deschampsia alpina</i>	9.91
<i>Rumex acetosella</i>	13.52	<i>Deschampsia cespitosa</i>	
<i>Saussurea alpina</i>	13.52	<i>subsp. cespitosa</i>	9.91
<i>Saxifraga aizoides</i>	13.52	<i>Elymus caninus</i>	9.91
<i>Saxifraga rosacea subsp.</i>		<i>Festuca ovina subsp.</i>	
<i>rosacea</i>	6.94	<i>ovina</i>	6.29
<i>Scorzonerooides autumnalis</i>	13.52	<i>Festuca rubra subsp.</i>	
<i>Senecio vulgaris</i>	13.52	<i>richardsonii</i>	6.29
<i>Sibbaldia procumbens</i>	13.52	<i>Festuca rubra</i>	6.29
<i>Silene acaulis</i>	13.52	<i>Festuca vivipara</i>	6.29
<i>Silene dioica</i>	13.52	<i>Hierochloë odorata</i>	9.91
<i>Solidago virgaurea</i>	13.52	<i>Melica nutans</i>	9.91
<i>Stellaria graminea</i>	6.94	<i>Milium effusum var.</i>	
<i>Stellaria media</i>	6.94	<i>effusum</i>	9.91
<i>Stellaria nemorum subsp.</i>		<i>Nardus stricta</i>	79.02
<i>nemorum</i>	6.94	<i>Phleum alpinum subsp.</i>	
<i>Succia pratensis</i>	13.52	<i>alpinum</i>	9.91
<i>Taraxacum ssp.</i>	13.52	<i>Poa alpina</i>	9.91
<i>Thalictrum alpinum</i>	6.94	<i>Poa glauca</i>	9.91
<i>Tofieldia pusilla</i>	6.94	<i>Poa pratensis</i>	9.91
<i>Trientalis europaea</i>	6.94	<i>Trisetum spicatum</i>	9.91
<i>Triglochin palustris</i>	6.29		
<i>Trollius europaeus</i>	15.34	sedges/rushes	
<i>Urtica dioica</i>	15.34	<i>Carex atrata</i>	11.62
<i>Valeriana sambucifolia</i>	15.34	<i>Carex bigelowii</i>	11.62
<i>Veronica alpina</i>	6.94	<i>Carex brunnescens</i>	11.62
<i>Veronica fruticans subsp.</i>		<i>Carex canescens subsp.</i>	
<i>fruticans</i>	6.94	<i>canescens</i>	11.62
<i>Vicia cracca</i>	6.94	<i>Carex capillaris</i>	11.62
<i>Viola biflora</i>	6.94	<i>Carex chordorrhiza</i>	11.62
<i>Viola canina</i>	6.94	<i>Carex diandra</i>	11.62
<i>Viola palustris subsp. palustris</i>	6.94	<i>Carex echinata subsp. echinata</i>	11.62
<i>Viola riviniana</i>	6.94	<i>Carex flava</i>	11.62
		<i>Carex lachenalii</i>	11.62
grasses		<i>Carex limosa</i>	11.62
<i>Agrostis ssp.</i>	9.91	<i>Carex lyngbyei</i>	11.62
<i>Anthoxanthum</i>		<i>Carex nigra</i>	11.62
<i>nipponicum</i>	9.91	<i>Carex norvegica</i>	11.62
<i>Anthoxanthum odoratum</i>	9.91	<i>Carex pallescens</i>	11.62
<i>Avenula pubescens</i>	9.91	<i>Carex paupercula</i>	11.62
<i>Calamagrostis lapponica</i>		<i>Carex rariflora</i>	11.62
<i>subsp. lapponica</i>	9.91	<i>Carex rostrata</i>	11.62
<i>Calamagrostis neglecta</i>	9.91	<i>Carex rupestris</i>	11.62
<i>Calamagrostis</i>		<i>Carex vaginata</i>	11.62
<i>phragmitoides</i>	9.91	<i>Eriophorum angustifolium</i>	11.62
<i>Dactylis glomerata</i>	9.91	<i>Eriophorum scheuchzeri</i>	11.62

<i>Eriophorum vaginatum</i>	11.62	evergreen shrubs	
<i>Juncus filiformis</i>	6.29	<i>Calluna vulgaris</i>	79.02
<i>Juncus trifidus</i>	6.29	<i>Cassiope tetragona</i> subsp.	
<i>Kobresia myosuroides</i>	6.29	<i>tetragona</i>	79.02
<i>Luzula multiflora</i>	11.62	<i>Dryas octopetala</i>	13.52
<i>Luzula pilosa</i>	11.62	<i>Empetrum nigrum</i>	79.02
<i>Luzula spicata</i> subsp. <i>spicata</i>	11.62	<i>Juniperus communis</i>	79.02
<i>Luzula sylvatica</i>	11.62	<i>Kalmia procumbens</i>	79.02
<i>Trichophorum cespitosum</i>		<i>Phyllodoce caerulea</i>	79.02
subsp. <i>cespitosum</i>	6.29	<i>Thymus praecox</i>	6.94
		<i>Vaccinium vitis-idaea</i>	35.46
deciduous shrubs			
<i>Alnus incana</i>	73.53	pteridophytes	
<i>Astragalus alpinus</i>	6.94	<i>Athyrium distentifolium</i>	15.34
<i>Betula nana</i>	73.53	<i>Athyrium filix femina</i>	15.34
<i>Betula pubescens</i>	73.53	<i>Botrychium lunaria</i>	13.52
<i>Ribes</i> ssp.	73.53	<i>Diphasiastrum alpinum</i>	13.52
<i>Rubus chamaemorus</i>	13.52	<i>Dryopteris expansa</i>	15.34
<i>Rubus idaeus</i>	13.52	<i>Dryopteris filix-mas</i>	15.34
<i>Rubus saxatilis</i>	73.53	<i>Equisetum arvense</i>	6.94
<i>Salix arctica</i>	73.53	<i>Equisetum fluviatile</i>	6.94
<i>Salix caprea</i> subsp.		<i>Equisetum hyemale</i>	6.94
<i>caprea</i>	73.53	<i>Equisetum palustre</i>	6.94
<i>Salix herbacea</i>	35.46	<i>Equisetum pratense</i>	6.94
<i>Salix lanata</i>	73.53	<i>Equisetum sylvaticum</i>	6.94
<i>Salix lapponum</i>	73.53	<i>Equisetum variegatum</i>	6.94
<i>Salix phylicifolia</i>	73.53	<i>Gymnocarpium dryopteris</i>	13.52
<i>Salix reticulata</i>	73.53	<i>Huperzia selago</i>	13.52
<i>Sorbus aucuparia</i>	73.53	<i>Lycopodium annotinum</i>	13.52
<i>Vaccinium myrtillus</i>	35.46	<i>Matteuccia struthiopteris</i> subsp.	
<i>Vaccinium</i>		<i>struthiopteris</i>	15.34
<i>uliginosum</i>	35.46	<i>Phegopteris connectilis</i>	13.52
		<i>Polystichum lonchitis</i>	13.52
		<i>Selaginella selaginoides</i>	13.52

Table S2. Fixed and random effects structure of linear mixed effects models. Models were used to test assumptions of contrasting productivity between different topographical units, and to test the effects of topography and grazing on alpha and beta diversity, based on two spatial grain sizes. All response variables were standardized to a mean of zero and a standard deviation of one.

aim of analyses	response variables	estimated effects (fixed)	design variables (random)
assumption of different productivity between landforms or elevations	pH, total C, total N, biomass	landform unit (convex vs. concave)	valley/slope aspect/elevation
	pH, total C, total N, biomass	elevation (high vs. low)	valley/slope aspect
diversity assessments on small spatial grain size	richness, Shannon	landform unit (convex vs. concave) grazing (un-grazed vs. grazed)	valley/slope aspect/elevation
	Jaccard, MG2	grazing (un-grazed vs. grazed)	valley/slope aspect/elevation
diversity assessments on large spatial grain size	richness, Shannon	elevation (high vs. low) grazing (un-grazed vs. grazed)	valley/slope aspect
	Jaccard, MG2	grazing (un-grazed vs. grazed)	valley/slope aspect

Table S3. Model estimates for alpha and beta diversity in Norway and Iceland – small grain size analyses

country	index	effects	effect size	std. error	df	t-value	p-value
Norway	species richness	convex vs. concave	0.28	0.14	99	1.99	0.050
		un-grazed vs. grazed	0.24	0.61	4	0.40	0.710
	Shannon Entropy	convex vs. concave	0.28	0.15	99	1.84	0.069
		un-grazed vs. grazed	-0.08	0.52	4	-0.16	0.880
	Jaccard	un-grazed vs. grazed	-0.24	0.37	4	-0.65	0.554
MG2	un-grazed vs. grazed	-0.19	0.32	4	-0.60	0.579	
Iceland	species richness	convex vs. concave	0.26	0.16	119	1.62	0.108
		un-grazed vs. grazed	-0.11	0.23	4	-0.48	0.656
	Shannon Entropy	convex vs. concave	0.28	0.15	119	1.95	0.053
		un-grazed vs. grazed	0.17	0.33	4	0.53	0.624
	Jaccard	un-grazed vs. grazed	-0.22	0.44	4	-0.50	0.641
MG2	un-grazed vs. grazed	-0.30	0.31	4	-0.97	0.387	

Table S4. Model estimates for alpha and beta diversity in Norway and Iceland – large grain size analyses

country	index	effects	effect size	std. error	df	t-value	p-value
Norway	species richness	high vs. low	-0.03	0.20	49	-0.13	0.896
		un-grazed vs. grazed	0.38	0.66	4	0.59	0.590
	Shannon Entropy	high vs. low	0.38	0.22	49	1.74	0.088
		un-grazed vs. grazed	-0.15	0.55	4	-0.27	0.799
	Jaccard	un-grazed vs. grazed	-0.36	0.53	4	-0.68	0.535
MG2	un-grazed vs. grazed	-0.57	0.60	4	-0.96	0.392	
Iceland	species richness	high vs. low	-0.46	0.22	59	-2.08	0.042
		un-grazed vs. grazed	-0.25	0.34	4	-0.74	0.499
	Shannon Entropy	high vs. low	0.15	0.20	59	0.76	0.449
		un-grazed vs. grazed	0.16	0.40	4	0.39	0.715
	Jaccard	un-grazed vs. grazed	-0.44	0.41	4	-1.09	0.338
MG2	un-grazed vs. grazed	-0.12	0.34	4	-0.34	0.750	

Figure S1. Number of plots that were subjectively assigned to a category of moisture for (A, B) convex and concave landforms; and (C, D) high and low elevations.

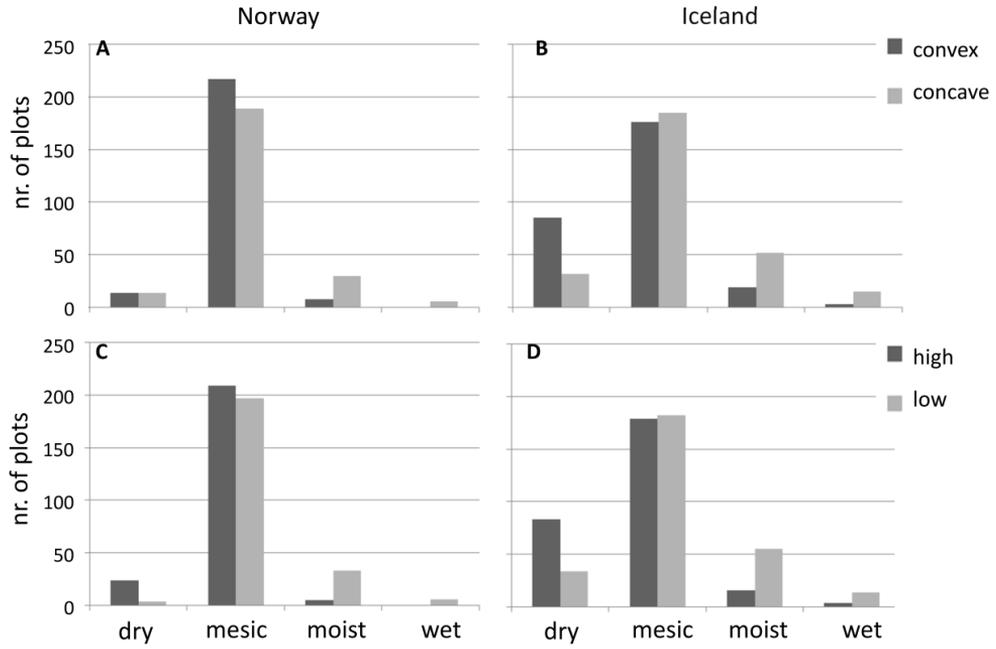


Figure S2. Average biomass ($\text{g}\cdot\text{m}^{-2}$) of plant growth forms for each elevation. Open symbols represent Norway, closed symbols represent Iceland. Error bars are 1 standard error. Observe that y-axes have different dimensions for growth forms due to large discrepancies in biomass.

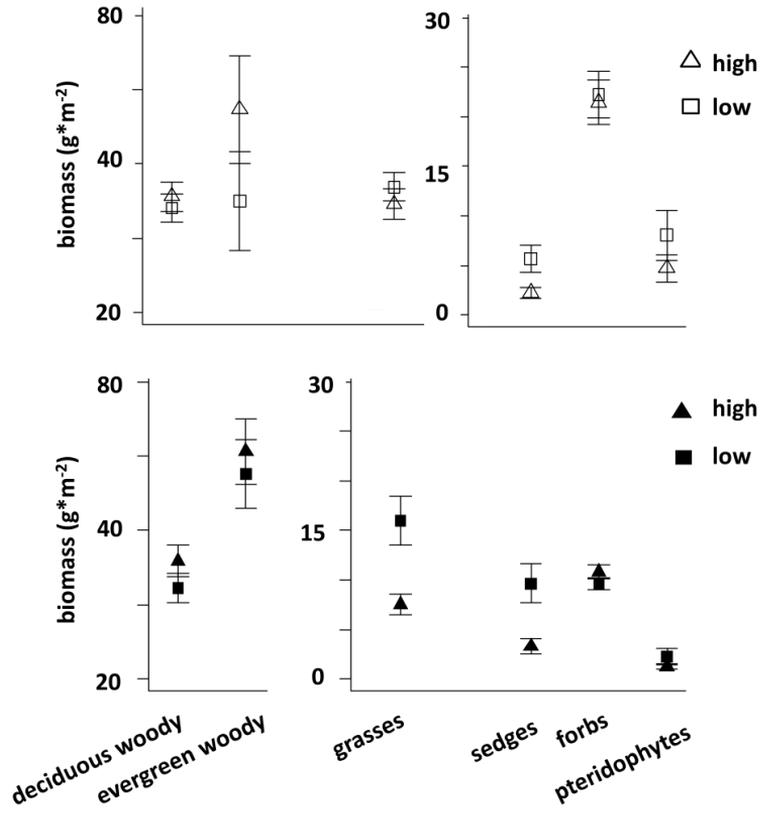


Figure S3. Average biomass ($\text{g}\cdot\text{m}^{-2}$) of plant growth forms for each grazing regime. Open symbols represent Norway, closed symbols represent Iceland. Error bars are 1 standard error. Observe that y-axes have different dimensions for growth forms due to large discrepancies in biomass.

