Effects of local and regional drivers on plant diversity within tundra landscapes

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Abstract

In tundra, the diversity within vascular plant communities (*alpha* diversity) is known to be determined by local drivers such as habitat productivity and ungulate grazing. However, little is known how such local drivers modify the diversity between communities (*beta* diversity). Furthermore, diversity patterns may be constrained by the size of the regional species pool, which in turn may mediate the effects of local drivers. Until now, these interactions have not been addressed in tundra habitats. The aim of this thesis was therefore to assess how local and regional drivers shape diversity patterns in tundra.

The thesis comprises three separate, but closely related studies. Firstly, to achieve comparability between studies, different methods of defining habitats for diversity assessments were evaluated. The results highlighted the importance of defining habitats explicitly. *Alpha* and *beta* diversity were assessed in Icelandic tundra valleys at several spatial scales, determined by topography, and contrasting regimes of sheep grazing. The same study design was applied at comparable locations in Norway, a mainland region with a greater species pool size than Iceland.

Diversity in Iceland was strongly driven by topography of contrasting landform curvature and elevation, representing different conditions of habitat productivity. Diversity was not affected by current contrasts in sheep grazing which is likely due to the persistence of historical grazing effects. Topography within Norway displayed similar effects, however, the comparison to Iceland provided the first evidence that a large species pool size may amplify diversity patterns that are shaped by local topography.

The thesis also highlights the importance of clarity and unambiguity when defining spatial scales for assessments, the appropriate diversity measures, and the levels of biological organization to be used. A clear definition concerning those aspects is essential when inferring effects of local and regional driving forces on vascular plant diversity within tundra.

Útdráttur

Tegundafjölbreytni innan plöntusamfélaga (*alpha*) í túndru endurspeglar staðbundna mótunarþætti svo sem framleiðni búsvæðisins og beit stórra grasbíta. Vísbendingar eru um að stórir grasbítar geti einnig haft áhrif á fjölbreytni milli samfélaga (*beta*). Áhrif staðbundnu þáttanna kunna einnig að ráðast að hluta af tegundaauðgi svæðanna en um það er lítið vitað. Markmið ritgerðarinnar var að greina hvernig staðbundnir og svæðisbundnir þættir móta tegundafjölbreytni æðplantna í túndru.

Áhersla var lögð á að skilgreina búsvæðaeiningar með ótvíráðum og gegnsæjum hætti þannig að sambærilegt úrtak fengist fyrir öll svæðin. Á Íslandi var *alpha* og *beta* fjölbreytni metin á nokkrum stærðarkvörðum sem réðust af landslagi og framleiðni búsvæða en einnig voru beitarfriðuð svæði borin saman við svæði með sauðfjárbeit. Sama nálgun var notuð á hliðstæðum svæðum í Noregi til að fá samanburð við meginlandssvæði með mun meiri tegundaauðgi en Ísland.

Fjölbreytni plantna á Íslandi var mjög mótuð af landslagi þar sem framleiðni búsvæða endurspeglaði landform (íhvolf/kúpt) og hæð yfir sjó. Niðurstöðurnar leiddu í ljós að landslag hefur mikil áhrif á fjölbreytni en þau eru samt háð því á hvaða stærðarkvarða matið er gert. Á Íslandi fannst enginn munur á milli beittra og nú beitarfriðaðra svæða sem sennilega skýrist af því hve langvinn beitaráhrifin eru. Landslag hafði hliðstæð áhrif á norsku svæðunum. Með samanburði milli landanna tveggja fengust í fyrsta skipti vísindalegar sannanir fyrir því að tegundaauðugt svæði (þ.e. tegundaauðugri flóra) geti magnað upp þau áhrif sem staðbundið landslag hefur á fjölbreytni. Rannsóknin staðfesti enn fremur hversu mikilvægt það er vanda til undirbúnings gagnasöfnunar og skilgreina með skýrum hætti þær vistfræðilegu og rúmfræðilegu einingar sem vinnan grundvallast á.

To my family and my friends

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The thesis is based on three papers of which one is published, one is submitted to a scientific journal and one is a manuscript to be submitted. Throughout the text, these papers are referenced using their respective number as follows:

- **Paper I:** Mörsdorf MA, Ravolainen VT, Støvern LE, Yoccoz NG, Jónsdóttir IS, Bråthen KA. 2015. Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities. PeerJ 3(3): e815.

- **Paper II***:* Mörsdorf MA, Ravolainen VT, Yoccoz NG, Thórhallsdóttir TE, Jónsdóttir IS. Topography drives patterns of tundra plant diversity – there is no difference, even 60 years after cessation of sheep grazing (submitted to Ecosystems)

- **Paper III:** Mörsdorf MA, Bråthen KA, Ravolainen VT, Jónsdóttir IS. Species pool size alters the diversity patterns shaped by local forces - an example from the tundra (manuscript)

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1 Background information and objectives of the thesis

1.1 Why study diversity?

The effects of productivity, disturbances and species pool size on *alpha* diversity – the diversity within communities – has received much attention in ecology (e.g. Grime 1973; Huston 1979; Ricklefs 1987; Tilman 1987; Cornell & Lawton 1992). In contrast, the understanding of what shapes diversity between communities in a landscape (*beta* diversity) is still limited, especially for some ecosystems such as the low arctic tundra. In addition to this, the interactive effects of regional species pool size with both productivity and disturbances have never been investigated for *alpha* and *beta* diversity within low arctic tundra ecosystems.

The conservation of biological diversity has entered political agendas as exemplified in the ”European council directive on the conservation of natural habitats and of wild fauna and flora” (FFH; The Council of the European Communities 1992). The awareness that biological diversity is a major determinant of ecosystem functioning and human well-being in combination with the potential threats to biological diversity stemming from global change and/or anthropogenic activities, necessitates the need for focused research efforts to identify the mechanisms driving biodiversity patterns (Sala 2000; Schmid et al. 2009; Cardinale 2012; Cardinale et al. 2012). Yet, the term biological diversity itself is complex and can refer to different levels of biological organization, and to differences in absolute or relative abundances of units both within and between communities (Hill 1973; Purvis & Hector 2000; Yoccoz et al. 2001; Jost 2006; Anderson et al. 2010; Tuomisto 2010 a,b).

In terms of the level of biological organization, this thesis focuses on the diversity of vascular plant species. Diversity will be defined on the basis of occurrence and relative abundances of those species. The degree to which different kinds of diversity can be distinguished at the species level will be clarified in the following sub-chapters.

1.2 Diversity as richness *versus* relative abundance of species

Species diversity is often investigated within a defined ecological community. An intuitive measure of species diversity is the number of species, or species richness within this community (Whittaker 1972). Plant species richness within a community is a widely used measure of plant species diversity in ecology and has been discussed with regard to potential drivers such as productivity (e.g. Grime 1973; Dickson & Foster 2011), disturbances (e.g. Connell 1978; Huston 1979; Shea et al. 2004) and species pool size (e.g. Ricklefs 1987, 2008; Cornell & Lawton 1992). However, the diversity within a community does not have to be regarded under the aspect of species richness only.

In certain contexts, the relative abundance of plant species can be more important than their absolute number (Whittaker 1972; Purvis & Hector 2000). Depending on the research questions asked and the hypothesized responses of species diversity within a community, there is a choice of diversity measures that represent relative species abundances. Commonly used measures include information criteria such as Shannon Entropy (Shannon 1948) or the Gini-Simpson index (Simpson 1949) (Table 1.1). Both these measures represent particular aspects of relative species abundances within a community, but differ in the way their values need to be interpreted.

Shannon Entropy for instance represents the evenness of the species distribution within a community, being equal to the uncertainty of species identity when one individual is picked at random from the community. Whilst the Gini-Simpson index represents the probability that two randomly drawn individuals from the community represent different species. Owing to differences in how such indices use abundance information, selecting a diversity measure as this will have major implications for the interpretation of data.

Due to the large number of measures that have been used to asses biological diversity, there have been a number of efforts to unify the concept. Here, the usage of number equivalents (Hill 1973) has recently been advocated as the only “true” concept to actually be called diversity (Jost 2006; Tuomisto 2010a). This refers to the number of equally abundant species that would be needed to produce a certain average abundance of species within a community. The advantage of number equivalents is that they are determined by an exponent “q” (see Table 1.1). This enables researchers to give species a different weight in their contribution to diversity, depending on their relative abundance within the community. However, the term “true diversity” prompted value laden discussions around the utility of this concept (e.g. Hoffmann & Hoffmann 2008), and undoubtedly, different concepts around the term diversity have their place in science (Purvis & Hector 2000; Anderson et al. 2010). Figure 1.1 shows in a simple way that diversity values depend on the diversity measure used.

Table 1.1. Measures of within community diversity (alpha)

Index	**Equation**	**Interpretation**
species richness	= sum (n_k) n_k: occurrence of species k within a community	The number of species found within a community
Shannon Entropy	= - sum (p_k * log $p_{k)}$ p_k: relative abundance of species k within the community	The uncertainty of species identity when one individual is picked at random from the community
Gini-Simpson index	= 1- sum (p_k^2) p_k: relative abundance of species k within the community	The probability that two randomly picked individuals from the community represent different species
Number equivalents	= sum $(p_k^q)^{1/(1-q)}$ p_k: relative abundance of species k within the community q: variable term to weigh species according to their relative abundance within the community	The number of equally abundant species that would be needed to produce a certain average abundance of species within a community. Depending on q, number equivalents are equal to the diversity measures above

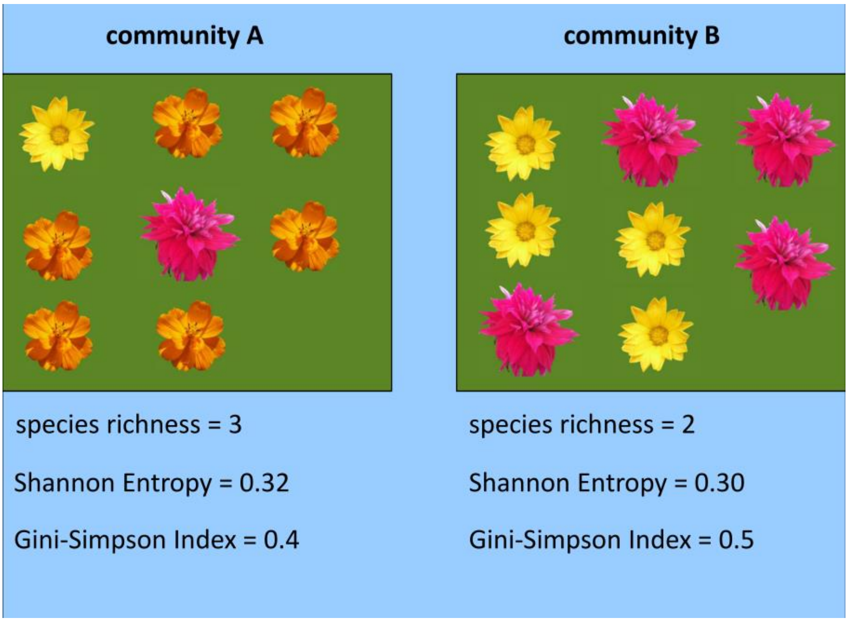

Figure 1.1. Species richness, Shannon Entropy and Gini-Simpson index for two plant communities (inspired by Purvis & Hector 2000). Outcomes of diversity assessments are thereby dependent on the diversity measure used.Community A has one more species than community B (species richness). Also the uncertainty of species identity when picking one species at random is higher in community A, reflected in higher Shannon Entropy. However, the probability of having different species when picking two individuals at random is higher in community B, being reflected in the Gini-Simpson index.

1.3 Diversity components: the concept of *alpha*, *beta* and *gamma* diversity

Whittaker (1960) was the first to expand the concept of diversity within communities towards different components of diversity that relate to its structuring within landscapes. Besides the diversity within communities, he also considered the heterogeneity among communities and the overall diversity of a region. Accordingly, he termed those components *alpha*, *beta* and *gamma* diversity. The assessment of *beta* diversity subsequently received great attention, because it provides important information when aiming to understand structuring of the overall diversity within a landscape or region (*gamma* diversity) (Whittaker 1960, 1972). Even though Whittaker explored many different ways of quantifying *beta* diversity, he suggested that the simplest way would be to use a multiplicative partitioning approach, where *beta* diversity is calculated based on the ratio between *gamma* and *alpha* diversity:

$$beta = gamma : alpha$$

An alternative concept was subsequently developed (Lande 1996; Veech et al. 2002) which suggested partitioning of diversity in an additive manner, with *beta* diversity being the difference between *gamma* and *alpha* diversity:

$$beta = gamma - alpha$$

Certainly, both approaches have their current utility, but care needs to be taken when interpreting their respective outcomes. Different diversity measures require either multiplicative or additive partitioning approaches due to mathematical reasons (Jost 2007). If number equivalents are used, multiplicative diversity partitioning yields *beta* diversity as the number of compositionally different communities (or other units) in the landscape or region (Jost 2007; Tuomisto 2013). *Gamma* diversity is thereby the total of number equivalents of a region and *alpha* diversity reflects the average of number equivalents per community. *Alpha* and *beta* diversity therefore relate to conceptually different phenomena. Additive partitioning would reveal *beta* diversity as the turnover of number equivalents and adds up to *gamma* diversity together with *alpha*. However, depending on the research question asked, it may be more applicable to compute *beta* diversity as a dissimilarity in terms of species information between communities.

Measures of multivariate dispersion are thereby an alternative to classical diversity partitioning, one which enables researchers to quantify the *beta* diversity of communities based on differences in species occurrence or abundances, depending on the measure used (Anderson et al. 2010; Tuomisto 2010c) (Table 1.2). Even though some researchers argued that measures of multivariate dispersion should not be termed *beta* diversity (Jost 2007; Tuomisto 2010a), they do quantify important aspects of community differentiation and are often found to be suitable to address the research question of interest (Legendre & Gauthier 2014). Yet, researchers need to be aware of what a specific dissimilarity measure quantifies and whether the properties of the measure are suitable to quantify the community parameters of interest. When selecting a suitable measure, the initial consideration is therefore whether the joint absence of a species from both communities should be used as information to quantify dissimilarity or not (Anderson et al. 2010). Depending on this decision, a suite of dissimilarity measures will have to be discarded as potential measures of *beta* diversity. Thereafter, researchers must decide whether to base calculations of community differentiation on species occurrences only, or whether to include information on relative species abundances. In the latter case, there is a choice of dissimilarity measures which have different strengths in how much emphasize is placed on the differences in abundance *versus* occurrence of a species between two communities. Common dissimilarity measures such as Chi-squared or Bray-Curtis distance inherit standardizations of species abundance information which leads to a stronger influence of rare species within both communities (Anderson et al. 2006).

Table 1.2. Jaccard-, Sørensen-, Bray-Curtis- and Modified Gower index as representatives for pairwise dissimilarity/distance measures that quantify differences in species diversity between two communities

Index	**Equation**	**Interpretation**
Jaccard	= (b+c)/(a+b+c) a: number of species shared by both communities b: number of species occurring in community one but not in community two c: number of species occurring in community two but not in community one	Proportion of unshared species to the total species number of two communities
Sørensen	= 2(b+c)/(2a+b+c) a: number of species shared by both communities b: number of species occurring in community one but not in community two c: number of species occurring in community two but not in community one	Proportion of unshared species to the average richness of two communities
Bray-Curtis	= sum (abs(x_{1k} - x_{2k})) /sum (x_{1k} + x_{2k}) x_{1k}: abundance of species k in community 1 x_{2k}: abundance of species k in community 2	Proportional dissimilarity between communities based on species abundances.
Modified Gower	= sum (w_k (abs(x'_{1k} – x'_{2k})) /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 $w_k = 1$	Average change in species abundance between two communities depending on the base of the logarithm. A log base of two gives a doubling of a species in one community the same weight as a compositional change of one species.

On the contrary, a dissimilarity measure that has been proposed by Anderson et al. (2006) enables researchers to define how much weight should be put on the difference in abundance *versus* occurrence of a species between communities (termed the Modified Gower Index). Using a logarithmic transformation of the data with a log base of two, this index places strongest weight on species abundance differences, where a doubling of a species in one community receives the same weight as a compositional change of one species.

Table 1.2 illustrates a small selection of pairwise dissimilarity/distance measures that are based on species occurrence or relative abundance information, and gives an explanation of how the outcome must be interpreted.

1.4 Spatial scales induce challenges of assessing diversity patterns

A challenge when assessing plant diversity within landscapes is posed by the spatial scale at which diversity is measured. The importance of how spatial scales affect studies of ecological patterns in nature has been emphasized by Wiens (1989) and Levin (1992). The processes underlying ecological patterns often operate at spatial scales that are different to the pattern of interest (Levin 1992). Therefore, in order to study the mechanisms that cause ecological patterns, consideration of several spatial scales of assessment is a necessity (Levin 1992; Huston 1999; Barton et al. 2013).

Essential decisions during the design of sampling protocols include for instance the determination of the smallest spatial resolution (or grain size) at which data are recorded and the complete geographical extent of the study (Wiens 1989). Grain size will affect the variation between units that can be assessed by the sampling, whereas the study extent determines how far results can be generalized by including or excluding specific types of units (Figure 1.2).

The definition of grain size and study extent is therefore important for the communication of scientific findings and the development of scientific theory (Wiens 1989). As there is no single “natural scale” (Levin 1992), the appropriate choice will be left to the researcher (Huston 1999; Jackson & Fahrig 2014).

In terms of plant diversity, the study of driving forces has repeatedly been shown to be affected by spatial scaling (e.g. Chaneton & Facelli 1991; Mittelbach et al. 2001; Normand et al. 2006). Researchers must therefore be aware of this issue, especially since grain size tends to increase with increasing study extent (Wiens 1989), making identification of processes that shape local diversity patterns difficult (Huston 1999).

Methods in recording plant diversity over large spatial extents, inherit problems that are strongly connected to this issue. Commonly used phytosociological approaches (Braun-Blanquet 1928) are efficient for assessing vegetation properties (including diversity) with a high spatial resolution (small grain size) while covering large geographical extents. However, plant communities are chosen based on indicator plant species in this approach, which has been shown to reveal biased estimates of plant community diversity (Chytrý 2001; Botta-Dukát et al. 2007; Hédl 2007). The basic problem is that plant communities are not clearly defined units (Kenkel et al. 1989). On the contrary, modern methods that rely on remote sensing techniques use sampling units in a transparent way which is, however, often accompanied by large grain sizes. Ecologists are therefore often confronted with a dilemma when aiming to assess diversity patterns over a range from small to large grain sizes, whilst also covering a large geographical extent.

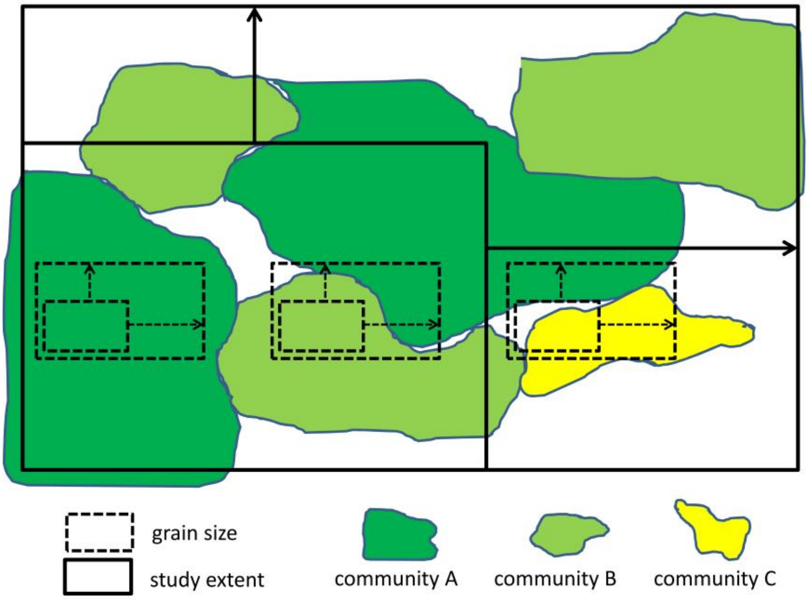

Figure 1.2. Visualizing the effects of grain size and study extent on information that can be retrieved for three communities. Using a small grain size compared to large grain size provides information about variation between communities A and B. Results based on a small study extent can only refer to community A and B in this example, whereas a large study extent includes information about community C as well.

1.5 Driving forces of species diversity

1.5.1 Local driving forces of species diversity

Over the past decades, researchers have established the importance of several driving forces that shape species *alpha* and *beta* diversity.

The importance of productivity in shaping diversity within communities was established early on by community ecologists (e.g. Grime 1973; Tilman 1987). The productivity within communities relates to different community processes that have been shown to create characteristic productivity – diversity relationships. The *Humped-Back Hypothesis* (Grime 1973) received great attention over the past decades, however, more recent meta-analyses have emphasized that productivity – diversity relationships are, belongs others, scale dependent, and can be positive, negative, humped-back, or even u-shaped (Waide et al. 1999; Mittelbach et al. 2001; Chase & Leibold, 2002; Whittaker & Heegaard 2003; Adler et al. 2011). However, it is also important that productivity-diversity relationships are altered as soon as external processes induce a disturbance of the community structure.

Under high productivity, competitive exclusion limits the diversity within plant communities, but disturbances can increase *alpha* diversity due to a reduction of highly productive and competitive species (Connell 1978; Huston 1979). Relationships have thereby been established between the intensity of disturbances and the diversity within communities as well. The *Intermediate Disturbance Hypothesis* (Connell 1978) states that *alpha* diversity increases when under moderate to intermediate intensities of disturbance, whereas high intensity of disturbance leads to a reduced *alpha* diversity (Shea et al. 2004). Disturbance effects, such as induced by grazing ungulates, are known to affect the diversity within plant communities (Milchunas et al. 1988; Olff & Ritchie 1998). However in general, grazing effects on plant diversity are dependent on the productivity of communities. Disturbances via grazing can cause a reduction in *alpha* diversity when plant productivity is low, which is explained by a lack of resource availability to recover from the disturbance (Proulx & Mazumder 1998; Bakker et al. 2006). On the contrary, the same intensity of disturbance can cause higher *alpha* diversity when productivity is high, due to the reduction of competitive exclusion or the enhancement of colonization by less competitive species (Proulx & Mazumder 1998; Bakker et al. 2006).

The shaping of *beta* diversity is also closely related to the effects of productivity and disturbances. Naturally, community differentiation within a landscape occurs due to a multitude of habitat conditions which have contrasting levels of potential plant productivity (Whittaker 1960). However, disturbances can change those patterns of *beta* diversity within a landscape (Chaneton & Facelli 1991; Olff & Ritchie 1998). Within tundra regions, grazing by reindeer (*Rangifer tarandus* L.) or sheep (*Ovies aries* L.) has been connected to a reduction of community differentiation, i.e. *beta* diversity. Reindeer are known to display preferences for productive plant species such as forbs, the results of which can lead to the homogenization of plant communities (Bråthen et al. 2007). Similar effects were shown for sheep grazing. In Icelandic tundra, Jónsdóttir (1984) found a reduced coverage of forbs and deciduous shrub species in grazing commons compared to communities on a neighboring island which was un-grazed. Grazed vegetation was strongly dominated by graminoids and community differentiation was less pronounced than on the un-grazed island. Similarly, an experimental study by Speed et al. (2013) found that the spatial turnover of plant species within heath communities was higher in a treatment of decreased sheep grazing. However in general, the effects of grazers on community heterogeneity can be expected to be scale dependent (Chaneton & Facelli 1991; Olff & Ritchie 1998; Adler et al. 2001; Austrheim & Eriksson 2001), which is presumably one of the reasons for seemingly contradictory results from separate studies that found indication for reduced (e.g. Ravolainen et al. 2010; Speed et al. 2013) and increased (e.g. Golodets et al. 2011) *beta* diversity resulting from ungulate grazing. Different types of grazers select food patches at a variety of spatial scales (Senft et al. 1987) and the interaction of grazing activity with spatial scales at which habitat productivity varies (Austrheim & Eriksson 2001) will determine the patterns of *beta* diversity within landscapes (Adler et al. 2001).

1.5.2 Relative effects of regional species pool size and local driving forces on species diversity

Early views in macro-ecology postulated that the size of regional species pools will ultimately limit the amount of species that can be found within communities and thus be the major determinant of *alpha* diversity (Ricklefs 1987, 2008; Taylor et al. 1990; Cornell & Lawton 1992; Zobel 1997). However, recent studies showed that the effects of regional species pool size have to be set in perspective to local effects such as habitat productivity and disturbances (e.g. Zobel & Pärtel 2008; Foster et al. 2004). The *Shifting Limitation Hypothesis* (SLH; Foster 2001) for instance states that in conditions of low productivity, *alpha* diversity will be limited by species pool size (Zobel & Liira 1997; Pärtel et al. 2000; Michalet et al. 2014). As soon as productivity increases, processes that relate to species interactions will become increasingly important (Foster et al. 2004; Dickson & Foster 2008; Michalet et al. 2014) and in conditions of high productivity, *alpha* diversity will be low due to the competitive exclusion of plant species (Figure 1.3). Yet, disturbances can shift this situation towards higher levels of productivity (Figure 1.3) (Foster et al. 2004; Dickson & Foster 2008). In situations of very high disturbances, *alpha* diversity will be entirely determined by the disturbance intensity (Michalet et al. 2014).

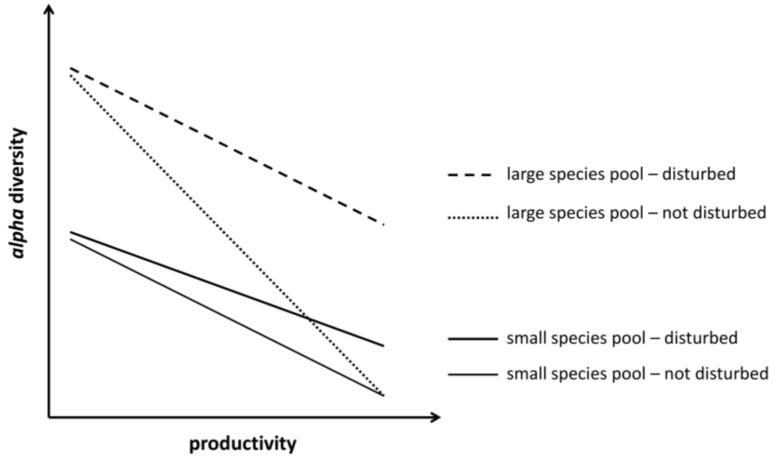

Figure 1.3. The shifting limitation hypothesis, exemplified for a negative linear relationship between alpha diversity and productivity. Alpha diversity under low productivity is determined by species pool size whereas alpha diversity under high productivity is determined by local species interactions. Grazing alters those relationships and very high grazing intensity can determine alpha diversity irrespectively of species pool size or productivity (not shown in figure). Observe that productivity - alpha diversity relationships are different under contrasting species pool sizes and disturbance regimes.

Beta diversity may also be influenced by both, the regional species pool size and local drivers. A large species pool size can be expected to create situations in which more plant species share the same habitat, as opposed to situations with small species pool size where the common pool of species occupying a particular habitat will be fewer. This situation may reduce the importance of interspecific competition, and niche width in regions of small species pool size will be larger, causing a reduced community differentiation in comparison to regions with a large species pool size (Steindórsson 1964). Also, regions that have small species pool size due to geographical isolation, such as islands, are usually dominated by species with high dispersal ability (McArthur & Wilson 1967), a trait that has been associated with low *beta* diversity (Qian 2009).

1.6 Knowledge gaps and objectives of this thesis

The central feature of this thesis work is the assessment of vascular plant diversity within tundra landscapes and the quantification of local and regional driving forces. As outlined above, driving forces shape plant diversity on several spatial scales, which necessitates assessments over several spatial grain sizes and potentially large study extents. A determination of sampling units on small spatial grain sizes is challenging. Subjective assignments of ecological sampling units may cause biased diversity estimates because researchers tend to select for communities with higher diversity. Also, subjective sampling approaches are not replicable. The first objective of this thesis was therefore to evaluate alternative methods of defining sampling units for vegetation assessments that rely on small grain sizes while covering large geographical extents. The outcome of this evaluation provides valuable information on the utility of alternative ways to define sampling units and will help to develop optimal sampling strategies that can be applied to plant diversity assessments in various tundra regions.

Grazing effects on within plant community properties have been well-studied in the low arctic tundra (e.g. Jónsdóttir 1984; Eskelinen & Oksanen 2006; Olofsson 2006; Austrheim et al. 2008), but knowledge about grazing effects on *beta* diversity is still limited. Studies from northern Norway that investigated the effects of reindeer on *beta* diversity indicated that ungulates cause homogenization of plant communities, i.e. reduction of *beta* diversity (Bråthen et al. 2007; Ravolainen et al. 2010). However, sheep, which have a major impact on plant communities throughout the north Atlantic region (Albon et al. 2007), can be expected to conduct food patch choices that are different compared to those of reindeer (Mysterud 2000). Only a few studies have addressed the effects of sheep grazing on *beta* diversity within tundra, indicating community homogenization as well (Jónsdóttir 1984; Speed et al. 2013). However, both studies were spatially confined and rely on only one spatial grain size of analysis. The question arises of whether sheep can alter *beta* diversity patterns, which are naturally shaped by contrasting habitat productivity, taking several ecologically defined spatial scales into consideration (see Adler et al. 2001; Austrheim & Eriksson 2001). The second objective of this thesis was to address this question.

Finally, our understanding of how the combined effects of regional species pool size and local driving forces such as contrasting productivity and disturbances influence *alpha* and *beta* diversity patterns is rudimentary, especially for some ecosystems such as the tundra. Existing case studies that addressed the effects of regional contexts on *beta* diversity have not directly included the size of species pools as a driving force of *beta* diversity and they were mainly conducted within tropical ecosystems (Graham et al. 2006; Normand et al.

2006; Davidar et al. 2007). Evidence for species pool size effects from higher latitudes are sparse and indicate that differences in *beta* diversity between regions rather relate to contrasts in historical habitat connectivity or the spatial heterogeneity of re-colonization sources after glaciation periods (Lenoir et al. 2010). Also the spatial scales of assessments can be assumed to affect the outcome of studies, addressing the relative importance of regional and local drivers of *beta* diversity (Normand et al. 2006). Regional driving forces determine *beta* diversity on large spatial grain sizes, whereas local driving forces determine *beta* diversity on small spatial grain sizes (Huston 1999; Normand et al. 2006), but this has not been assessed in tundra ecosystems either. The third objective of this thesis was therefore to evaluate the relative importance of habitat productivity and sheep grazing as local drivers of *alpha* and *beta* diversity in tundra regions under different contexts of species pool size.

2 Methods

2.1 Establishing replicable methods to assess diversity patterns within tundra

The first objective was to assess how alternative ways of defining sampling units affected certain response variables within the lower tundra. This was addressed in **Paper I** which compared a subjective *versus* a formal approach to defining sampling units, the latter approach being based on replicable criteria as opposed to the subjective approach. Response variables of interest were plant community characteristics such as *alpha* diversity and the biomass of different plant functional groups.

A hierarchically nested vegetation survey was conducted across Varanger peninsula in northern Norway (Figure 2.1 A). On higher spatial hierarchies, the sampling design was stratified to contrasting bedrock material and reindeer densities.

The sampling units of interest were mesic and snowbed habitat types. In the formal approach, *a priori* habitat characteristics were defined, ones which could be identified on large spatial grain sizes via a digital elevation model in GIS (ESRI ArcGIS, Version 8.3.0). Here, potential sampling units needed to have a concave topography and a slope between 5 and 30 degrees because the habitats of interest were known to be situated in such conditions (Fremstad 1997). To ensure sampling within low arctic tundra habitats, units needed to be less than 350 m above sea level and have a minimum distance of 500 m to birch forest. Further stratifications were done to account for logistic considerations (see Material and Methods in **Paper I** for details). In the field, potential sampling units were chosen for vegetation assessments based on the fulfillment of simple criteria. The vegetation within potential landforms needed to indicate the presence of both habitat types, which was simply assessed via a visual shift in vegetation characteristics. Furthermore, the visually estimated vegetation cover needed to be at least 75% and the landform needed to be large enough to conduct vegetation assessments along two transects (see Material and Methods in **Paper I** for details).

In close proximity to the selected sampling units, mesic and snowbed habitats were chosen in a subjective way. This choice was based on a survey of mesic and snowbed habitats within the study area (Figure 2.1 B, C). If vegetation was found with plant growth forms that were indicative of mesic and snowbed conditions (see Material and Methods in **Paper I** for details), those habitats were considered as sampling units for the study as long as the criteria for vegetation cover and minimum size for conducting sampling along two transects were fulfilled.

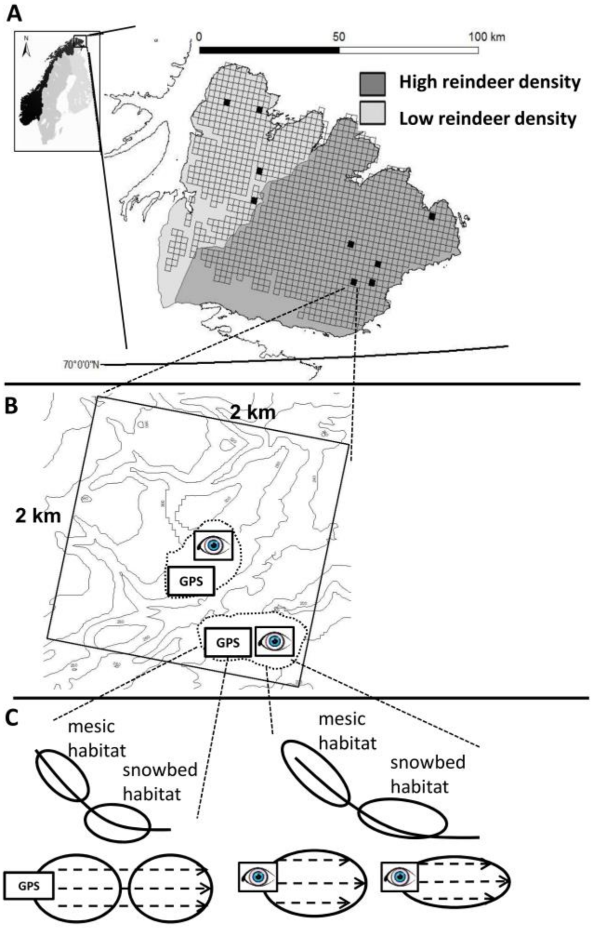

Figure 2.1. The hierarchical nestedness of the sampling design. (A) Shows the geographical location of the sampling region (Varanger peninsula, northern Norway). The shades of gray delimit the districts of contrasting reindeer density. Open squares show 2×2 km landscape areas where major roads, power lines, glaciers and large water bodies have been omitted. Black squares correspond to landscape areas that adhered to allother delimitations in our design (see Materials and Methods section of Paper I for details). (B) One landscape area contained up to two study areas (dashed line) which inherited a pair of formally (GPS) and subjectively (eye) defined sampling units. (C) Each sampling unit contained both a mesic and a snowbed habitat. The recording of vegetation characteristics within each habitat was conducted along transects (dashed lines within habitats).

In the data analyses, linear mixed effects models were used to assess the effects of the subjective *versus* the formal approach of defining sampling units on plant community properties, such as *alpha* diversity and the biomass of several plant functional groups (see Material and Methods in **Paper I** for details). Those effects were assessed for the two districts that differed in density of reindeer.

2.2 *Alpha* and *beta* diversity under contrasting habitat productivity and grazing regimes within tundra

The second objective was to identify whether sheep can alter plant diversity patterns which are naturally shaped by contrasting habitat productivity. This was addressed by recording plant diversity within glacially eroded valley landscapes in Iceland over a set of spatial scales (**Paper II**). The various valley landscapes where sampling was conducted represented contrasting regimes of sheep grazing.

Many farms in remote regions of Iceland were abandoned after agricultural modernization in the 1940's. This historical development created opportunities for studying un-grazed vegetation states up to 60 years after the cessation of sheep grazing. Vegetation assessments were stratified to three un-grazed valleys in North and Northwest Iceland, and compared to three presently grazed valleys (Figure 2.2 A). All valleys were similar in terms of bedrock and had a U-shaped profile (Figure 2.2 B) due to glacial erosion during the last glacial maxima which peaked approximately 11 000 year ago (Norðdahl et al. 2008).

Topography alters habitat condition and productivity in terms of moisture and nutrients in tundra ecosystems (Daubenmire 1980; Evans et al. 1989; Ostendorf & Reynolds 1998) and is therefore a strong driver of plant community characteristics within tundra valleys. For the valleys selected in this study, the prevailing wind direction from east and north-east leads to contrasting growth conditions for plants between the slopes with east and west facing aspects; the latter being subjected to higher snow accumulation and later snow disappearance than the former (Einarsson 1976; Evans et al. 1989). Valley slopes are generally of concave character, which also causes contrasts in snow distribution and moisture conditions within valley slopes. High elevations are characterized by a shorter duration of snow cover, xeric conditions and low nutrient stocks whereas the opposite conditions prevail at low elevations. Within those slopes, small streams and alluvial fans cause a horizontal pattern of altering convex and concave landforms which leads to similar contrasts in habitat conditions within the same elevation. Topographical units shape habitat productivity within valleys and as topographical units can be regarded as spatially nested, habitat productivity was assessed at three different spatial scales (Figure 2.2 C).

Within each convex and concave landform, occurrences and relative abundances of vascular plant species were recorded using the five point intercept method (Bråthen & Hagberg 2004; see Materials and Methods in **Paper II** for details). Calculations of *alpha* and *beta* diversity for plant communities within and between topographical units were based on species occurrence and relative abundance information. For *alpha* diversity, species richness and the Gini-Simpson index were chosen. For *beta* diversity Jaccard dissimilarities and MG2 distances between communities were calculated.

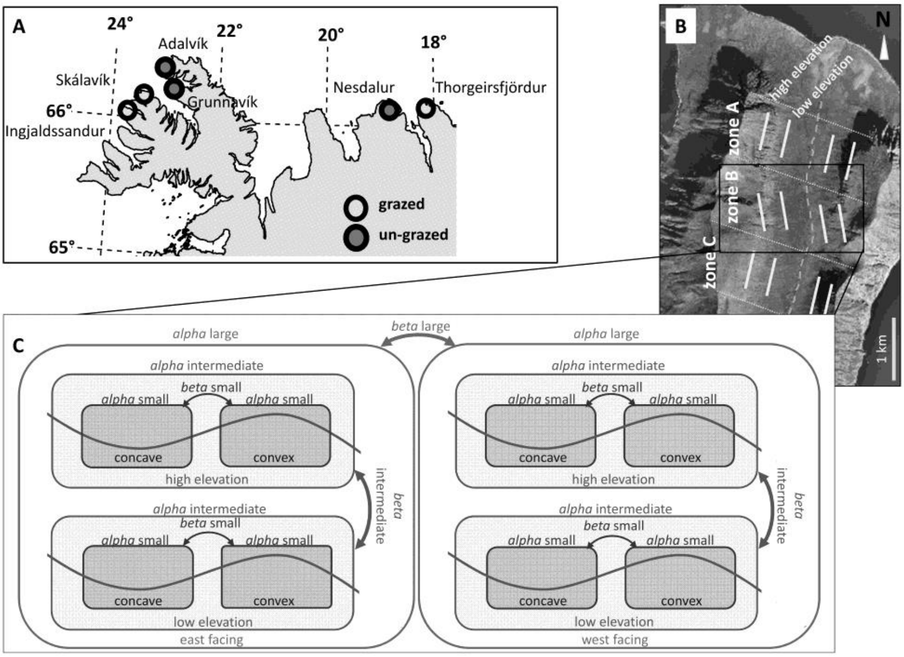

Figure 2.2. (A) Location of sampling sites in grazed and un-grazed valleys in Iceland. (B) Each valley was split up into three zones (zone A, zone B, zone C) to spread sampling throughout the valley. (C) Within each zone, the major topographical contrasts were covered; landform curvature (small grain size), elevation (intermediate grain size) and slope aspect (large grain size). Vegetation sampling was performed within 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.

Linear mixed effects models were used to assess how patterns of *alpha* diversity were shaped by topography and different grazing regimes (see Materials and Methods in **Paper II** for details). Effects of the grazing regime were also assessed for *beta* diversity using the same approach. All analyses were conducted for the three nested spatial grain sizes that were determined by topography (Figure 2.2). In addition, the biomass of plant growth forms within topographical units was estimated using linear mixed effects models, to improve interpretation of the diversity analyses.

2.3 Relative effects of contrasting species pool size, habitat productivity and grazing regimes within tundra

The third objective was to evaluate the relative importance of local drivers under contrasting species pool size. This was addressed by comparing *alpha* and *beta* diversity patterns of tundra plant communities from regions of large- to small species pool size. Furthermore, the effects of contrasting habitat productivity and sheep grazing within those regions were assessed under consideration of two spatial grain sizes (**Paper III**).

Northern Norway and the North/Northwest Iceland were selected as study regions with contrasting species pool size (see Material and Methods of **Paper III** for details on locations). The Norwegian flora lists approximately six times as many species as the Icelandic flora (Lid & Lid 2005; Kristinsson 2010). Although it was considered that this contrast of national species lists may have no direct relevance to the specific geographical areas chosen for this study, species lists from the study confirmed that species pool size differed as expected. In Norway 179 vascular plant species were recorded, whilst only 116 species were recorded in Iceland.

Within both countries, sampling was stratified to glacially eroded U-shaped valleys with similar climate and bedrock chemistry, using the WorldClim data base (Hijmans et al. 2005) and geological bedrock maps (http://geo.ngu.no/kart/berggrunn/; Jóhannesson & Sæmundsson 2009). Half of the valleys were used as grazing commons for sheep whereas the other half were un-grazed.

Within valleys, the differentiation of plant communities was assumed to be shaped by topography, just as described for **Paper II**. However, pairs of grazed and un-grazed valleys in Norway had different general exposure and for two valleys (Kvalvikdalen and Lyngsdalen), grazing contrasts existed only for the south facing slopes. For this reason, only landforms of different curvature (convex *versus* concave) and different elevations (high *versus* low) were considered as spatial grain sizes for the analyses (see Materials and Methods in **Paper III** for details).

Average *alpha* and *beta* diversity was assessed for both study regions. Relative effects of local contrasts in habitat productivity and grazing were analyzed within each study region using linear mixed effects models (see Materials and Methods in **Paper III** for details) and discussed with respect to contrasts in regional species pool size.

3 Results and discussions

3.1 Transparency needed: definition of sampling units alters community estimates

Paper I revealed that the method used to define sampling units can have profound effects on estimates of diversity and functional group biomass within communities. A subjective definition of sampling units rendered higher *alpha* diversity estimates than a formal definition for the mesic habitat type (Figure 3.1 A, B, C), whereas in snowbed habitats, a subjective definition caused either higher or lower *alpha* diversity estimates, depending on the district of contrasting reindeer density where the data was sampled (Figure 3.2 A, B, C).

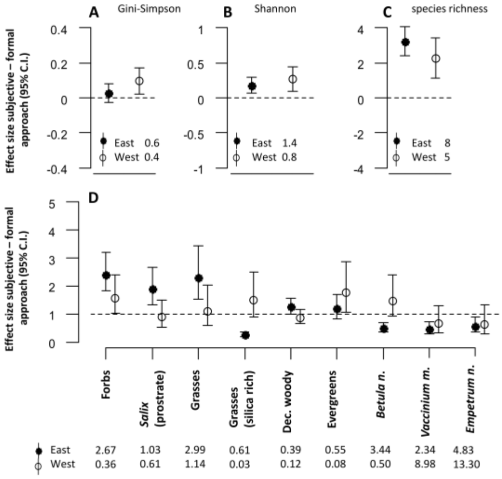

Figure 3.1. Model estimates for the mesic habitat. Effect sizes (mean ±95% confidence interval) of the response difference between the subjective and the formal approach of defining sampling units are shown for (A, B, C) estimates of diversity and (D) estimates of biomass of dominant plant species and functional groups. Effect sizes above or below the dotted line can be interpreted as the subjective approach having higher or lower estimates respectively than the formal approach. The numbers at the base of each figure are predicted model values of diversity or plant biomass in the formal approach. Closed symbols represent estimates for the eastern district with high reindeer density, whereas open symbols represent estimates for the western district with low reindeer density.

The definition of sampling units also affected estimates of plant functional group biomass. For both habitat types, clear dependence of effect sizes on the district where data was sampled was also observed (Figure 3.1 D, Figure 3.2 D). Differences in estimates between the formal and subjective approach are thus not consistent, indicating that the choice of approach has the potential to beget conclusions from ecological studies.

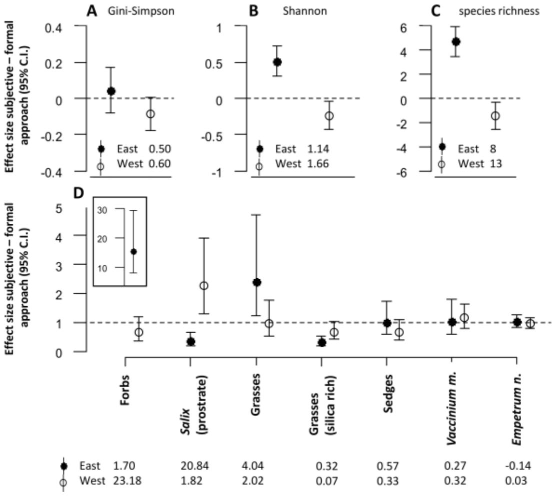

Figure 3.2. Model estimates for the snow bed habitat. All other information as for Figure 3.1.

"Ill-defined" units are common in ecology (Whittaker et al. 1973; Kenkel et al. 1989; Franklin et al. 2002) and a formal, replicable definition can be challenging, especially in the case of habitats (Whittaker et al. 1973). However, ecological knowledge builds strongly upon evidence and comparison of outcomes from case studies (Shrader-Frechette & McCoy 1994). Potential idiosyncrasies between studies (Chase et al. 2000; Hedlund et al. 2003; Badano & Cavieres 2006) could be solely due to the effects of different definitions of sampling units such as those based on habitat types. In general, the outcome of **Paper I** guided the use of transparent criteria to define sampling units when developing sampling approaches for plant diversity in tundra.

3.2 Effects of topography and grazing on tundra plant diversity

Paper II revealed effects of topography, representing contrasting habitat productivity, on patterns of plant diversity. By contrast, there was no difference in diversity between grazed and un-grazed valleys. Topographical effects were also scale-dependent.

Topography was a key determinant of *alpha* diversity in Iceland. Different species richness was found between landforms of opposite curvature and between different elevations (Figure 3.3 A, Figure 3.4 A), but there was no effect of different slope aspects (see **Paper II** for details).

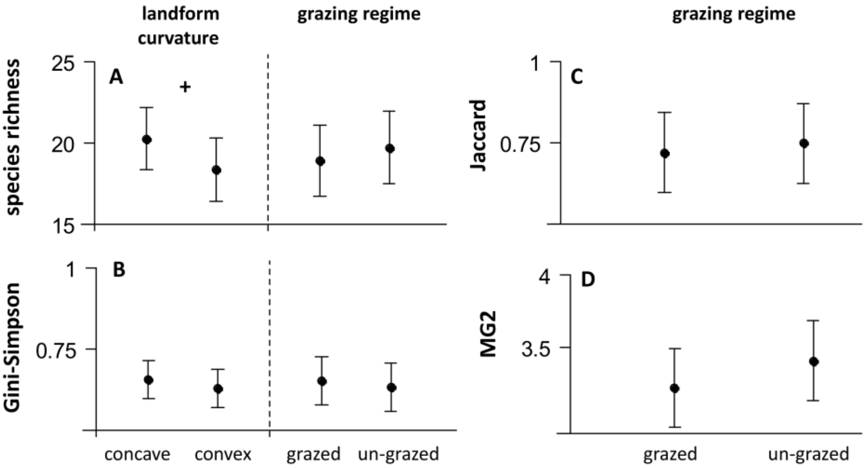

Figure 3.3. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using a small spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of landform curvature and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity 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 based on a 10% level. Error bars represent 95% confidence intervals.

Measurements of soil pH, total nitrogen (N) and total carbon (C) concentrations were additionally conducted in this study and indicated higher potential plant productivity in concave compared to convex landforms, as well as within low compared to high elevations. Whereas analyses of landform curvature effects revealed higher species richness within productive, concave landforms, analyses of elevation effects revealed the opposite pattern (higher species richness in less productive high elevations). However, standard soil measurements such as used in this study may not always reflect site fertility (or potential plant productivity), because acquisition of plant nutrients can take many forms in the tundra, including the uptake of different pools of nitrogen (Miller & Bowman 2002; Eskelinen et al. 2009).

The biomass of different plant growth forms can provide valuable insights into habitat conditions as well and is as important as abiotic growing conditions in determining *alpha* diversity within tundra (Bråthen & Ravolainen 2015). High *alpha* diversity in this study for instance was associated with topographical units having a high abundance of species with facilitating characteristics in terms of nutrient turnover, such as forbs, or with deciduous woody plants which may provide shelter for other plant species (Bråthen &

Lortie 2015; Bråthen & Ravolainen 2015) (Figure 3.5 A, B). Decreased species richness in low compared to high elevations was additionally associated with a high biomass of graminoids, which can potentially cause competition for light with other species and reduce species richness in tundra (Figure 3.5 B; Bråthen & Lortie 2015).

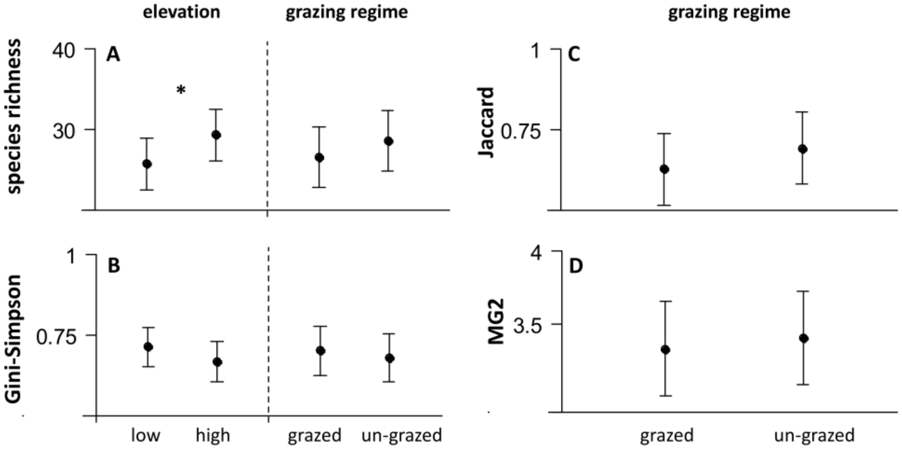

Figure 3.4. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using an intermediate spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of elevation and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity 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 based on a 5% level. Error bars represent 95% confidence intervals.*

There was no difference in either *alpha* (Figure 3.3 A, B; Figure 3.4 A, B) or *beta* (Figure 3.3 C, D; Figure 3.4 C, D) diversity between contrasting grazing regimes. This outcome was somewhat surprising, especially given that the selected valleys currently represented the strongest contrasts in sheep grazing in Iceland. It is acknowledged that present contrasts in sheep grazing are not an equivalent to a control of grazing impacts because all un-grazed valleys in this study have been grazed for centuries in the past (Erlendsson et al. 2009). It was therefore interpreted that sheep grazing has set tundra vegetation into states which are characteristic of grazed conditions (van der Wal 2006). Those vegetation states can persist for long time periods as a consequence of historical filtering of the propagule pool due to grazing (Milchunas et al. 1988), and low resource availability within habitats (Cingolani et al. 2013).

A long history of grazing is expected to select for species with high grazing tolerance (Milchunas et al. 1988; Cingolani et al. 2013). Sheep grazing in Iceland was claimed to have maintained graminoid dominated vegetation, thereby preventing re-growth of forbs or shrubs which originally dominated the landscape before human settlement (Kristinsson

1995; Thórhallsdóttir 1996). Forbs were a growth form which had low abundance in this study as well, but woody plants were the most common growth form, followed by grasses (Figure 3.5 C). Valleys in this study do presumably not represent vegetation states that are as strongly impacted by sheep grazing as other landscapes in Iceland, but based on growth form abundances, vegetation states are comparable to tundra landscapes in northern Norway, which are grazed by semi-domesticated reindeer (Bråthen et al. 2007; Ravolainen et al. 2010).

The only difference between grazed and un-grazed valleys was a marginally higher biomass of thicket-forming *Betula pubescens* and *Salix* plants in the un-grazed valleys (Figure 3.5 C). However, the data showed that recovery of those plants occurs very slowly. Shrubs within tundra can generally be expected to have slow growth rates, relying on favorable growing conditions, including high temperatures, during growing season (Büntgen et al. 2015) but in addition, a low resource availability can substantially delay recovery of vegetation after grazing (Cingolani et al. 2013). Recovery of vegetation after grazing cessation in nutrient poor ecosystems can thereby take many decades (Laycock 1991; Ransijn et al. 2015), and this, in conjunction with centuries of intense grazing pressure, and regular removal of animal biomass from the system, could have further deteriorated nutrient stocks in the present study. This mechanisms is exemplified in many grazing commons in Iceland, which has led to a persistent state of un-vegetated landscapes and severe problems due to soil erosion (Arnalds & Barkarson 2003; Arnalds 2015).

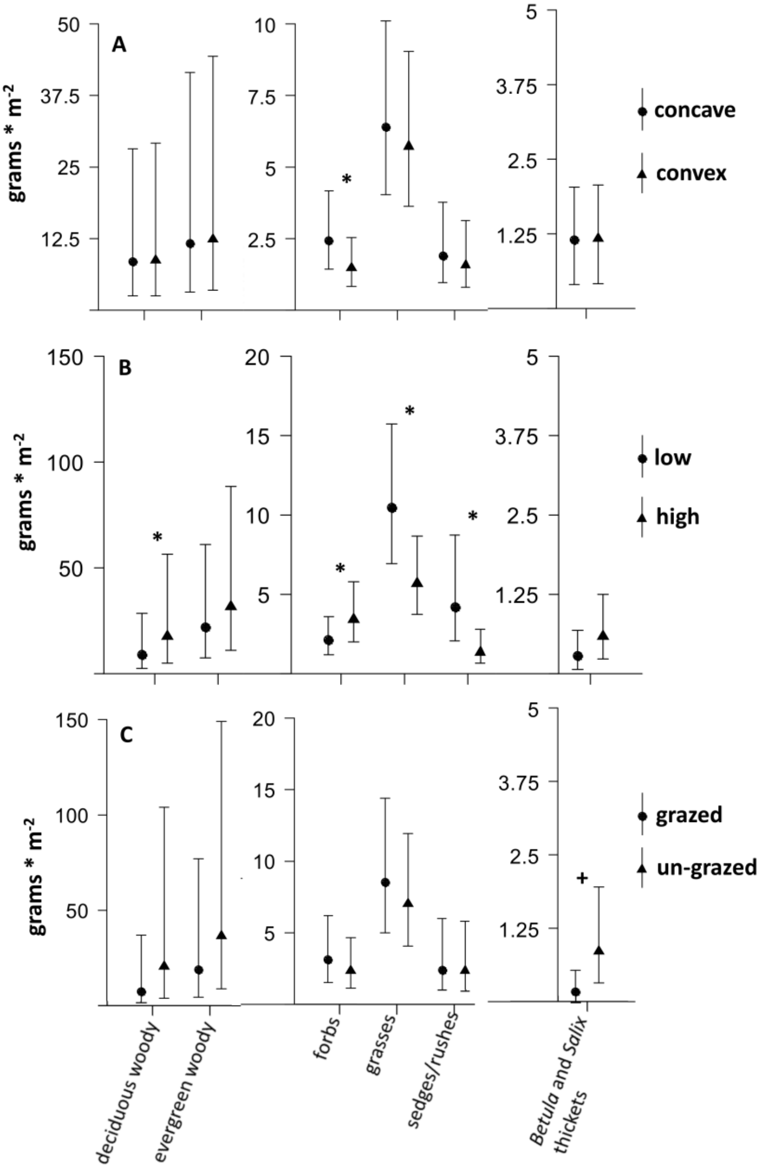

Figure 3.5. Model estimates of biomass of plant growth forms in contrasting landforms, elevations and grazing regimes. The symbols represent geometric means that were derived via back transforming model estimates [g/m^2]. "" indicates statistically significant effects on a 5% significance level, whereas "+" indicates marginally significant effects based on a 10% level. 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.*

3.3 Species pool size alters effects of topography within tundra

Paper III confirmed that topography is a strong driver of diversity, but the results also indicated that species pool size modifies topographical effects.

The results supported prior assumptions that actual species pool size was larger in Norway than in Iceland. The regional contrasts in species spool size were also found on a valley scale (on average, 87 species in Norway and 74 species in Iceland). Average *alpha* diversity was thereby higher in Norway than in Iceland (see Results section of **Paper III** for further details). As sampling within both regions was stratified to similar environmental conditions, those differences in *alpha* diversity appear related to the larger species pool size in Norway, allowing more species to colonize target communities (Zobel 1997). There were no clear differences in *beta* diversity between study regions. Only a few studies have investigated regional and local effects on *beta* diversity, but these suggest that relative effects are scale dependent (Normand et al. 2006). On a large scale, *beta* diversity may be determined by regional effects which are connected to environmental history and the existing propagule pool (Normand et al. 2006; Lenoir et al. 2010). High prevalence of species with high dispersal ability in the species pool may decrease *beta* diversity at large scales (Normand et al 2006). However, at relatively small spatial grain sizes such as in this study, *beta* diversity is strongly driven by environmental heterogeneity (Normand et al. 2006).

In terms of environmental heterogenetiety and contrasting habitat conditions, **Paper III** revealed strong effects of topography in both Norway and Iceland. Species richness and Shannon Entropy were higher in concave than in convex landforms and effect sizes had similar strength in both countries (Figure 3.6 A, B). However, investigations of soil variables revealed that landform curvatures were more strongly distinguished in Iceland than in Norway. The combination of both findings indicated that topographically-induced differences in productivity have a greater impact in regions with a large compared to a small species pool size. It was previously emphasized that species spool size affects productivity – diversity relationships on a global scale (Zobel & Pärtel 2008), because a larger species pool size may inherit a large number of species that are able to establish under conditions of very low or very high productivity (Pärtel et al. 2000; Zobel & Pärtel 2008). As opoosed to a context of small species pool size, more species are thereby available to potentially exploit existing resources (Tilman et al. 1997).

Analyses on a large spatial grain size showed that plant interactions are important determinants of *alpha* diversity in Iceland, but not Norway.

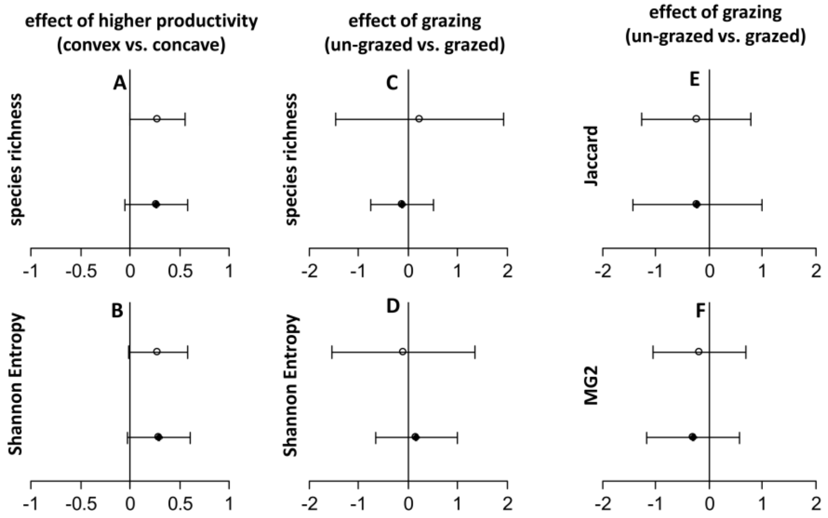

Figure 3.6. Model estimates representing the effects of landform and grazing on alpha and beta diversity, based on a small grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes. (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.

As opposed to diversity assessments in relation to different landform curvatures, the assessment of elevation effects captured a decreasing phase of species richness with increasing productivity in Iceland, whereas there were no elevation effects on species richness in Norway (Figure 3.7 A). As outlined in **Paper II**, the lower species richness in low elevations was related to potential competitive exclusion, which might be induced by a high biomass of graminoids (Bråthen & Lortie 2015).

Examination of the Shannon Entropy values revealed an entirely different outcome compared with species richness for those analyses (Figure 3.7 B). Shannon entropy in Norway was higher in low compared to high elevations, wereas there was no effect in Iceland. The results therefore highlight that productivity *versus* species richness relationships cannot simply be transferred to other measures of diversity (Svensson et al. 2012).

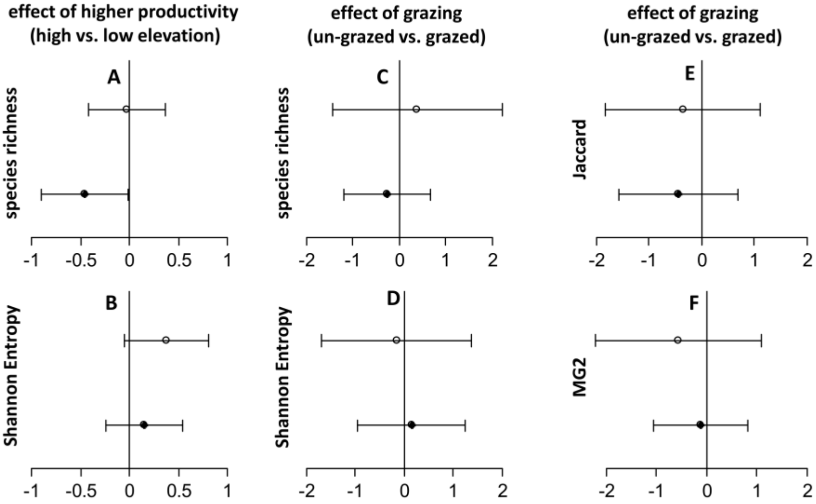

Figure 3.7. Model estimates representing the effects of elevation and grazing on alpha and beta diversity, based on a large grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes. (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.

There were no sheep grazing effects on *alpha* or *beta* diversity in either Norway or Iceland (Figure 3.6 C-F; Figure 3.7 C-F). As outlined above, persistence of historical grazing effects might be the reason for the lack of contrasts between un-grazed and grazed tundra valleys. An obvious difference between Norwegian and Icelandic valleys is that the former ones were stronger dominated by forbs and grasses. Vegetation assessments within Norwegian tundra showed that ungulates select for nutrient rich plants such as forbs and grasses (Bråthen at al. 2007), which may be interpreted such that historical or present grazing impacts were stronger in Iceland than in Norway. However, under high animal densities, ungulates also cause high abundance of especially grasses due to their high grazing tolerance and their ability of effective inorganic nutrient utilization (Augustine & McNaughton 1998). Without detailed information about grazing history within all valleys, it was thus not possible to relate the different vegetation states to intensities in historical or present sheep grazing.

4 Synthesis of study outcomes and future perspectives

A synthesis of the papers in this thesis reveals that integrating objective, robust sampling design, with a thorough assessment of scale dependence are essential considerations for accurately estimating how local and regional drivers shape vascular plant diversity within tundra.

Assessments in both, Iceland and Norway, revealed that topography was a strong driver of diversity. The sampling designs in **Paper II** and **III** were adapted to capture contrasting topography, and were based on the outcomes of **Paper I**. Sampling was stratified to maximise similarity in environmental conditions and topography between Norwegian and Icelandic sites, but it was also emphasized that definition of sampling units followed exactly the same criteria to enable a robust comparison between regions (Loehle 2004). When aiming for diversity assessments within habitats of contrasting productivity, a definition based on topography had several advantages as opposed to habitat selection based on plant community characteristics.

Topography is defined by simple criteria, and the procedure for its assessment can be easily replicated by other researchers. Additionally, potential differences in how topography covers the range of productivity between different surveys can be related to other ecosystem parameters such as soil conditions (see e.g. **Paper III**). Replicability in defining habitats for assessments of tundra plant diversity has therefore clear benefits when communicating study outcomes and interpreting data. Although vegetation reflects the potential productivity within habitats as well, choosing vegetation types subjectively is not transparent and causes biased diversity estimates (Chytrý 2001; Botta-Dukát et al. 2007; Hédl 2007). It is also circular to measure differences in plant community characteristics, such as diversity, based on a prior choice of communities that show visually different characteristics before measurements are initiated. To improve understanding of what shapes patterns of tundra plant diversity, units within which diversity is assessed need to be defined in a replicable way.

As opposed to many other studies in tundra (e.g. Jónsdóttir 1984; Speed et al. 2013), there were no effects of sheep grazing in either Iceland or Norway. As outlined above, this outcome was somewhat surprising because sampling in both regions captured the strongest known contrasts in sheep grazing, respecting similar environmental conditions between valleys. The lack of grazing effects is likely related to historical grazing activity, although it must be noted that sampling designs used here were not specifically tailored to capture effects of gazing history. However, instead of regarding this as a shortcoming of this thesis, I argue that the two papers (**Paper II** and **Paper III**) call for more research around the issue of ungulate grazing and stable states within tundra. Opposed to the studies presented here (**paper II** and **III**), experimental evidence from tundra in southern Norway showed that cessation of sheep grazing can lead to relatively rapid shifts in vegetation states, requiring only a few years to record changes in dominant plant species (Speed et al. 2014). However, sheep grazing had a longer history and was presumably more intense than in the valleys assessed in this thesis. Also the environmental conditions such as moisture regimes were different than in the papers presented here. Considering that resilience depends on factors such as the resource availability within habitats (Cingolani et al. 2013), more studies that represent sites of different habitat productivity throughout the tundra are clearly needed. Assessing the resilience of tundra vegetation after cessation of ungulate grazing requires sophisticated experiments, including strong control on initial grazing intensity in the respective sites, but such studies have been rarely conducted so far (e.g. Olofsson 2006).

Disturbance effects by ungulate grazing need also more attention with respect to the species pool size. As outlined above, species pool size may exert especially strong effects on diversity in conditions of low productivity and because grazing relaxes competitive interactions between species, the species pool size has presumably stronger effects on diversity in grazed compared to un-grazed conditions (Foster et al. 2004; Dickson & Foster 2008). Also, grazing history affects species prevalence within the propagule pool (Milchunas et al. 1988) and species left after a long history of grazing may have different properties in terms of dispersal or resource exploitation which are traits that affect productivity diversity relationships as well (Pärtel & Zobel 2007; Zobel & Pärtel 2008; Xiao et al. 2010). For those reasons, studies aimed at assessing grazing effects on tundra vegetation states must be designed as long term projects to potentially monitor vegetation changes and recovery over long time periods and include considerations of the species pool.

Paper III represents also the first evidence that species pool size alters topographical effects on diversity patterns within tundra landscapes. Yet, the soil measurements that were used here do not necessarily reflect the differences between tundra habitats in the best way because different plant types in tundra make use of different resource pools (e.g. Miller & Bowman 2002). The conclusion of **Paper III,** that a large species pool size alters diversity patterns that are created by differences in habitat productivity within tundra, should therefore be used as a working hypothesis for further studies. Here, sophisticated soil measurements in combination with a focus on potential niche exploitation of species found within communities, considering regions with contrasting species pool size, may provide further evidence for this finding. Potential experiments should also consider incorporation of grazing effects, as those are expected to alter productivity – diversity relationships under different species pool contexts, such as outlined above.

Besides the points raised so far, this thesis revealed methodological dependencies when assessing diversity patterns in tundra. Topographical effects on diversity depended on the spatial grain size of the analyses. Here, spatial scales were based on nested topographical units but in principal, many additional spatial scales could have been defined based on the spatial hierarchy of the sampling design (Jackson & Fahrig 2014). Also, the diversity measures used have determined the outcomes of diversity assessments throughout this thesis. The choice of diversity measure is essential for diversity assessment and in principal one could rely on other levels of biological organization than species as well (Yoccoz et al. 2001). Ungulate grazing, for instance, was frequently related to within and between community alterations in terms of both species (Chaneton & Facelli 1991;

Eskelinen & Oksanen 2006; Ravolainen et al. 2010; Speed et al. 2013) and various plant group classifications (Augustine & McNaughton 1998; Eskelinen & Oksanen 2006; Bråthen et al. 2007; Austrheim et al. 2008). A further analysis of the Icelandic dataset in this thesis can be used to exemplify that all three aspects, the spatial scale, the diversity measure and the level of biological organization contribute to the conclusions from diversity assessments.

I therefore conducted an additive diversity partitioning analysis (Couteron & Pelissier 2004) over all spatial hierarchies of the sampling design in Iceland using three ways of quantifying diversity: 1. based on species occurrences (species richness), 2. based on species but highlighting species abundances (Gini-Simpson index), 3. based on growth forms (such as applied in **Paper II**) and highlighting growth form abundances (Gini-Simpson based on growth forms). The approach quantifies the turnover of diversity that is induced by all spatial hierarchies of the sampling design. Although those analyses are not suitable to directly assess the effects of grazing, I conducted additive partitioning of diversity separately for grazed and un-grazed valleys. Spatial hierarchies that significantly contribute to the turnover of diversity over all spatial scales were assessed by applying Monte Carlo tests, using 1000 permutations.

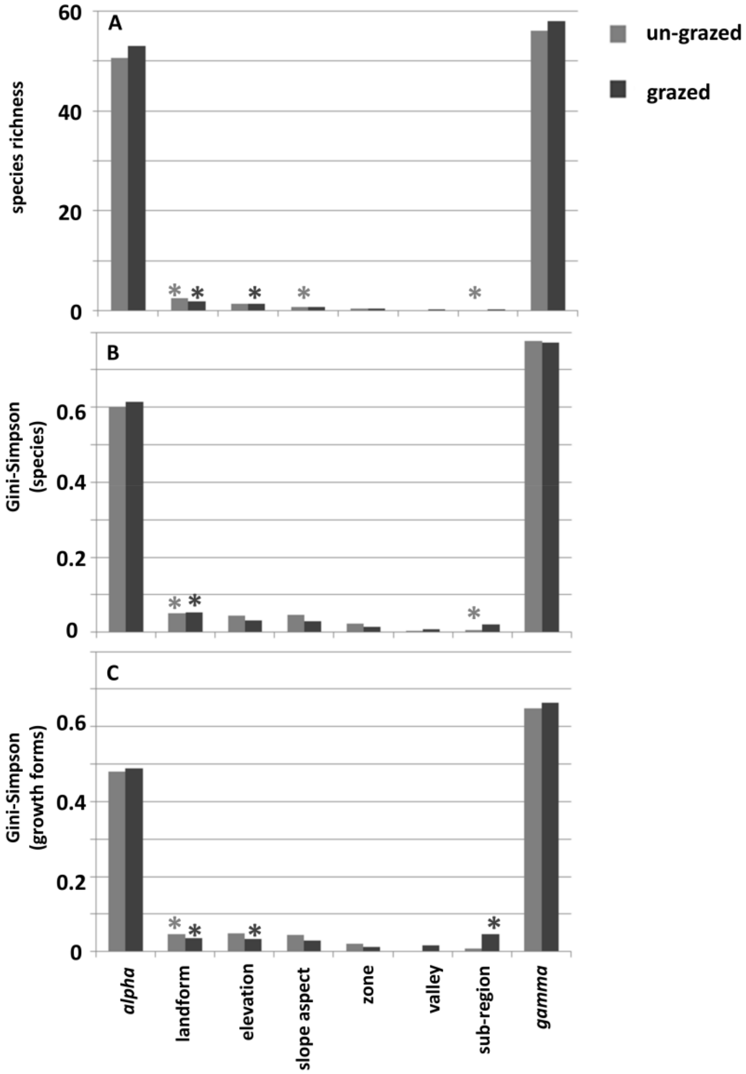

Figure 4.1. Additive diversity partitioning of the Icelandic dataset across all spatial hierarchies of the sampling design. "" indicates statistically significant turnover components of the respective spatial scale for either un-grazed (light gray) or grazed (dark gray) valleys. Statistical significance is based on a 5% significance level using Monte Carlo-test, with 1000 permutations.*

Figure 4.1 A shows similar within community (*alpha*) and overall species richness (*gamma*) for both grazing regimes. The turnover of species richness differs between both grazing regimes though. For example, landform curvature can exert significant species turnover in both un-grazed and grazed conditions, but elevation only contributes to a significant species turnover in grazed conditions. Conversely, slope aspect and the sub-region of sampling (North Iceland *versus* Northwest Iceland) contributed to a significant species turnover in un-grazed conditions only. However using the Gini-Simpson index for quantifying the turnover component of diversity reveals different patterns (Figure 4.1 B). As before, the landform curvature exerts significant effects on the turnover of the Gini-Simpson index under both grazing regimes, but effects of elevation or slope aspect were not revealed for those analyses. If turnover of the Gini-Simpson index is based on growth forms, patterns are different again (Figure 4.1 C). Landform curvature exerted significant effects on turnover of diversity, but in grazed conditions, elevation and sub-region contributed significantly to the turnover of diversity as well.

Diversity partitioning, as presented here, is simply an example to visualize how diversity patterns can depend on the spatial scale of consideration, the diversity measure and the level of biological organization that is used for calculating diversity. However, the results do suggest that all three factors may influence outcomes of diversity assessments. Figure 4.2 incorporates the definition of sampling units (**paper I**) to this finding and exemplifies in a more structured way that several steps are essential for the assessment of biological diversity. Those steps are related to a set of questions that correspond to previous suggestions regarding the monitoring of biological diversity, emphasizing that clarification of “why”-, “what”- and “how” to monitor is important (Yoccoz et al. 2001).

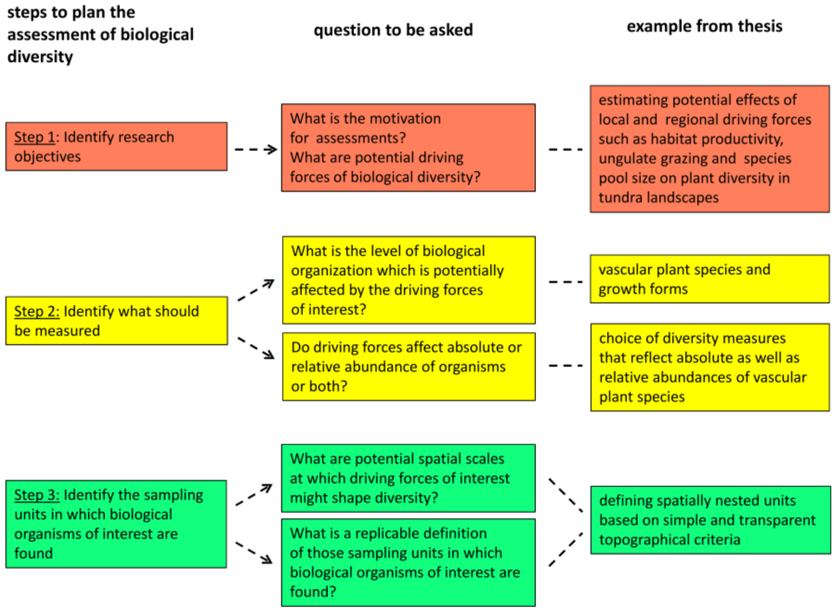

Figure 4.2. Important steps to the assessment of biological diversity

5 Conclusions

The thesis revealed new insights into the effects of local and regional drivers of plant *alpha* and *beta* diversity and highlighted important considerations that are required for diversity assessments within tundra landscapes.

I. The definition of sampling units has strong effects on estimates of *alpha* diversity and other plant community parameters. In order to make diversity assessments throughout the tundra comparable and repeatable, it is necessary that sampling units are defined in a replicable way.

II. *Alpha* and *beta* diversity of tundra plant communities are driven by topography but there was no difference between valleys that are presently grazed by sheep and valleys that were not grazed by sheep for several decades. Many landscapes throughout the tundra have a long history of ungulate grazing, and grazed vegetation states can have long persistence due to filtering towards grazing tolerant species and environmental constraints on re-growth. Assessments of grazing impacts in tundra therefore require considerations of grazing history within the landscapes of interest.

III. Besides topography, the species pool size is a strong determinant of plant diversity in tundra. A large species pool size can amplify productivity – diversity patterns that are caused by topography, but there was indication that species interactions may limit species richness in highly productive habitats as well.

IV. In general, findings throughout this thesis highlight the importance of explicit determination of spatial scales of assessments, the diversity measure and the levels of biological organization that are used to measure diversity. All three factors will determine the outcome of studies addressing effects of local and regional driving forces on *alpha* and *beta* diversity within tundra.

References

Adler B, Raff A, Lauenroth K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128: 465–479.

Adler PB, Seabloom EW, Borer ET, Hillebrand H, Hautier Y, Hector A, Harpole WS, O´Halloran LR, Grace JB, Anderson TM, Bakker JD, Biederman LA, Brown CS, Buckley YM, Calabrese LB, Chu C-J, Cleland EE, Collins SL, Cottingham KL, Crawley MJ, Damschen EI, Davies KF, DeCrappeo NM, Fay PA, Firn J, Frater P, Gasarch EI, Gruner DS, Hagenah N, Lambers JHR, Humphries H, Jin VL, Kay AD, Kirkman KP, Klein JA, Knops JMH, La Pierre KJ, Lambrinos JG, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchel CE, Moore JL, Morgan JW, Mortensen B, Orrock JL, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Wang G, Wragg PD, Wright JP, Yang LH. 2011. Productivity is a poor predictor of plant species richness. Science 333: 1750–1753.

Albon SD, Brewer MJ, O'Brien S, Nolan AJ, Cope D. 2007. Quantifying the grazing impacts associated with different herbivores on rangelands. Journal of Applied Ecology 44: 1176–1187.

Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of *beta* diversity. Ecology Letters 9: 683–693.

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG. 2010. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14: 19–28.

Arnalds O, Barkarson BH. 2003. Soil erosion and land use policy in Iceland in relation to sheep grazing and government subsidies. Environmental Science and Policy 6: 105–113.

Arnalds O. 2015. The soils of Iceland. Springer Science+Business Media, Dordrecht.

Augustine DJ, McNaughton SJ. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of Wildlife Management 62: 1165–1183.

Austrheim G, Eriksson O. 2001. Plant species diversity and grazing in the Scandinavian mountains - patterns and processes at different spatial scales. Ecography 24: 683–695.

Austrheim G, Mysterud A, Pedersen B, Halvorsen R, Hassel K, Evju M. 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. Oikos 117: 837–846.

Badano EI, Cavieres LA. 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? Journal of Biogeography 33: 304–313.

Bakker ES, Ritchie ME, Olff H, Milchunas DG, Knops JMH. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9: 780–788.

Barton PS, Cunningham SA, Manning AD, Gibb H, Lindenmayer DB, Didham RK. 2013. The spatial scaling of *beta* diversity. Global Ecology and Biogeography 22: 639–647.

Botta-Dukát Z, Kovács-Láng E, Rédei T, Kertész M, Garadnai J. 2007. Statistical and Biological Consequences of Preferential Sampling in Phytosociology: Theoretical Considerations and a Case Study. Folia Geobotanica 42: 141–152.

Braun-Blanquet J. 1928. Pflanzensoziologie; Grundzüge der Vegetationskunde. Biologische Studienbücher VII. Springer, Berlin.

Bråthen KA, Hagberg O. 2004. More Efficient Estimation of Plant Biomass. Journal of Vegetation Science 15: 653–660.

Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. Ecosystems 10: 773–789.

Bråthen KA, Lortie C. 2015. A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Functional Ecology. doi:10.1111/1365-2435.12458

Bråthen KA, Ravolainen VT. 2015. Niche construction by growth forms is as strong a predictor of species diversity as environmental gradients. Journal of Ecology 103: 701–713.

Büntgen U, Hellmann L, Tegel, W, Normand S, Myers-Smith I, Kirdyanov, AV, Nievergelt D, Schweingruber FH. 2015. Temperature-induced recruitment pulses of arctic dwarf shrub communities. Journal of Ecology 103: 489–501.

Cardinale B. 2012. Impacts of biodiversity loss. Science 336: 552–553.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S. 2012. Biodiversity loss and its impact on humanity. Nature 486: 59–67.

Chaneton EJ, Facelli JM. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. Vegetatio 93: 143–155.

Chase J.M, Leibold MA. 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416: 427–430.

Chase JM, Leibold MA, Downing AL, Shurin JB. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81: 2485–2497.

Chytrý M. 2001. Phytosociological data give biased estimates of species richness. Journal of Vegetation Science 12: 441–444.

Cingolani AM, Noy-Meir I, Díaz S. 2013. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological Applications 15: 757–773.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cornell HV, Lawton JH. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. Journal of Animal Ecology 61: 1–12.

Couteron P, Pelissier R. 2004. Additive apportioning of species diversity: towards more sophisticated models and analyses. Oikos 107: 215–221.

Daubenmire R. 1980. Mountain topography and vegetation patterns. Northwest Science 54: 146–152.

Davidar P, Rajagopal B, Mohandass D, Puyravaud J-P, Condit R, Wright SJ, Leigh Jr EG. 2007. The effect of climatic gradients, topographic variation and species traits on the *beta* diversity of rain forest trees. Global Ecology and Biogeography 16: 510–518.

Dickson TL, Foster BL. 2008. The relative importance of the species pool, productivity and disturbance in regulating grassland plant species richness: a field experiment. Journal of Ecology 96: 937–946.

Dickson TL, Foster BL. 2011. Fertilization decreases plant biodiversity even when light is not limiting. Ecology Letters 14: 380–388.

Einarsson MÁ. 1976. Veðurfar á Íslandi. Reykjavík: Iðunn: 150.

Erlendsson E, Edwards KJ, Buckland PC. 2009. Vegetational response to human colonisation of the coastal and volcanic environments of Ketilsstaðir, southern Iceland. Quaternary Research 72: 174–187.

Eskelinen A, Oksanen J. 2006. Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. Journal of Vegetation Science 17: 245–254.

Eskelinen A, Stark S, Männistö M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. Oecologia 161: 113–23.

Evans BM, Walker DA, Benson CS, Nordstrand EA, Petersen GW. 1989. Spatial interrelationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska. Oikos 12: 270–278.

Foster BL. 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4: 530–535.

Foster BL, Dickson TL, Murphy CA, Karel IS, Smith VH. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. Journal of Ecology 92: 435–449.

Franklin AB, Noon BR, George TL. 2002. What is habitat fragmentation? Studies in Avian Biology 25: 20–29.

Fremstad E. 1997. Vegetasjonstyper i Norge: 1–279.

Golodets C, Kigel J, Sternberg M. 2011. Plant diversity partitioning in grazed Mediterranean grassland at multiple spatial and temporal scales. Journal of Applied Ecology 48: 1260–1268.

Graham CH, Moritz C, Williams SE. 2006. Habitat history improves prediction of biodiversity in rainforest fauna. Proceedings of the National Academy of Sciences of the United States of America 103: 632–636.

Grime JP. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344–347.

Hédl R. 2007. Is sampling subjectivity a distorting factor in surveys for vegetation diversity? Folia Geobotanica 42: 1991–1998.

Hedlund K, Regina IS, Van der Putten WH, Leps J, Diaz T, Korthals GW, Lavorel S, Brown VK, Gormsen D, Mortimer SR, Rodríguez BC, Roy J, Smilauer P, Smilauerová M, Van Dijk C. 2003. Plant species diversity, plant biomass and responses of the soil community on abandoned land across Europe: idiosyncracy or above-belowground time lags. Oikos 103: 45–58.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.

Hoffmann S, Hoffmann A. 2008. Is there a “true” diversity? Ecological Economics 65: 213–215.

Huston MA. 1979. A general hypothesis of species diversity. The American Naturalist 113: 81–101.

Huston MA. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393–401.

Jackson HB, Fahrig L. 2014. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24: 52–63.

Jóhannesson H, Sæmundsson K. 2009. Geological Map of Iceland - 1: 600 000. Icelandic Institute of Natural History.

Jónsdóttir IS. 1984. Effects of grazing on the vegetation on Audkúluheidi heathland, Northern Iceland. Nátúrufrædingurinn 53: 19-40.

Jost L. 2006. Entropy and diversity. Oikos 113: 363–375.

Jost L. 2007. Partitioning diversity into independent *alpha* and *beta* components. Ecology 88: 2427–2439.

Kenkel NC, Juhász-Nagy P, Podani J. 1989. On sampling procedures in population and community ecology. Vegetatio 83: 195–207.

Kristinsson H. 1995. Post-settlement history of Icelandic forests. Icelandic Agricultural Science 9: 31–35.

Kristinsson H. 2010. Flóra Íslands (The Flora of Iceland). Mál og menning, Reykjavík.

Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5–13.

Laycock W. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. Journal of Range Management 44: 427–433.

Legendre P, Gauthier O. 2014. Statistical methods for temporal and space-time analysis of community composition data. Proceedings of the Royal Society B 281: 20132728.

Lenoir J, Gégout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Grytnes J-A, Virtanen R, Svenning J-C. 2010. Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. PloS One 5: e15734. doi:10.1371/journal.pone.0015734

Levin SA. 1992. The problem of pattern and scale in ecology: The Robert H . MacArthur Award Lecture. Ecology 73: 1943–1967.

Lid J, Lid DT. 2005. Norsk flora. Det Norske Samlaget.

Loehle C. 2004. Challenges of ecological complexity. Ecological Complexity 1: 3–6.

MacArthur R, Wilson EO. 1967. The theory of island biogeography. Princeton University Press.

Michalet R, Maalouf J-P, Choler P, Clément B, Rosebery D, Royer J-M, Schöb C, Lortie CJ. 2014. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. Ecography 37: 1-11

Milchunas DG, Sala OE, Lauenroth WK. 1988. A Generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132: 87–106.

Miller AE, Bowman WD. 2002. Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species : do species partition by nitrogen form ? Oecologia 130: 609–616.

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001. What is the observed relationship between species richness and productivity? Ecology 82: 2381–2396.

Mysterud A. 2000. Diet overlap among ruminants in Fennoscandia. Oecologia 124: 130–137.

Normand S, Vormisto J, Svenning JC, Grández C, Balslev H. 2006. Geographical and environmental controls of palm *beta* diversity in paleo-riverine terrace forests in Amazonian Peru. Plant Ecology 186: 161–176.

Norðdahl H, Ingólfsson Ó, Pétursson HG, Hallsdóttir M. 2008. Late Weichselian and Holocene environmental history of Iceland. Jökull 58: 343-364.

Olff H, Ritchie ME. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13: 261–265.

Olofsson J. 2006. Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. Journal of Ecology 94: 431–440.

Ostendorf B, Reynolds JF. 1998. A model of arctic tundra vegetation derived from topographic gradients. Landscape Ecology 13: 187–201.

Pärtel M, Zobel M. 2007. Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. Journal of Ecology 95: 90–94.

Pärtel M, Zobel M, Liira J, Zobel K. 2000. Species richness limitations in productive and oligotrophic communities. Oikos 90: 191–193.

Proulx M, Mazumder A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79: 2581–2592.

Purvis A, Hector A. 2000. Getting the measure of biodiversity. Nature 405: 212–219.

Qian H. 2009. *Beta* diversity in relation to dispersal ability for vascular plants in North America. Global Ecology and Biogeography 18: 327–332.

Ransijn J, Kepfer-Rojas S, Verheyen K, Riis-Nielsen T, Schmidt IK. 2015. Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. Journal of Vegetation Science 26: 254–266.

Ravolainen VT, Yoccoz NG, Bråthen KA., Ims RA, Iversen M, González VT. 2010. Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. Ecosystems 13: 157–170.

Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. Science 235: 167–171.

Ricklefs RE. 2008. Disintegration of the ecological community. The American Naturalist 172: 741–50.

Sala OE. 2000. Global Biodiversity Scenarios for the Year 2100. Science 287: 1770–1774.

Schmid B, Balvanera P, Cardinale BJ, Godbold J, Pfisterer AB, Raffaelli D, Solan M, Srivastava DS. 2009. Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (EDS), Biodiversity, ecosystem functioning, and human wellbeing - an ecological and economic perspective (pp 14–29). Oxford University Press.

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift D. M. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789–795+798–799.

Shannon C. 1948. A mathematical theory of communication. The Bell System Technical Journal 27: 379–423.

Shea K, Roxburgh SH, Rauschert ESJ. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology Letters 7: 491–508.

Shrader-Frechette K, McCoy ED. 1994. Applied ecology and the logic of case studies. Philosophy of Science 61:228–249.

Simpson E. 1949. Measurement of diversity. Nature 163: 688.

Speed JDM, Austrheim G, Mysterud A. 2013. The response of plant diversity to grazing varies along an elevational gradient. Journal of Ecology 101: 1225–1236.

Speed JDM, Martinsen V, Mysterud A, Mulder J, Holand Ø, Austrheim G. 2014. Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem. Ecosystems 17: 1138–1150.

Steindórsson S. 1964. Gróður á Íslandi (Vegetation on Iceland). Almenna bókafélagið.

Svensson JR, Lindegarth M, Jonsson PR, Pavia H. 2012. Disturbance-diversity models: what do they really predict and how are they tested? Proceedings of the Royal Society B 279: 2163–2170.

Taylor DR, Aarssen LW, Loehle C. 1990. On the relationship between r/K selection and environmental carrying capacity: A new habitat templet for plant life history strategies. Oikos 58: 239–250.

The Council of the European Communities. 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities 206: 7–50.

Thórhallsdóttir THE. 1996. Áhrif búsetu á landið. In: Grímsdóttir GÁ (ED), Umlandnám á Íslandi — fjórtán erindi (pp. 149–170). Vísindafélag Íslendinga, Reykjavík.

Tilman D. 1987. The importance of the mechanisms of interspecific competition. The American Naturalist 129: 769–774.

Tilman D, Lehman CL, Thomson KT. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences of the United States of America 94: 1857–1861.

Tuomisto H. 2010a. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164: 853–860.

Tuomisto H. 2010b. A diversity of *beta* diversities: straightening up a concept gone awry. Part 1. Defining *beta* diversity as a function of *alpha* and *gamma* diversity. Ecography 33: 2–22.

Tuomisto H. 2010c. A diversity of *beta* diversities: straightening up a concept gone awry. Part 2. Quantifying *beta* diversity and related phenomena. Ecography 33: 23–45.

Tuomisto H. 2013. Defining, measuring, and partitioning species diversity. In: Levin SA (ED), Encyclopedia of Biodiversity (pp. 434–446). Elsevier Inc., Waltham MA-Academic Press.

Van der Wal R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114: 177–186.

Veech JA, Summerville KS, Crist TO, Gering JC. 2002. The additive partitioning of species diversity: recent revival of an old idea. Oikos 99: 3–9.

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257–300.

Whittaker RH. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279–338.

Whittaker RH. 1972. Evolution and measurement of species diversity. Taxon 21(2/3): 213–251.

Whittaker RH, Levin SA, Root RB. 1973. Niche, habitat, and ecotope. The American Naturalist 107: 321–338.

Whittaker RJ, Heegaard E. 2003. What is the observed relationship between species richness and productivity? comment. Ecology 84: 3384–3390.

Wiens JA. 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.

Xiao S, Zobel M, Szava-Kovats R, Pärtel M. 2010. The effects of species pool, dispersal and competition on the diversity-productivity relationship. Global Ecology and Biogeography 19: 343–351.

Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution 16: 446–453.

Zobel M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12: 266–269.

Zobel K, Liira J. 1997. A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities. Oikos 80: 325–332.

Zobel M, Pärtel M. 2008. What determines the relationship between plant diversity and habitat productivity? Global Ecology and Biogeography 17: 679–684.

PAPER I

Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities

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- Conceived of or designed study: VTR, LES, KAB
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- Analyzed the data: MAM, VTR, NGY, KAB
- Wrote the paper: MAM, VTR, LES, NGY, ISJ, KAB

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Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities

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ABSTRACT

In ecology, expert knowledge on habitat characteristics is often used to define sampling units such as study sites. Ecologists are especially prone to such approaches when prior sampling frames are not accessible. Here we ask to what extent can different approaches to the definition of sampling units influence the conclusions that are drawn from an ecological study? We do this by comparing a formal versus a subjective definition of sampling units within a study design which is based on well-articulated objectives and proper methodology. Both approaches are applied to tundra plant communities in mesic and snowbed habitats. For the formal approach, sampling units were first defined for each habitat in concave terrain of suitable slope using GIS. In the field, these units were only accepted as the targeted habitats if additional criteria for vegetation cover were fulfilled. For the subjective approach, sampling units were defined visually in the field, based on typical plant communities of mesic and snowbed habitats. For each approach, we collected information about plant community characteristics within a total of 11 mesic and seven snowbed units distributed between two herding districts of contrasting reindeer density. Results from the two approaches differed significantly in several plant community characteristics in both mesic and snowbed habitats. Furthermore, differences between the two approaches were not consistent because their magnitude and direction differed both between the two habitats and the two reindeer herding districts. Consequently, we could draw different conclusions on how plant diversity and relative abundance of functional groups are differentiated between the two habitats depending on the approach used. We therefore challenge ecologists to formalize the expert knowledge applied to define sampling units through a set of well-articulated rules, rather than applying it subjectively. We see this as instrumental for progress in ecology as only rules based on expert knowledge are transparent and lead to results reproducible by other ecologists.

Subjects Biodiversity, Ecology, Plant Science
Keywords Sampling design, Expert knowledge, Formal rules, Sampling frame, Snowbed habitat, Mesic habitat

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INTRODUCTION

Sampling in ecology can be challenging. Ecological systems are characterized by complexity (*Loehle, 2004*) about which there is a paucity of information (*Carpenter, 2002*). Hence, ecological sampling is often accompanied by unknown characteristics that may unintentionally cause estimates to be dependent on the sampling designs, even to the extent that they "beget conclusions", as was shown for the impact of the Exxon Valdez oil spill (*Peterson et al., 2001*; *Peterson et al., 2002*). The bases for achieving unbiased estimates are study- or sampling designs that include well-articulated objectives along with proper methodology (*Olsen et al., 1999*; *Yoccoz, Nichols & Boulinier, 2001*; *Albert et al., 2010*). In addition, sampling designs need to be transparent, enabling others to repeat the study. Accordingly, ecologists have been encouraged to use formal approaches (*Legendre et al., 2002*; *Edwards et al., 2005*; *Edwards et al., 2006*; *Albert et al., 2010*). However, whilst sources of bias and a call for formal rules in sampling designs have received attention, the seemingly simple task of defining a sampling unit, such as a study site, also merits thorough consideration, especially in community ecology. Indeed, the definition of sampling units is often a task that demands expert knowledge. Expert knowledge can be applied in such a way that sampling units are formally defined but in ecology, expert knowledge implies often a subjective definition of sampling units before data collection is initiated (*Whittaker, Levin & Root, 1973*; *Kenkel, Juhász-Nagy & Podani, 1989*; *Franklin, Noon & George, 2002*; *Loehle, 2004*; *McBride & Burgman, 2012*).

In situations where sampling units are not clearly defined, the availability of relevant sampling units is not known before entering the field, i.e., there is no well-defined sampling frame and in its vacancy, a subjective definition of sampling units is applied in order to guide sampling to ecological units that are determined to be suitable in the field. In principle, the selection of any subjectively defined sampling unit can never be sufficiently articulated as to enable other researchers to repeat the study, or to allow generalizations of results to a specific target population (in a statistical sense) (*Olsen et al., 1999*; *Schreuder, Gregoire & Weyer, 2001*). Moreover, in phytosociological studies it has been documented that individual preferences in selecting sampling units that were defined subjectively can lead to biased estimates (*Chytrý, 2001*; *Botta-Dukát et al., 2007*; *Hédl, 2007*). The criticism of using a subjective definition of sampling units is both theoretically and empirically based, but it may merely reflect a study-specific bias between subjective and more formal approaches. Therefore, in this study we want to compare a subjective *versus* a formal definition of sampling units in the same study system in order to assess whether subjective definition merely introduces bias, overstating findings, or if the way of defining sampling units even begets conclusions.

Studies that have compared formal *versus* subjective sampling have investigated sampling units based on existing geographical data (e.g., *Edwards et al., 2006*; *Hédl, 2007*; *Michalcová et al., 2011*). A formal *a priori* definition of sampling unit criteria could therefore be done before sampling was initiated. However, ecologists might often not have access to such data which is especially the case when the spatial extent of sampling units is smaller than the spatial resolution of previously existing geographical data (*Roleček et al.,* *2007*). As a way of making the definition of units more transparent in such situations, a few studies used formal criteria for suitable sampling units that are defined *a priori* to the field sampling (e.g., *Ravolainen et al., 2010*).

Habitats are perhaps some of the most difficult sampling units to define (*Whittaker, Levin & Root, 1973*; *Franklin, Noon & George, 2002*), but are central to many conservation programs such as the "European council directive on the conservation of natural habitats and of wild fauna and flora" (FFH) (*The Council of the European Communities, 1992*) or the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (*IUCN, 2013*). Despite the acknowledged importance of habitats, definitions differ greatly among conservation programs worldwide. Whereas some conservation initiatives rely on formal definitions of habitat criteria (*Jeffers, 1998*; *Jongman et al., 2006*), others rely on a subjective definition of habitats in the field (*Jennings et al., 2009*). In this paper, we focus on habitats and address the question of whether subjective or formal definitions of sampling units lead to different estimates of habitat properties. We therefore compared a formal approach, where the final selection of these habitats involved an *a priori* definition of sampling units, to an approach involving only a subjective definition (*sensu Gilbert, 1987*).

For both approaches we aimed at two habitats typical for tundra. These habitats are characterized by their difference in growing conditions and are found in sloping, concave terrain. Here, slopes of intermediate steepness provide intermediate moisture conditions (mesic habitats) and gently inclined slopes have wetter conditions combined with a long lasting snow cover (snowbed habitats) (*Fremstad, 1997*). For the formal approach of defining sampling units, we used explicit criteria of the aforementioned habitat terrain and a terrain model in order to extract a list of potential sampling units. Because we expected that some of these would not be suitable for sampling (e.g., because of boulder fields), we pre-defined additional habitat criteria to be applied in the field. For the subjective approach of defining sampling units, habitats were solely subjectively selected in the field. Both approaches were applied within the same sampling design that ensured balanced sampling with respect to major ecological gradients.

The research questions, i.e., what are the plant community characteristics that describe mesic and snowbed habitats, and the measurement of plant community characteristics, were the same in both approaches. For all sampling units, estimates of standing crop of the most abundant plant species and plant functional groups were assessed as well as within plant community diversity. Finally, to evaluate whether different approaches to defining sampling units lead to different estimates of habitat properties, we tested the effect of using formal *versus* subjective definition of sampling units on the estimates of these plant community characteristics.

MATERIALS AND METHODS

Ecosystem characteristics

The field sampling for the current study was conducted during peak growing season between 20th and 30th of July 2011 on Varanger Peninsula, the north-eastern part of Finnmark County in northern Norway (Fig. 1A). The Varanger Peninsula is delineated

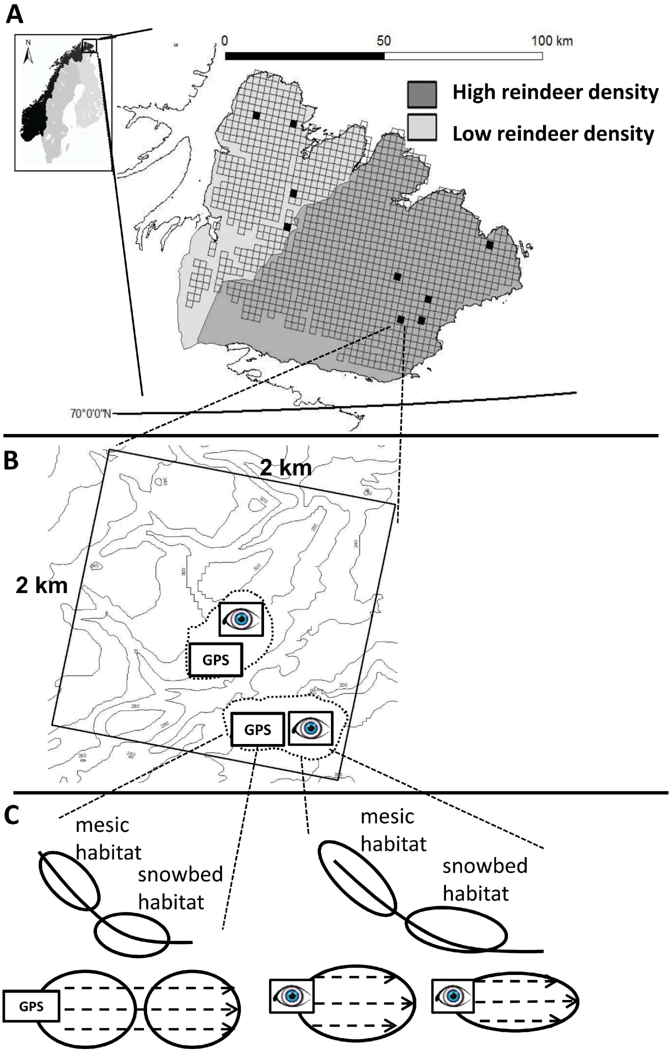

Figure 1 The figure represents the hierarchical nestedness of the sampling design. (A) The figure shows the geographical location of the sampling region (Varanger Peninsula, northern Norway) and nestedness of the sampling design. The shades of gray delimit the districts of contrasting reindeer density. Open squares show the raster of 2 × 2 km landscape areas where major roads, power lines, glaciers and large water bodies have been omitted. Black squares correspond to landscape areas that adhered to all other delimitations in our design (see Materials and Methods section for details). (B) One landscape area contained up to two study areas (dashed line) which inherited a pair of formally (GPS) and subjectively (eye) defined sampling units. (C) Each sampling unit contained both a mesic and a snowbed habitat. The recording of vegetation characteristics within each habitat was conducted along transects (dashed lines within habitats).

by the Barents Sea towards the north and birch forests towards the south. Sandstone, sandstone intermingled with schist, and sandstone intermingled with schist and calcareous bedrock are among the most common geological parental materials (The Geological survey of Norway; www.ngu.no). The topography is characterized by a mixture of plateaus and gently sloping hills (maximum height of approximately 500 m) that are intersected by river valleys. The plateaus build a border with steep slopes towards the Barents Sea. During the growing season (July to August) average (monthly) precipitation is 47.7 mm (range 38–55 mm) and temperature is 8.7 °C (range 6.2–10.5 °C) (30 year averages from 1960 to 1990, Norwegian Meteorological Institute, www.met.no).

We conducted our study in the low alpine zone. The vegetation of the low alpine zone in this region is generally classified as low shrub tundra (*Walker et al., 2005*) with mountain birch *(Betula pubescens* Ehrh.) forming the tree line (*Oksanen & Virtanen, 1995*). Topography affecting snow accumulation and moisture conditions creates habitats that are differentiated into exposed ridges, and steep and gentle parts of slopes, creating a sequence from xeric to mesic and very moist conditions with increasing duration of snow cover (*Fremstad, 1997*). These habitat characteristics give rise to distinct vegetation types such as ridge, mesic and snowbed vegetation (*Fremstad, 1997*). In this study we targeted mesic and snowbed habitats. Commonly occurring plant species in mesic habitats on the Varanger Peninsula include tall stature forbs (e.g., *Alchemilla* spp., *Geranium sylvaticum* L., *Ranunculus acris* L., *Rhodiola rosea* L.) in combination with grasses (e.g., *Phleum alpinum* L., *Poa pratense* ssp. *alpigena* (Fr.) Hiit., *Festuca rubra* L.). Snowbed habitats are characterized by prostrate *Salix* species (*Salix herbacea* L.) in combination with other grasses (e.g., *Festuca rubra* L., *Poa alpina* L.) and forbs (e.g., *Cerastium sp.*) of lower stature. Mosses such as *Dicranum* spp. or *Polytrichum* spp. are also prevalent here.

Semi-domesticated reindeer (*Rangifer tarandus* L.) that are managed by indigenous Sami people are the most common large herbivores in eastern Finnmark. In summer, reindeer herds are kept in the coastal mountains in large districts, which range in area from about 300 to 4000 km^2, with most reindeer migrating inland during winter. Densities of reindeer have increased during the past two decades in some of these summer grazing districts, whilst remaining constant in others (see Table 2 in *Ravolainen et al., 2010*). This was evident on Varanger Peninsula during the period of our study, with contrasting reindeer densities observed in the two neighboring districts (Fig. 1). Other large herbivores present on Varanger peninsula are moose (*Alces alces* L.) and locally occurring domestic sheep *(Ovis aries* L.). Ptarmigans (*Lagopus lagopus* L. and *Lagopus muta* Montin), Norwegian lemming (*Lemmus lemmus* L.), root vole (*Microtus oeconomus* Pallas) and grey-sided vole (*Myodes rufocanus* Sund.) are also found in the area (*Henden et al., 2011*).

Sampling design

We employed a hierarchical, nested sampling design. Our protocol for selecting sampling units that corresponded to the habitats of interest involved several levels of selection (Fig. 1). Using the Varanger Peninsula as the sampling region (Fig. 1A) we covered both districts of contrasting reindeer density. We used information retrieved from a digital elevation model (DEM) to locate landscape areas that had potential sampling units representing the habitats of interest: Using GIS (ESRI ArcGIS with ArcMap. Version 8.3.0) we placed a raster of 2 × 2 km landscape areas over a 25 × 25 m pixel DEM (produced by Norwegian Mapping Authorities on the basis of elevation contour lines) covering the entire peninsula (Fig. 1A). Potential sampling units needed to have at least two 25 × 25 m neighboring pixels of concave topography with a mean slope between 5 °and 30 °. We restricted sampling to units that were a minimum distance of 500 m from birch forests and to an altitude of below 350 m above sea level in order to stay within the low alpine tundra. Finally we avoided lakes, glaciers, major roads and power lines, and only considered units that were within a one day's walking distance from a road in order to be accessible. We then only selected landscape areas that according to the DEM included at least three potential sampling units that followed these criteria. This limited us to a total of 21 landscape areas over the whole peninsula. Out of time constraints we ultimately sampled nine of these landscape areas, divided between the two reindeer districts and with a good geographic spread (Fig. 1A).

Within each landscape area, the selection of sampling units was based on two different approaches of defining them (Fig. 1B). In the first approach (formal approach), we applied expert knowledge by defining *a priori* criteria in two steps. First, we defined topographical criteria to locate habitats in GIS (as described above). However, the spatial resolution of our DEM was too coarse for an *a priori* distinction of the two target habitats. Therefore, secondly, we defined additional criteria to be evaluated in the field. Here, the sampling unit had to show characteristics indicating both target habitats (i.e., mesic and snowbed) to be present. This criterion corresponded to a visible shift in plant species composition. In addition, the visually estimated vegetation cover had to be higher than 75%, and the habitat's grain size had to be large enough to include a minimum of two transects for vegetation measurements (with at least one transect having a length of 10 m and every transect being 5 m apart; see more details below). If a potential sampling unit failed to meet any of these criteria, it was discarded and the next most accessible potential sampling unit was visited and inspected for possible field analyses. The sampling units of the formal approach correspond to the sampled habitats in *González et al. (2010)* and *Ravolainen et al. (2010)*.

In the second approach (subjective approach), we based the selection of sampling units on a subjective definition as follows. As we entered the landscape areas, we subjectively assessed topography to locate sloping, concave terrain for the habitats of interest. When a typical plant community that either indicated a mesic or a snowbed habitat was found, it was considered as part of a sampling unit and it was analyzed as long as habitat size complied to the additional field criteria used in the formal approach (i.e., a vegetation cover of minimum 75% over a habitat area large enough to include a minimum of two transects, with at least one of them being 10 m long and each transect being horizontally spaced 5 m apart from each other). For both approaches, the final study unit was delineated either by convex areas of heath vegetation or a maximum transect length of 50 m.

Sometimes we sampled two sampling units per approach within one landscape area, in which case the closest set of sampling units, i.e., one from each of the two approaches, were termed "study area" being nested within landscape area (Fig. 1B).

Table 1 The sample sizes are presented for each of the hierarchical levels of the sampling design, for each of the two approaches and their summarized sample size. The formal and the subjective approach share samples at both levels above the level of sampling units.

	Nested hierarchy	Replication of units		
		Formal	Subjective	Total for both approaches
Mesic habitat	Landscape area	9	9	9
	Study area	11	11	11
	Habitats/sampling units	11	11	22
	Transects	30	25	55
	Plots	199	152	351
Snowbed habitat	Landscape area	6	6	6
	Study area	7	7	7
	Habitats/sampling units	7	7	14
	Transects	18	16	34
	Plots	85	103	188

Measurement of plant community characteristics

Within each selected habitat, measurement of plant community characteristics was identical for both approaches, except for the placement of transects. In the formal approach, the starting point of each transect was given by the initial GPS coordinates; in the subjective approach, starting points were chosen subjectively so that transects would cover the longest spatial extent of the targeted habitats (Fig. 1C). For both approaches, each transect was marked with a measuring tape running downslope from the starting point, with 5 m in horizontal distance between transects. Depending on the spatial extent of the habitats, we sampled between 2 and 5 transects with lengths varying from 4 m to 32 m. Thereafter, we recorded plant species abundance using the point intercept method according to *Bråthen & Hagberg (2004)*. A frame of 40 cm × 40 cm with 5 pins of 2 mm diameter attached, one to each of the four frame corners and one to the center (see *Ravolainen et al., 2010*), was placed at fixed intervals of 2 m along the measuring tape. For each placement of the frame (i.e., for each plot), intercepts between pins and above ground vascular plant parts were recorded for each species separately. Species within the frame that were not hit by a pin were recorded with the value of 0.1. Table 1 presents a list of replication of all study units according to the spatial hierarchy of our design.

Response variables for data analyses

We converted point intercept data into biomass (g/plot) using weighted linear regression (*Bråthen & Hagberg, 2004*) and established calibration models (see Table S1 in *Ravolainen et al., 2010*), after which plant community measures were calculated for each plot in the data set. First we calculated three commonly used measures of within community (alpha-) diversity (Gini-Simpson index, Shannon entropy and species richness). Then we calculated biomass of the most dominant species (*Betula nana* L., *Empetrum nigrum* L. Hagerup. and *Vaccinium myrtillus* L.) and biomass of plant functional groups (as in *Bråthen et al.,*

Table 2 **Major plant functional groups and their associated species encountered in mesic and snowbed habitats.** The letters “M” (mesic) and “S” (snowbed) indicate the occurrence of each species within the respective target habitat. The nomenclature follows the Pan Arctic Flora (http://nhm2.uio.no/paf/).

Forbs		**Grasses**	
Alchemilla alpina (M,S)	*Ranunculus acris* (M, S)	*Agrostis mertensii* (M, S)	*Juncus filiformis* (M, S)
Antennaria alpina (M)	*Rhodiola rosea* (M, S)	*Anthoxanthum nipponicum* (M, S)	*Luzula multiflora* (M, S)
Antennaria dioica (M, S)	*Rubus chamaemorus* (M, S)	*Avenella flexuosa* (M, S)	*Luzula spicata* (M, S)
Bartsia alpina (M, S)	*Rumex acetosa* (M, S)	*Calamagrostis neglecta* (M, S)	*Luzula wahlenbergii* (S)
Bistorta vivipara (M, S)	*Sagina saginoides* (S)	*Calamagrostis phragmitoides* (M)	
Caltha palustris (M)	*Saussurea alpina* (M, S)	*Festuca ovina* (M, S)	**Deciduous woody plants**
Chamaepericlymenum suecicum (M)	*Saxifraga cespitosa* (M)	*Festuca rubra* (M, S)	*Arctous alpina* (M)
Campanula rotundifolia (M, S)	*Sibbaldia procumbens* (M, S)	*Phleum alpinum* (M, S)	*Vaccinium uliginosum* (M, S)
Comarum palustre (M)	*Silene acaulis* (M)	*Poa alpina* (M, S)	
Draba glabella (M)	*Solidago virgaurea* (M, S)	*Poa pratensis* (M)	**Evergreen woody plants**
Epilobium anagallidifolium (S)	*Stellaria nemorum* (S)	*Vahlodea atropurpurea* (M)	*Andromeda polifolia* (M)
Epilobium hornemannii (M)	*Taraxacum croceum aggregate* (M, S)		*Dryas octopetala* (M)
Euphrasia frigida (M,S)	*Thalictrum alpinum* (M, S)	**Silica rich grasses**	*Harrimanellahypnoides* (M, S)
Euphrasia wettsteinii (M, S)	*Trientalis europaea* (M, S)	*Deschampsia cespitosa* (M, S)	*Juniperus communis* (M)
Geranium sylvaticum (M, S)	*Trollius europaeus* (M, S)	*Nardus stricta* (M, S)	*Kalmia procumbens* (M, S)
Geum rivale (M)	*Veronica alpina* (M, S)		*Linnaea borealis* (M)
Listera cordata (M)	*Viola biflora* (M, S)	**Sedges/Rushes**	*Orthilia secunda* (M)
Melampyrum sylvaticum (M)	*Viola palustris* (M)	*Carex aquatilis* (S)	*Phyllodoce caerulea* (M)
Omalotheca norvegica (M, S)		*Carex bigelowii* (M, S)	Pyrola minor (M, S)
Omalotheca supina (M, S)	**Prostrate *Salix* species**	*Carex brunnescens* (M)	*Pyrola grandiflora* (M, S)
Oxyria digyna (S)	*Salix herbacea* (M, S)	*Carex canescens* (M, S)	*Vaccinium vitis-idaea* (M, S)
Parnassia palustris (M, S)	*Salix reticulata* (M)	*Carex lachenalii* (M, S)	
Pedicularis lapponica (M, S)		*Carex vaginata* (M, S)	**Dominant plant species**
Pinguicula vulgaris (M)		*Eriophorum angustifolium* (M)	*Betula nana* (M, S)
Potentilla crantzii (M)		*Eriophorum vaginatum* (M)	*Empetrum nigrum* (M, S)
Potentilla erecta (M)		*Juncus arcticus* (S)	*Vaccinium myrtillus* (M, S)

2007). Certain plant functional groups such as hemi-parasites had very low abundance and were therefore merged into the group of forbs (Table 2). Species and plant functional groups differed between the two habitats of interest, reflecting the fact that the mesic and the snowbed habitats were generally different in their species composition.

Statistical analysis

We analyzed the three measures of (within-) community diversity and the biomass of different species and plant functional groups as response variables separately for each habitat type. When fitting linear mixed effect models, the approach to defining sampling units (formal *versus* subjective), the reindeer district (east *versus* west) and their interaction were used as fixed factors in the models. Bedrock type was included as a factor with three levels (sandstone; sandstone intermingled with schist; sandstone intermingled with schist and calcareous rock) and used as a co-variate (Table S2). The landscape areas and the study areas were set as random factors to account for spatial autocorrelation within areas. For some of the response variables we had to exclude study areas from the random effects structure because data existed for one study area per landscape area only. Models that had biomass of dominant plant species or biomass of functional groups as response variable were $\log_e(x+v)$ transformed in order to assure model assumptions, with (v) representing the smallest biomass value of the sampled data in order to avoid negative values for plots with zero abundance. Diversity measures were not transformed. We used standard diagnostics to assess constancy and normality of residuals and controlled for outliers. All models were run using the lme function as part of the nlme package (*Pinheiro et al., 2012*) in R (version 2.12.1; *R Development Team, 2010*). A list of all models, containing Akaike's Information Criterion and test statistics for the used fixed factors, can be found in Tables S3 and S4.

RESULTS

Mesic habitat

The approach to defining sampling units affected almost all estimates of plant community diversity in the mesic habitat (Figs. 2A–2C). The estimates of the diversity indices were in most cases significantly higher in the subjective compared with the formal approach. However, for one of the indices (Gini-Simpson), estimates were only higher in the western district (Fig. 2A).

Estimates of plant functional group biomass and biomass of dominant plant species were significantly different between the two approaches (Fig. 2D). The biomass of forbs was estimated to be consistently higher when using the subjective approach in both districts. However, there were interaction effects between the approach type and the reindeer district. For many response variables, differences between the two approaches were only significant in one of the two districts (prostrate *Salix*, grasses, evergreens, deciduous woody species, *Vaccinium myrtillus*, *Empetrum nigrum* L.). Biomass estimates of other response variables (silica rich grasses and *Betula nana*) were lower in the eastern, but higher in the western district when the subjective approach was used.

Snowbed habitat

The approach to defining sampling units also had significant effects on the diversity estimates for the snowbed habitat (Figs. 3A–3C). For both Shannon entropy and species richness, the subjective approach revealed higher estimates in the eastern but lower estimates in the western district (Figs. 3B and 3C).

Significant differences between the two approaches were also found for the biomass estimates of dominant plant species and of different plant functional groups (Fig. 3D). Similar to the mesic habitat, there were significant interaction effects between the approach to define sampling units and the reindeer district. Biomass estimates of some plant functional groups were only affected by the approach in one of the two districts (forbs, grasses, silica rich grasses). For prostrate *Salix*, we found opposite effects of the approach between the two districts. The biomass was estimated to be significantly lower in the eastern, but significantly higher in the western district when using the subjective approach.

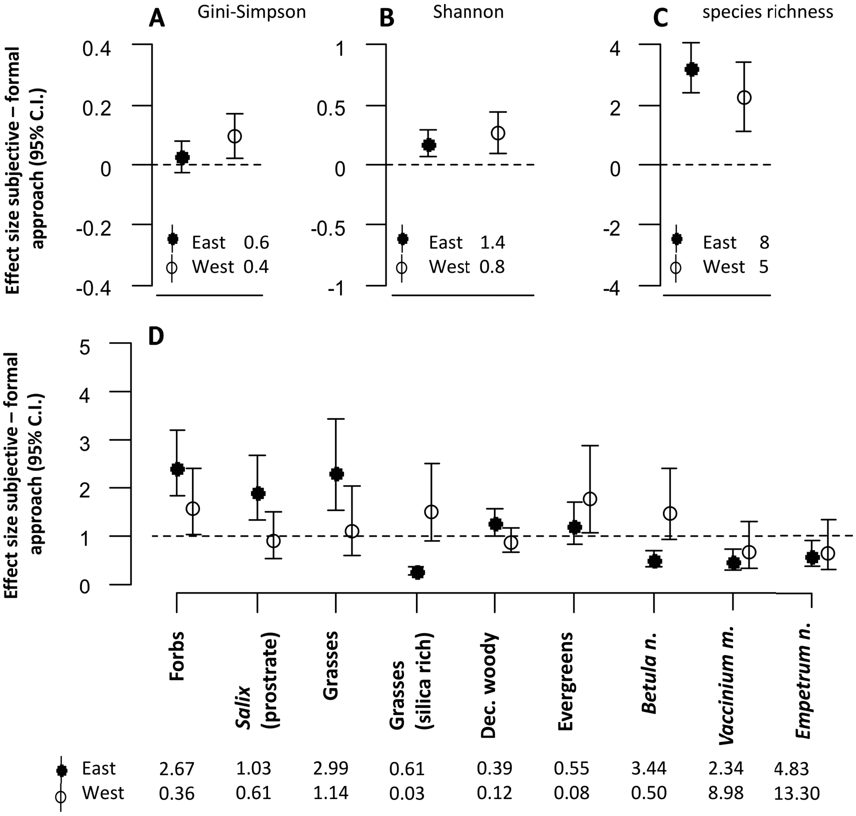

Figure 2 **The figure represents all model estimates for the mesic habitat.** Effect sizes (mean ±95% confidence interval) of the response difference between the subjective and the formal approach of defining sampling units within the mesic habitat are shown for estimates of diversity (A, B, C) and estimates of biomass of dominant plant species and functional groups (D). Effect sizes above or below the dotted line can be interpreted as the subjective approach having higher or lower estimates than the formal approach. Effect sizes of biomass estimates are back transformed values from a logarithmic scale, using the exponential on effect sizes from our model, and may be interpreted as the ratio of the subjective/formal approach. The numbers at the base of each figure represent estimates of the respective diversity index (A, B, C) and the geometric mean of the biomass estimates (D) from the formal approach for each respective response variable. Geometric means can be interpreted as approximate biomass estimates for the respective district.

DISCUSSION

Differences in defining sampling units affect community estimates depending on ecological context

In our study, the sampling approach based on a subjective definition of sampling units revealed significant effects on many of our response variables in comparison to the approach based on formal rules.

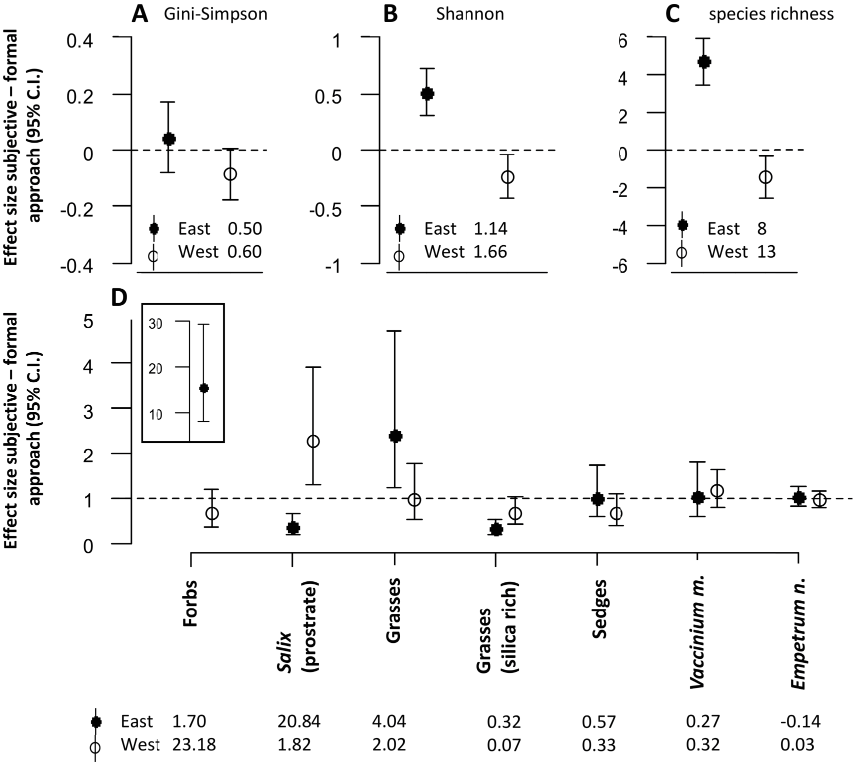

Figure 3 **The figure represents all model estimates for the snowbed habitat.** Effect sizes (mean ± 95% confidence interval) of the response difference between the subjective and the formal approach of defining sampling units within the snowbed habitat are shown for estimates of diversity (A, B, C) and estimates of biomass of dominant plant species and functional groups (D). Effect sizes above or below the dotted line can be interpreted as the subjective approach having higher or lower estimates than the formal approach. Effect sizes of biomass estimates are back transformed values from a logarithmic scale, using the exponential on effect sizes from our model, and may be interpreted as the ratio of the subjective/formal approach. The numbers at the base of each figure represent estimates of the respective diversity index (A, B, C) and the geometric mean of the biomass estimates (D) from the formal approach for each respective response variable. Geometric means can be interpreted as approximate biomass estimates for the respective district, hence the slightly negative value for *Empetrum nigrum* which had very low biomass recordings in the eastern district.

For instance, from our subjective approach our conclusion would be that mesic and snowbed habitats had very low but comparable biomass of silica rich grasses within the two reindeer districts where data were collected. In contrast, our results based on a formal definition of sampling units show a considerably higher abundance of silica rich grasses in the eastern district where also reindeer density is higher. The role of silicate rich plants in plant herbivore interactions (*Vicari & Bazely, 1993*) indicate that the acceptance of one conclusion or the other could lead to very different ecological outcomes and highlight the need for careful consideration in the definition of sampling units in ecological studies.

Hence, the way sampling units were defined begets ecological conclusions to be drawn (*Peterson et al., 2001*).

Previous studies have documented how individual preferences for certain sampling units could result in biased estimates, with for instance higher estimates of species richness compared to probabilistic sampling approaches (*Chytrý, 2001*; *Botta-Dukát et al., 2007*; *Diekmann, Kühne & Isermann, 2007*). However, the subjective selection in this study only rendered constantly higher estimates of species richness in the mesic habitats, while species richness in the snowbed habitats was only increased by the subjective approach in the eastern district. We can only speculate on the reasons for this lack of consistency. For the mesic habitat, the consistently higher estimates of species richness in the subjective approach might be due to the fact that we focused on habitats with many indicator species that can be easily distinguished visually, such as different forb species (see Fig. 2D). Such a preference could also explain the higher estimates of species richness and forbs of snowbeds in the eastern district, where high reindeer abundance might lead to generally low abundance of facilitating plant species such as forbs (*Bråthen et al., 2007*). The lower species richness estimates of the snowbed habitat in the western district might be due to a preference of the sampling units that were visually more strongly impacted by snow, causing a higher probability of selecting for late snowbeds as opposed to earlier snowbeds. Late emergence from snow causes marginal growing conditions for vascular plants and reduced species richness (*Björk & Molau, 2007*). However, the fact that these interpretations would only account for one specific district shows that the bias caused by the subjective definition of sampling units in species richness depends on ecological context. We found similar context dependencies for other diversity indices and for many of the biomass response variables in our study (Figs. 2 and 3).

How to define sampling units to ensure comparability between studies?

Context dependency of the differences in estimates between the two approaches could also have relevance to the comparability of ecological studies. Idiosyncratic results from work on similar study systems are often found in ecological research (*Chase et al., 2000*; *Hedlund et al., 2003*; *Badano & Cavieres, 2006*). Our results indicate that idiosyncratic results within studies or among different studies may have their roots in the way sampling units have been defined. With context dependency being one of the greatest challenges of ecology today (*Wardle et al., 2011*), additional context dependency enforced by the way ecological sampling units are defined will make it even more difficult to tackle this challenge (see e.g., *Franklin, Noon & George, 2002*).

The definition of sampling units in our formal approach involved abiotic characteristics known to represent the habitats in question (e.g., slope and curvature). Such terrain criteria were applied in a way that allowed us to accurately document each sampling unit characteristic, although at the coarse scale of the DEM. In contrast, we did not apply biotic criteria such as the usage of indicator plant species or indicator functional groups in an *a priori* way in this approach, for two reasons. First, plant composition was largely unknown across the potential sampling units of the two habitats, reflecting the absence of vegetation maps (at the grain size of our habitats) for the study area. Secondly, any preference for plant indicators was likely to interfere with the outcome of our research question (*Ewald, 2003*), i.e., what are the plant community characteristics of mesic and snowbed habitats? However, because our focus was on plants, simple biotic criteria of vegetation cover and a visual shift in type of plant community were not considered to interfere with our conclusions. Although the rules applied in the formal approach were quite simple, they were considered relevant to the research questions set. Clearly, more specific research questions would demand more refined formal rules.

For applications in ecology, the reproducibility of studies and the comparison between studies are essential (*Shrader-Frechette & McCoy, 1994*). Therefore, for any true comparison between studies to be made, discrete sampling units such as habitats must be defined in the same way (*Loehle, 2004*). Our study shows that even slight deviations in the definition of sampling units could affect the comparability of results, even within the same study system. That is, only the formal approach to defining sampling units is concomitantly transparent (i.e., by the set of formal rules applied), and produced results that fulfill the premise on which further ecological understanding can be developed. Hence, as sampling procedures that allow reproducibility and comparisons between studies are essential, so are the sampling procedures to allow accumulation of ecological knowledge. Therefore, we believe that the call for formal approaches in study designs (*Legendre et al., 2002*; *Edwards et al., 2005*; *Edwards et al., 2006*; *Albert et al., 2010*) should also be extended to formal approaches to the definition of sampling units.

The application of expert knowledge is a matter of discussion in several fields of ecology. There are a number of studies that address ways of eliciting expert knowledge for decision making in conservation or landscape ecology (*Burgman et al., 2011*; *Martin et al., 2011*; *McBride & Burgman, 2012*), including the use of expert opinion for modeling (*Booker & McNamara, 2004*; *Kuhnert, Martin & Griffiths, 2010*; *Martin et al., 2011*). In landscape ecology, the use of expert knowledge has recently been challenged to adhere to the same scientific rigor as other sampling approaches (*Morgan, 2014*). We believe the application of expert knowledge deserves equal attention in terms of the definition of sampling units, and especially in the definition of habitats, which should be done in a transparent way (*Whittaker, Levin & Root, 1973*; *Franklin, Noon & George, 2002*).

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Virve T. Ravolainen is an employee at the Norwegian Polar Institute and Leif Einar Støvern is an employee at the Norwegian Institute for Forest and Landscape Research. Nigel G. Yoccoz is an Academic Editor for PeerJ.

Author Contributions

- Martin A. Mörsdorf analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Virve T. Ravolainen and Kari Anne Bråthen conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, reviewed drafts of the paper.
- Leif Einar Støvern conceived and designed the experiments, performed the experiments, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Nigel G. Yoccoz analyzed the data, wrote the paper, reviewed drafts of the paper.
- Ingibjörg Svala Jónsdóttir wrote the paper, reviewed drafts of the paper.

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REFERENCES

Albert CH, Yoccoz NG, Edwards Jr TC, Graham CH, Zimmermann NE, Thuiller W. 2010. Sampling in ecology and evolution–bridging the gap between theory and practice. *Ecography* **33**:1028–1037 DOI 10.1111/j.1600-0587.2010.06421.x.

Badano EI, Cavieres LA. 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography* **33**:304–313 DOI 10.1111/j.1365-2699.2005.01384.x.

Björk RG, Molau U. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research* **39**:34–43 DOI 10.1657/1523-0430(2007)39[34:EOASAT]2.0.CO;2.

Booker JM, McNamara LA. 2004. Solving black box computation problems using expert knowledge theory and methods. *Reliability Engineering and System Safety* **85**:331–340 DOI 10.1016/j.ress.2004.03.021.

Botta-Dukát Z, Kovács-Láng E, Rédei T, Kertész M, Garadnai J. 2007. Statistical and biological consequences of preferential sampling in phytosociology: theoretical considerations and a case study. *Folia Geobotanica* **42**:141–152 DOI 10.1007/BF02893880.

Bråthen KA, Hagberg O. 2004. More efficient estimation of plant biomass. *Journal of Vegetation Science* **15**:653–660 DOI 10.1111/j.1654-1103.2004.tb02307.x.

Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* **10**:773–789 DOI 10.1007/s10021-007-9058-3.

Burgman M, Carr A, Godden L, Gregory R, McBride M, Flander L, Maguire L. 2011. Redefining expertise and improving ecological judgment. *Conservation Letters* **4**:81–87 DOI 10.1111/j.1755-263X.2011.00165.x.

Carpenter SR. 2002. Ecological futures: building an ecology of the long now. *Ecology* **83**:2069–2083 DOI 10.1890/0012-9658(2002)083[2069:EFBAEO]2.0.CO;2.

Chase JM, Leibold MA, Downing AL, Shurin JB. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* **81**:2485–2497 DOI 10.1890/0012-9658(2000)081[2485:TEOPHA]2.0.CO;2.

Chytrý M. 2001. Phytosociological data give biased estimates of species richness. *Journal of Vegetation Science* **12**:441–444 DOI 10.1111/j.1654-1103.2001.tb00190.x.

Diekmann M, Kühne A, Isermann M. 2007. Random vs non-random sampling: effects on patterns of species abundance, species richness and vegetation-environment relationships. *Folia Geobotanica* **42**:179–190 DOI 10.1007/BF02893884.

Edwards Jr TC, Cutler DR, Zimmermann NK, Geiser L, Alegria J. 2005. Model-based stratification for enhancing the detection of rare ecological events. *Ecology* **86**:1081–1090 DOI 10.1890/04-0608.

Edwards Jr TC, Cutler DR, Zimmermann NE, Geiser L, Moisen GG. 2006. Effects of sample survey design on the accuracy of classification tree models in species distribution models. *Ecological Modelling* **199**:132–141 DOI 10.1016/j.ecolmodel.2006.05.016.

Ewald J. 2003. A critique for phytosociology. *Journal of Vegetation Science* **14**:291–296 DOI 10.1111/j.1654-1103.2003.tb02154.x.

Franklin AB, Noon BR, George L. 2002. What is habitat fragmentation? *Studies in Avian Biology* **25**:20–29.

Fremstad E. 1997. Vegetasjonstyper i Norge. *NINA Temahefte* **12**:1–279.

Gilbert RO. 1987. *Statistical methods for environmental pollution monitoring.* New York: John Wiley and Sons.

González VT, Bråthen KA, Ravolainen VT, Iversen M, Hagen SB. 2010. Large-scale grazing history effects on arctic-alpine germinable seed banks. *Plant Ecology* **207**:321–331 DOI 10.1007/s11258-009-9676-2.

Hédl R. 2007. Is sampling subjectivity a distorting factor in surveys for vegetation diversity? *Folia Geobotanica* **42**:1991–1998 DOI 10.1007/BF02893885.

Hedlund K, Regina IS, Van der Putten WH, Lepš J, Díaz T, Korthals GW, Lavorel S, Brown VK, Gormsen D, Mortimer SR, Barrueco CR, Roy J, Smilauer P, Smilauerová M, Van Dijk C. 2003. Plant species diversity, plant biomass and responses of the soil community on abandoned land across Europe: idiosyncracy or above-belowground time lags. *Oikos* **103**:45–58 DOI 10.1034/j.1600-0706.2003.12511.x.

Henden J-A, Ims RA, Yoccoz NG, Sørensen R, Killengreen ST. 2011. Population dynamics of tundra voles in relation to configuration of willow thickets in southern arctic tundra. *Polar Biology* **34**:533–540 DOI 10.1007/s00300-010-0908-7.

IUCN. 2013. *The IUCN red list of threatened species*. Version 2013.2. *Available at www.iucnredlist.org* (accessed 21 November 2013).

Jeffers JNR. 1998. The statistical basis of sampling strategies for rivers: an example using river habitat survey. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**:447–454 DOI 10.1002/(SICI)1099-0755(199807/08)8:4<447::AID-AQC288>3.0.CO;2-R.

Jennings MD, Faber-Langendoen D, Loucks OL, Peet RK, Roberts D. 2009. Standards for associations and alliances of the US national vegetation classification. *Ecological Monographs* **79**:173–199 DOI 10.1890/07-1804.1.

Jongman RHG, Bunce RGH, Metzger MJ, Mücher CA, Howard DC, Mateus VL. 2006. Objectives and applications of a statistical environmental stratification of Europe. *Landscape Ecology* **21**:409–419 DOI 10.1007/s10980-005-6428-0.

Kenkel NC, Juhász-Nagy P, Podani J. 1989. On sampling procedures in population and community ecology. *Vegetatio* **83**:195–207 DOI 10.1007/BF00031692.

Kuhnert PM, Martin TG, Griffiths SP. 2010. A guide to eliciting and using expert knowledge in Bayesian ecological models. *Ecology Letters* **13**:900–914 DOI 10.1111/j.1461-0248.2010.01477.x.

Legendre P, Dale MRT, Fortin M-J, Gurevitch J, Hohn M, Myers D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* **25**:601–615 DOI 10.1034/j.1600-0587.2002.250508.x.

Loehle C. 2004. Challenges of ecological complexity. *Ecological Complexity* **1**:3–6 DOI 10.1016/j.ecocom.2003.09.001.

Martin TG, Burgman MA, Fidler F, Kuhnert PM, Low-Choy S, McBride M, Mengersen K. 2011. Eliciting expert knowledge in conservation science. *Conservation Biology* **26**:1–10 DOI 10.1111/j.1523-1739.2011.01806.x.

McBride MF, Burgman MA. 2012. What is expert knowledge, how is such knowledge gathered, and how do we use it to address questions in landscape ecology? In: Perera AH, Drew CA, Johnson CJ, eds. *Expert knowledge and its application in landscape ecology*. New York: Springer Science + Business Media, 11–38.

Michalcová D, Lvoncík S, Chytrý M, Hájek O. 2011. Bias in vegetation databases? A comparison of stratified-random and preferential sampling. *Journal of Vegetation Science* **22**:281–291 DOI 10.1111/j.1654-1103.2010.01249.x.

Morgan MG. 2014. Use (and abuse) of expert elicitation in support of decision making for public policy. *Proceedings of the National Academy of Sciences of the United States of America* **111**:7176–7184 DOI 10.1073/pnas.1319946111.

Oksanen L, Virtanen R. 1995. Topographic, altitudinal and regional patterns in continental and sub-oceanic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica* **153**:1–80.

Olsen AR, Sedransk J, Edwards D, Gotway CA, Liggett W, Rathbun S, Reckhow K, Young L. 1999. Statistical issues for monitoring ecological and natural resources in the United States. *Environmental Monitoring and Assessment* **54**:1–45 DOI 10.1023/A:1005823911258.

Peterson CH, McDonald LL, Green RH, Erickson WP. 2001. Sampling design begets conclusions: the statistical basis for detection of injury to and recovery of shore- line communities after the “Exxon Valdez” oil spill. *Marine Ecology Progress Series* **210**:255–283 DOI 10.3354/meps210255.

Peterson CH, McDonald LL, Green RH, Erickson WP. 2002. The joint consequences of multiple components of statistical sampling designs. *Marine Ecology Progress Series* **231**:309–314 DOI 10.3354/meps231309.

Pinheiro J, Bates D, DebRoy S, Sarkar D. 2012. *nlme: linear and nonlinear mixed effects models*. R package version 3.1-104.

R Development Team. 2010. *R: a language and environment for statistical computing*. Vienna: The R Foundation for Statistical Computing.

Ravolainen VT, Yoccoz NG, Bråthen KA, Ims RA, Iversen M, González VT. 2010. Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. *Ecosystems* **13**:157–170 DOI 10.1007/s10021-009-9308-7.

Roleček J, Chytrý M, Hájek M, Lvončik S, Tichý L. 2007. Sampling design in large-scale vegetation studies: Do not sacrifice ecological thinking to statistical purism! *Folia Geobotanica* **42**:199–208 DOI 10.1007/BF02893886.

Schreuder HT, Gregoire TG, Weyer JP. 2001. For what applications can probability and non-probability sampling be used? *Environmental Monitoring and Assessment* **66**:281–291 DOI 10.1023/A:1006316418865.

Shrader-Frechette K, McCoy ED. 1994. Applied ecology and the logic of case studies. *Philosophy of Science* **61**:228–249 DOI 10.1086/289797.

The Council of the European Communities. 1992. Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities* **206**:7–50 *Available at: http://eur-lex.europa.eu/legalcontent/EN/TXT/?uri=CELEX:31992L0043*.

Vicari M, Bazely DR. 1993. Do grasses fight back? The case for antiherbivore defences. *Trends in Ecology and Evolution* **8**:137–141 DOI 10.1016/0169-5347(93)90026-L.

Walker DA, Raynolds MK, Daniëls FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA, CAVM Team. 2005. The circumpolar Arctic vegetation map. *Journal of Vegetation Science* **16**:267–282 DOI 10.1111/j.1654-1103.2005.tb02365.x.

Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH. 2011. Terrestrial ecosystem responses to species gains and losses. *Science* **332**:1273–1277 DOI 10.1126/science.1197479.

Whittaker RH, Levin SA, Root RB. 1973. Niche, habitat, and ecotope. *The American Naturalist* **107**:321–338 DOI 10.1086/282837.

Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* **16**:446–453 DOI 10.1016/S0169-5347(01)02205-4.

Supplemental Information

Table S1. Number of habitats per district and approach and their corresponding bedrock type. We used information obtained from bedrock maps (The Geological survey of Norway; www.ngu.no), assigning each target habitat with the correct bedrock type after the field session.

				formal approach	**subjective approach**
mesic habitat	**district**	**east**	sandstone	3	2
			sandstone, schist	2	3
			sandstone, schist, calc.	1	1
		west	sandstone	3	2
			sandstone, schist	0	0
			sandstone, schist, calc.	1	2
snowbed habitat	**district**	**east**	sandstone	1	1
			sandstone, schist	2	2
			sandstone, schist, calc.	0	0
		west	sandstone	2	2
			sandstone, schist	0	1
			sandstone, schist, calc.	2	1

Table S2. Replication of plots according to fixed factors of the mixed models. Mixed models contained the approach of defining sampling units, the two districts of different reindeer density and the three bedrock categories as fixed factors.

				formal approach	**subjective approach**
mesic habitat	**district**	**east**	sandstone	58	34
			sandstone, schist	32	39
			sandstone, schist, calc.	25	16
		west	sandstone	46	33
			sandstone, schist	0	0
			sandstone, schist, calc.	16	30
snowbed habitat	**district**	**east**	sandstone	21	20
			sandstone, schist	18	24
			sandstone, schist, calc	0	0
		west	sandstone	26	27
			sandstone, schist	0	16
			sandstone, schist, calc.	20	16

Table S3. Linear Mixed Effect Models for the mesic habitat type. The table shows Akaike´s Information Criterion (AIC) for each model. "Value" indicates effects of factor levels compared to the Intercept which is followed by a t-test statistic.

Response	**Model AIC**	**Fixed Factors**	**Value**	**Std.Error**	**DF**	**t-value**	**p-value**
log (bm forbs + 0.7092)	958.69	Intercept - formal approach in eastern district	1.22	0.32	316	3.86	0.000
		sand, schist, calc.	0.29	0.31	316	0.96	0.340
		sand, schist	-1.16	0.31	316	-3.72	0.000
		subjective approach	0.88	0.14	316	6.15	0.000
		western district	-1.15	0.45	7	-2.55	0.038
		subjective approach in western district	-0.44	0.26	316	-1.69	0.092
log (bm prost. *Salix* + 0.7092)	1098.47	Intercept - formal approach in eastern district	0.56	0.35	316	1.57	0.118
		sand, schist, calc.	0.83	0.36	316	2.28	0.023
		sand, schist	-0.53	0.37	316	-1.41	0.161
		subjective approach	0.64	0.18	316	3.57	0.000
		western district	-0.27	0.50	7	-0.55	0.602
		subjective approach in western district	-0.76	0.32	316	-2.39	0.017
log (bm grasses + 0.1258)	1197.04	Intercept - formal approach in eastern district	1.13	0.45	316	2.55	0.011
		sand, schist, calc.	-0.31	0.44	316	-0.70	0.483
		sand, schist	-1.26	0.45	316	-2.81	0.005
		subjective approach	0.83	0.21	316	4.00	0.000
		western district	-0.90	0.64	7	-1.41	0.202
		subjective approach in western district	-0.73	0.37	316	-1.96	0.051
log (bm grasses silica + 0.1258)	1112.86	Intercept - formal approach in eastern district	-0.31	0.31	316	-1.01	0.312
		sand, schist, calc.	-0.40	0.34	316	-1.19	0.236
		sand, schist	-0.51	0.36	316	-1.43	0.154
		subjective approach	-1.39	0.18	316	-7.62	0.000
		western district	-1.58	0.43	7	-3.66	0.008
		subjective approach in western district	1.79	0.32	316	5.60	0.000
log (bm dec. woody + 0.7092)	806.85	Intercept - formal approach in eastern district	0.10	0.12	316	0.77	0.441
		sand, schist, calc.	0.06	0.15	316	0.42	0.672
		sand, schist	-0.58	0.17	316	-3.51	0.001
		subjective approach	0.23	0.11	316	2.01	0.046
		western district	-0.28	0.17	7	-1.62	0.149
		subjective approach in western district	-0.37	0.19	316	-1.98	0.049
log (bm evergreens + 0.2704)	1106.36	Intercept - formal approach in eastern district	-0.19	0.25	316	-0.79	0.432
		sand, schist, calc.	-0.02	0.28	316	-0.06	0.955
		sand, schist	-0.33	0.31	316	-1.05	0.297
		subjective approach	0.17	0.18	316	0.93	0.352
		western district	-0.85	0.34	7	-2.49	0.042
		subjective approach in western district	0.39	0.31	316	1.27	0.205
log (bm *Betula n.*+ 1.4706)	1051.02	Intercept - formal approach in eastern district	1.59	0.34	314	4.72	0.000
		sand, schist, calc.	-0.32	0.34	314	-0.95	0.345
		sand, schist	0.13	0.38	314	0.35	0.729
		subjective approach	-0.70	0.18	314	-3.92	0.000
		western district	-0.91	0.49	7	-1.88	0.102
		subjective approach in western district	1.09	0.30	314	3.61	0.000
log (bm *Vaccinium m.*+ 0.7092)	1252.04	Intercept - formal approach in eastern district	1.12	0.70	316	1.59	0.112
		sand, schist, calc.	-1.01	0.54	316	-1.89	0.060
		sand, schist	2.63	0.53	316	5.00	0.000
		subjective approach	-0.78	0.22	316	-3.45	0.001
		western district	1.15	1.02	7	1.13	0.296
		subjective approach in western district	0.35	0.42	316	0.83	0.406

log (bm *Empetrum h.*+ 1.5804)	1295.20	Intercept - formal approach in eastern district	1.86	0.71	316	2.61	0.010
		sand, schist, calc.	-0.86	0.57	316	-1.51	0.131
		sand, schist	2.68	0.56	316	4.80	0.000
		subjective approach	-0.57	0.24	316	-2.39	0.018
		western district	0.84	1.04	7	0.81	0.443
		subjective approach in western district	0.12	0.44	316	0.27	0.790
Gini-Simpson Index	-169.07	Intercept - formal approach in eastern district	0.60	0.05	314	12.40	0.000
		sand, schist, calc.	-0.01	0.05	314	-0.16	0.872
		sand, schist	-0.11	0.06	314	-1.93	0.055
		subjective approach	0.03	0.03	314	1.02	0.308
		western district	-0.16	0.07	7	-2.22	0.062
		subjective approach in western district	0.07	0.05	314	1.51	0.133
Shannon Index	368.23	Intercept - formal approach in eastern district	1.41	0.17	316	8.29	0.000
		sand, schist, calc.	-0.05	0.13	316	-0.39	0.699
		sand, schist	-0.83	0.13	316	-6.23	0.000
		subjective approach	0.18	0.06	316	3.09	0.002
		western district	-0.57	0.25	7	-2.30	0.055
		subjective approach in western district	0.09	0.11	316	0.88	0.378
Species Richness	1579.33	Intercept - formal approach in eastern district	7.81	1.24	314	6.30	0.000
		sand, schist, calc.	-0.39	0.91	314	-0.43	0.668
		sand, schist	-3.26	1.02	314	-3.20	0.002
		subjective approach	3.24	0.42	314	7.74	0.000
		western district	-2.41	1.97	9	-1.22	0.253
		subjective approach in western district	-0.96	0.72	314	-1.34	0.180

Table S4. Linear Mixed Effect Models for the snowbed habitat type. The table shows Akaike´s Information Criterion (AIC) for each model. "Value" indicates effects of factor levels compared to the Intercept which is followed by a t-test statistic.

Response	**Model AIC**	**Fixed Factors**	**Value**	**Std.Error**	**DF**	**t-value**	**p-value**
log (bm forbs + 0.1388)	679.46	Intercept - formal approach in eastern district	0.61	2.33	178	0.26	0.794
		sand, schist, calc.	-6.25	0.82	178	-7.60	0.000
		sand, schist	-3.43	0.44	178	-7.73	0.000
		subjective approach	2.73	0.33	178	8.31	0.000
		western district	2.54	2.86	4	0.89	0.425
		subjective approach in western district	-3.15	0.45	178	-7.07	0.000
log (bm prost. *Salix* + 0.7092)	667.86	Intercept - formal approach in eastern district	3.07	0.25	176	12.49	0.000
		sand, schist, calc.	0.27	0.29	176	0.93	0.355
		sand, schist	-0.40	0.24	176	-1.66	0.099
		subjective approach	-1.01	0.30	176	-3.35	0.001
		western district	-2.14	0.34	6	-6.40	0.001
		subjective approach in western district	1.82	0.41	176	4.47	0.000
log (bm grasses + 0.1258)	690.53	Intercept - formal approach in eastern district	1.43	0.85	178	1.68	0.094
		sand, schist, calc.	-0.10	0.74	178	-0.13	0.895
		sand, schist	-0.96	0.43	178	-2.21	0.028
		subjective approach	0.88	0.34	178	2.57	0.011
		western district	-0.66	1.06	4	-0.63	0.563
		subjective approach in western district	-0.93	0.46	178	-2.03	0.044
log (bm grasses silica + 0.1258)	578.58	Intercept - formal approach in eastern district	-0.81	0.24	176	-3.38	0.001
		sand, schist, calc.	-0.19	0.33	176	-0.57	0.568
		sand, schist	0.10	0.24	176	0.43	0.670
		subjective approach	-1.16	0.26	176	-4.46	0.000
		western district	-0.82	0.33	6	-2.45	0.050
		subjective approach in western district	0.76	0.34	176	2.25	0.026
log (bm Sedges + 0.2324)	617.52	Intercept - formal approach in eastern district	-0.22	0.43	178	-0.52	0.601
		sand, schist, calc.	-0.10	0.48	178	-0.21	0.831
		sand, schist	0.56	0.32	178	1.77	0.079
		subjective approach	0.01	0.28	178	0.02	0.982
		western district	-0.35	0.54	4	-0.65	0.553
		subjective approach in western district	-0.42	0.37	178	-1.14	0.256
log (bm *Vaccinium m.*+ 0.7092)	494.60	Intercept - formal approach in eastern district	-0.02	0.50	176	-0.05	0.961
		sand, schist, calc.	0.51	0.48	176	1.06	0.291
		sand, schist	-0.13	0.34	176	-0.38	0.706
		subjective approach	0.03	0.28	176	0.09	0.928
		western district	0.05	0.66	4	0.08	0.942
		subjective approach in western district	0.11	0.33	176	0.34	0.737
log (bm *Empetrum h.*+ 1.5804)	265.37	Intercept - formal approach in eastern district	0.36	0.15	178	2.35	0.020
		sand, schist, calc.	0.21	0.18	178	1.16	0.249
		sand, schist	0.26	0.12	178	2.22	0.028
		subjective approach	0.02	0.10	178	0.23	0.817
		western district	0.11	0.20	4	0.58	0.596
		subjective approach in western district	-0.06	0.14	178	-0.45	0.650

Gini-Simpson Index	1.60	Intercept - formal approach in eastern district	0.50	0.07	176	7.06	0.000
		sand, schist, calc.	-0.24	0.10	176	-2.42	0.017
		sand, schist	-0.02	0.07	176	-0.24	0.812
		subjective approach	0.05	0.06	176	0.72	0.475
		western district	0.09	0.10	4	0.94	0.399
		subjective approach in western district	-0.13	0.08	176	-1.71	0.089
Shannon Index	268.49	Intercept - formal approach in eastern district	1.14	0.47	178	2.44	0.016
		sand, schist, calc.	-1.42	0.26	178	-5.47	0.000
		sand, schist	-0.59	0.14	178	-4.18	0.000
		subjective approach	0.51	0.11	178	4.81	0.000
		western district	0.52	0.58	4	0.90	0.419
		subjective approach in western district	-0.75	0.14	178	-5.19	0.000
Species Richness	916.34	Intercept - formal approach in eastern district	8.26	4.51	178	1.83	0.069
		sand, schist, calc.	-13.95	1.58	178	-8.84	0.000
		sand, schist	-6.06	0.85	178	-7.12	0.000
		subjective approach	4.73	0.63	178	7.51	0.000
		western district	4.64	5.54	4	0.84	0.449
		subjective approach in western district	-6.16	0.86	178	-7.20	0.000

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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(*submitted*)

Authors contributions:

- 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

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

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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.

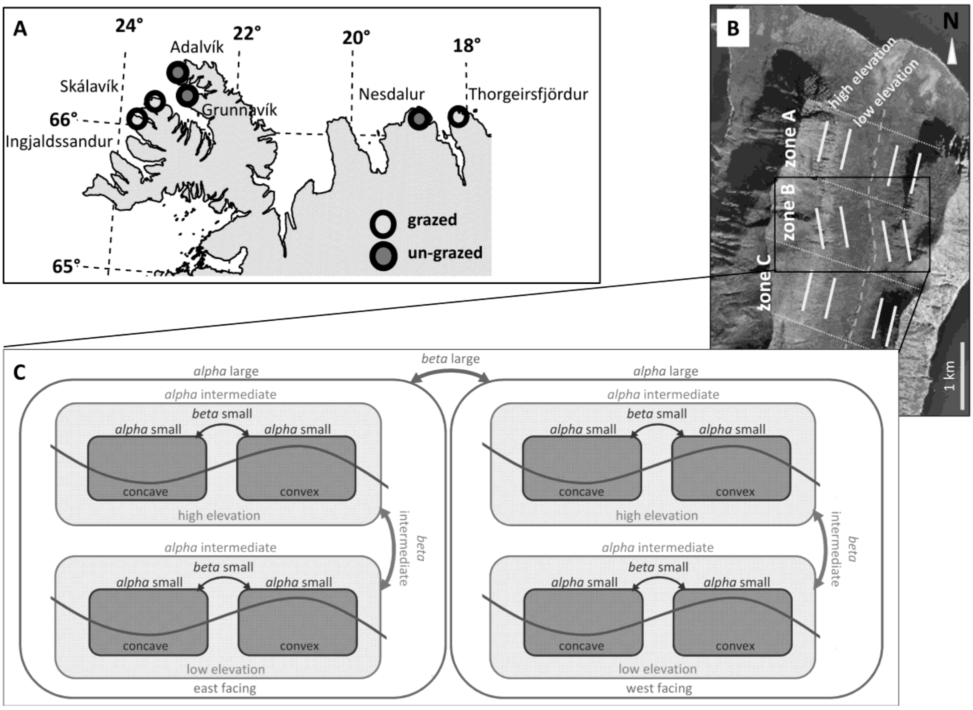

Figure 1. (A) Location of sampling sites in grazed and un-grazed valleys in Iceland. (B) Each valley was split up into three zones (zone A, zone B, zone C) to spread sampling throughout the valley. (C) Within each zone, we covered the major topographical contrasts; landform curvature (small grain size), 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

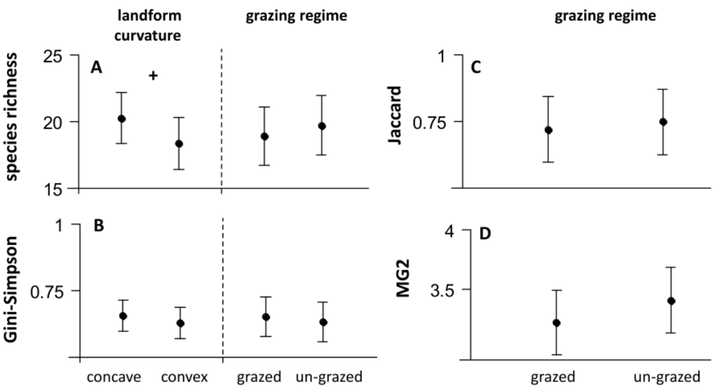

Figure 2. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using a small spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of landform curvature and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity 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.

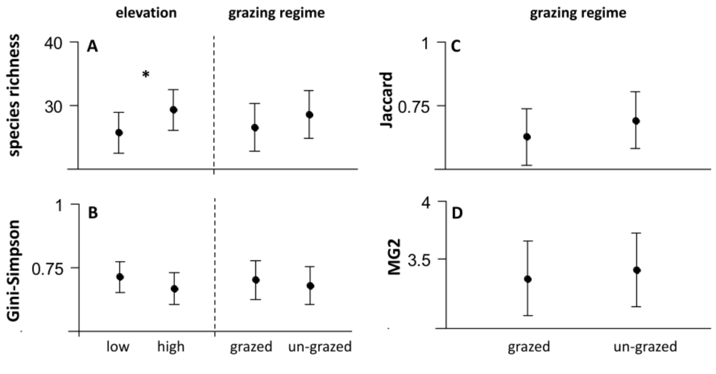

Figure 3. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using an intermediate spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of elevation and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity 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.

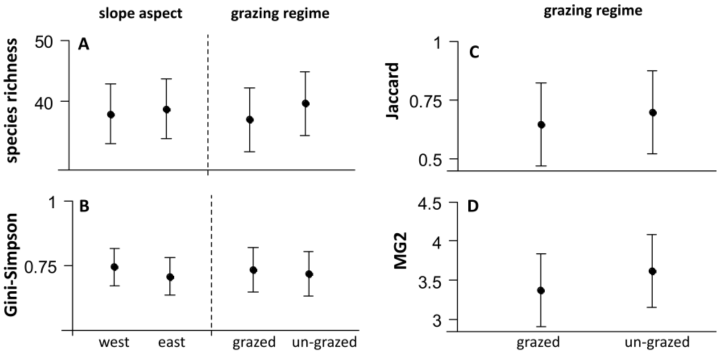

Figure 4. Plant diversity in Icelandic tundra within (alfa) and between (beta) plant communities, using a large spatial grain size. (A, B) Alfa diversity (species richness and Gini-Simpson) is presented given the influence of slope aspect and grazing regime. (C, D) Beta diversity (Jaccard dissimilarity 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

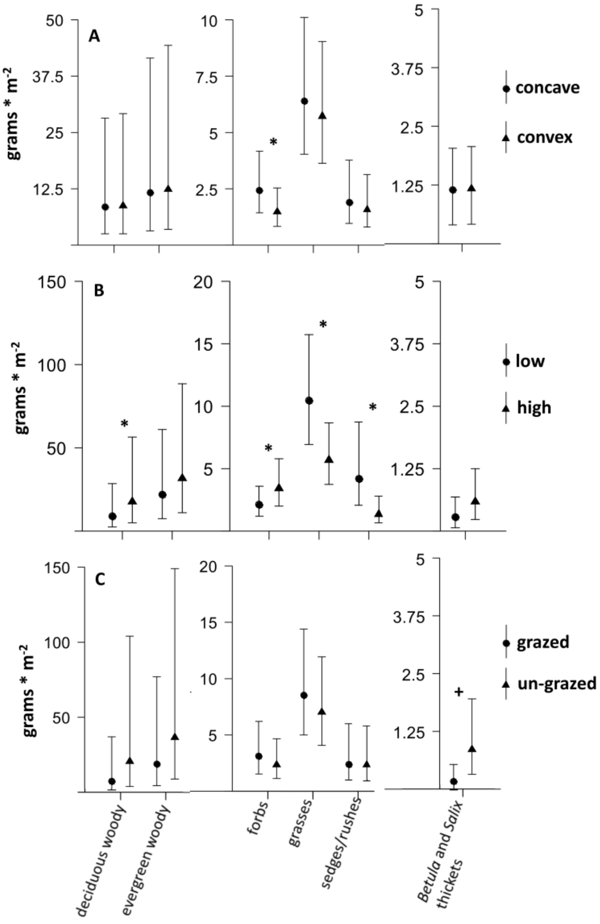

*Figure 5. Model estimates of biomass of plant growth forms in contrasting landforms, elevations and grazing regimes. The symbols represent geometric means (g*m2) that were derived via back transforming model estimates. "*" indicates statistically significant effects on a 5% significance level, whereas "+" 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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References

Adler B, Raff A, Lauenroth K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128: 465–479.

Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of *beta* diversity. Ecology Letters 9: 683–693.

Arnalds O. 2015. The soils of Iceland. Springer Netherlands: Springer Science+Business Media Dordrecht.

Augustine DJ, McNaughton SJ. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of Wildlife Management 62: 1165–1183.

Austrheim G, Eriksson O. 2001. Plant species diversity and grazing in the Scandinavian mountains - patterns and processes at different spatial scales. Ecography 24: 683–695.

Austrheim G, Mysterud A, Pedersen B, Halvorsen R, Hassel K, Evju M. 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. Oikos 117: 837–846.

Bakker ES, Ritchie ME, Olff H, Milchunas DG, Knops JMH. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9: 780–788.

Blakemore LC, Searle PL, Daly BK. 1987. Methods for chemical analysis of soil. New Zealand Soil Bureau Report 80.

Bouahim S, Rhazi L, Amami B, Sahib N, Rhazi M, Waterkeyn A, Zouahri A, Mesleard F, Muller SD, Grillas P. 2010. Impact of grazing on the species richness of plant communities in Mediterranean temporary pools (western Morocco). Comptes Rendus Biologies 333: 670–679.

Bråthen KA, Hagberg O. 2004. More efficient estimation of plant biomass. Journal of Vegetation Science 15: 653–660.

Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. Ecosystems 10: 773–789.

Bråthen KA, Lortie C. 2015. A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Functional Ecology. doi: 10.1111/1365-2435.12458

Bråthen KA, Ravolainen VT. 2015. Niche construction by growth forms is as strong a predictor of species diversity as environmental gradients. Journal of Ecology 103: 701–713.

Brown JL, Simpson IA, Morrison SJL, Adderley WP, Tisdall E, Vésteinsson O. 2012. Shieling areas: Historical grazing pressures and landscape responses in northern Iceland. Human Ecology 40: 81–99.

Büntgen U, Hellmann L, Tegel, W, Normand S, Myers-Smith I, Kirdyanov, AV, Nievergelt D, Schweingruber FH. 2015. Temperature-induced recruitment pulses of arctic dwarf shrub communities. Journal of Ecology 103: 489–501.

CAVM Team. 2003. Circumpolar Arctic Vegetation Map (1:7,500,000 scale). Conservation of arctic flora and fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Chaneton EJ, Facelli JM. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. Vegetatio 93: 143–155.

Cingolani AM, Noy-Meir I, Díaz S. 2013. Grazing effects on rangeland diversity: A synthesis of contemporary models. Ecological Applications 15: 757–773.

Daubenmire R. 1980. Mountain topography and vegetation patterns. Northwest Science 54: 146–152.

Einarsson MÁ. 1976. Veðurfar á Íslandi. Reykjavík: Iðunn: 150.

Erlendsson E, Edwards KJ, Buckland PC. 2009. Vegetational response to human colonisation of the coastal and volcanic environments of Ketilsstaðir, southern Iceland. Quaternary Research 72: 174–187.

Eskelinen A, Oksanen J. 2006. Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. Journal of Vegetation Science 17: 245–254.

Eskelinen A, Stark S, Männistö M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. Oecologia 161: 113–23.

Evans BM, Walker DA, Benson CS, Nordstrand EA, Petersen GW. 1989. Spatial interrelationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska. Oikos 12: 270–278.

Fisk MC, Schmidt SK, Seastedt TR. 1998. Topography patterns of above- and bellowground production and Nitrogen cycling in alpine tundra. Ecology 79: 2253–2266.

Golodets C, Kigel J, Sternberg M. 2011. Plant diversity partitioning in grazed Mediterranean grassland at multiple spatial and temporal scales. Journal of Applied Ecology 48: 1260-1268.

Gough L, Shaver GR, Carroll J, Royer DL, Laundre JA. 2000. Vascular plant species richness in Alaskan arctic tundra: The Importance of Soil pH. Journal of Ecology 88: 54–66.

Huston MA. 1979. A general hypothesis of species diversity. The American Naturalist 113: 81–101.

Jóhannesson H, Sæmundsson K. 2009. Geological Map of Iceland - 1: 600 000. Reykjavík: Icelandic Institute of Natural History (1st edition).

Jonasson S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52: 101–106.

Jónsdóttir IS. 1984. Effects of grazing on the vegetation on Audkúluheidi heathland, Northern Iceland. Nátúrufrædingurinn 53: 19-40.

Jónsdóttir IS, Magnússon B, Gudmundsson J, Elmarsdóttir A, Hjartarson H. 2005. Variable sensitivity of plant communities in Iceland to experimental warming. Global Change Biology 11: 553–563.

Kohyani P, Bossuyt B, Bonte D, Hoffmann M. 2008. Grazing as a management tool in dune grasslands: Evidence of soil and scale dependence of the effect of large herbivores on plant diversity. Biological Conservation 141: 1687–1694.

Körner C. 1995. Alpine plant diversity: a global survey and functional interpretations. - In: Chapin, F. S. III and Körner, C. (eds). Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. Springer: 45-62.

Kristinsson H. 1995. Post-settlement history of Icelandic forests. Icelandic Agricultural Science 9: 31–35.

Lawson IT, Gathorne-Hardy FJ, Church MJ, Newton AJ, Edwards KJ, Dugmore AJ, Einarsson Á. 2007. Environmental impacts of the Norse settlement: palaeoenvironmental data from Mývatnssveit, northern Iceland. Boreas 36: 1–19.

Laycock W. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. Journal of Range Management 44: 427–433.

Levin SA. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology 73: 1943–1967.

Lezama F, Baeza S, Altesor A, Cesa A, Chaneton EJ, Paruelo JM. 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. Journal of Vegetation Science 25: 8–21.

Matsuura T, Suzuki W. 2012. Analysis of topography and vegetation distribution using a digital elevation model: case study of a snowy mountain basin in northeastern Japan. Landscape and Ecological Engineering 9: 143–155.

Milchunas DG, Sala OE, Lauenroth WK. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132: 87-106.

Mörsdorf MA, Ravolainen VT, Støvern LE, Yoccoz NG, Jónsdóttir IS, Bråthen KA. 2015. Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities. PeerJ 3(3): e815.

Mulder CPH. 1999. Vertebrate herbivores and plants in the Arctic and Subarctic: effects on individuals, populations, communities and ecosystems. Perspectives in Plant Ecology, Evolution and Systematics 2: 29–55.

Mysterud A. 2000. Diet overlap among ruminants in Fennoscandia. Oecologia 124: 130–137.

Norðdahl H, Ingólfsson Ó, Pétursson HG, Hallsdóttir M. 2008. Late Weichselian and Holocene environmental history of Iceland. Jökull 58: 343-364.

Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H. 2013. vegan: Community ecology package. R package version 2.0-7.

Olff H, Ritchie ME. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13: 261–265.

Olofsson J. 2006. Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. Journal of Ecology 94: 431–440.

Ostendorf B, Reynolds JF. 1998. A model of arctic tundra vegetation derived from topographic gradients. Landscape Ecology 13: 187–201.

Pinheiro J, Bates B, DebRoy S, Sarkar D. 2004. nlme: Linear and nonlinear mixed effects models. R package 3rd edn.

Proulx M, Mazumder A. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79: 2581–2592.

Ransijn J, Kepfer-Rojas S, Verheyen K, Riis-Nielsen T, Schmidt IK. 2015. Hints for alternative stable states from long-term vegetation dynamics in an unmanaged heathland. Journal of Vegetation Science 26: 254–266.

Ravolainen VT, Yoccoz NG, Bråthen KA, Ims RA, Iversen M, González VT. 2010. Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. Ecosystems 13: 157–170.

Ravolainen VT, Bråthen KA, Yoccoz NG, Nguyen JK, Ims RA. 2014. Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. Journal of Applied Ecology 51: 234–241.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Senft RL, Coughenour MB, Bailey DW., Rittenhouse LR, Sala OE, Swift DM. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789–795+798–799.

Soil Survey Staff. 2011. Soil survey laboratory information manual. Soil survey investigations report No. 45, Version 2.0. R. Burt (ed.). U.S. Department of Agriculture, Natural Resources Conservation Service.

Speed JDM, Austrheim G, Mysterud A. 2013. The response of plant diversity to grazing varies along an elevational gradient. Journal of Ecology 101: 1225–1236.

Streeter R, Dugmore A. 2014. Late-Holocene land surface change in a coupled social–ecological system, southern Iceland: a cross-scale tephrochronology approach. Quaternary Science Reviews 86: 99–114.

Sundqvist MK, Giesler R, Graae BJ, Wallander H, Fogelberg E, Wardle DA. 2011. Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. Oikos 120: 128–142.

Thórhallsdóttir THE. 1996. Áhrif búsetu á landið. In: Grímsdóttir GÁ (ed.) Um Landnám á Íslandi – fjórtán erindi. Reykjavík- Vísindafélag Íslendinga: 149–170.

Unnsteinsdóttir ER, Hersteinsson P. 2009. Surviving north of the natural range: the importance of density independence in determining population size. Journal of Zoology 277: 232–240.

Van der Wal R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114: 177–186.

Vickers K, Erlendsson E, Church MJ, Edwards KJ, Bending J. 2011. 1000 years of environmental change and human impact at Stóra-Mörk, southern Iceland: A multiproxy study of a dynamic and vulnerable landscape. The Holocene 21: 979–995.

Walker DA, Raynolds MK, Daniëls FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA, CAVM Team. 2005. The circumpolar arctic vegetation map. Journal of Vegetation Science 16: 267–282.

Westoby M, Walker B, Noy-Meir I. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42: 266–274.

Wiens JA. 1989. Spatial Scaling in Ecology. Functional Ecology 3: 385–397.

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

Alchemilla alpina - **13.52**

Alchemilla filicaulis **- 13.52***

Alchemilla glomerulan **- 13.52***

Alchemilla wichurae **- 13.52***

Angelica archangelica agg. - **15.34***

Armeria maritima - **6.94***

Bartsia alpina **- 13.52**

Bistorta vivipara - **13.52**

Caltha palustris - **13.52**

Cardaminae pratensis agg. - **13.52***

Cerastium alpinum - **6.94***

Cerastium cerastoides - **6.94**

Cerastium fontanum - **6.94**

Chamaepericlymenum suecicum **- 6.94***

Coeloglossum viridae - **6.94***

Epilobium alsinifolium **- 6.94**

Epilobium palustre - **6.94**

Erigeron borealis - **6.94**

Euphrasia frigida - **6.94**

Gentianopsis detonsa - **6.94***

Geranium sylvaticum - **15.34**

Galium boreale - **6.94**

Galium normanii - **6.94**

Galium verum - **6.94**

Hieracium alpinum agg. - **13.52***

Hieracium thaectolepiun - **13.52***

Listera cordata - **6.94**

Menyanthes trifoliate - **13.52***

Micranthes nivalis - **6.94**

Omalotheca norwegica - **13.52**

Oxyria digyna - **6.94**

Parnassia palustris - **13.52**

Pinguicula vulgaris - **6.94**

Plantago maritima - **6.94**

Limnorchis dilatata - **6.94***

Potentilla cranztii - **13.52**

Pyrola minor - **13.52**

Ranunculus acris - **15.34**

Rhinanthus minor - **13.52**

Rumex acetosa - **13.52**

Saxifraga rosacea - **6.94**

Scorzoneroides autumnalis **- 13.52**

Sibbaldia procumbens - **13.52**

Silene acaulis - **13.52**

Taraxacum officinale - **13.52**

Thalictrum alpinum - **6.94**

Triglochin palustris - **6.94**

Veronica alpina - **6.94**

Viola canina - **6.94**

Viola palustris - **6.94**

Viola riviniana - **6.94**

Grasses

Agrostis capillaris - **9.91**

Agrostis vinealis - **9.91**

Anthoxanthum odoratum - **9.91**

Avenella flexuosa - **6.29**

Calamagrostis neglecta - **9.91**

Deschampsia alpina - **9.91**

Deschampsia cespitosa - **9.91**

Festuca rubra ssp. richardsonii - **6.29**

Festuca vivipara - **6.29**

Hierochloë odorata - **9.91**

Nardus stricta - **6.29**

Phleum alpinum - **9.91**

Poa glauca - **9.91**

Poa pratensis - **9.91**

Trisetum spicatum - **9.91**

sedges and rushes

Carex atrata - **11.62**

Carex bigelowii - **11.62**

Carex canescens - **11.62**

Carex capillaris - **11.62**

Carex chordorrhizza - **11.62**

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

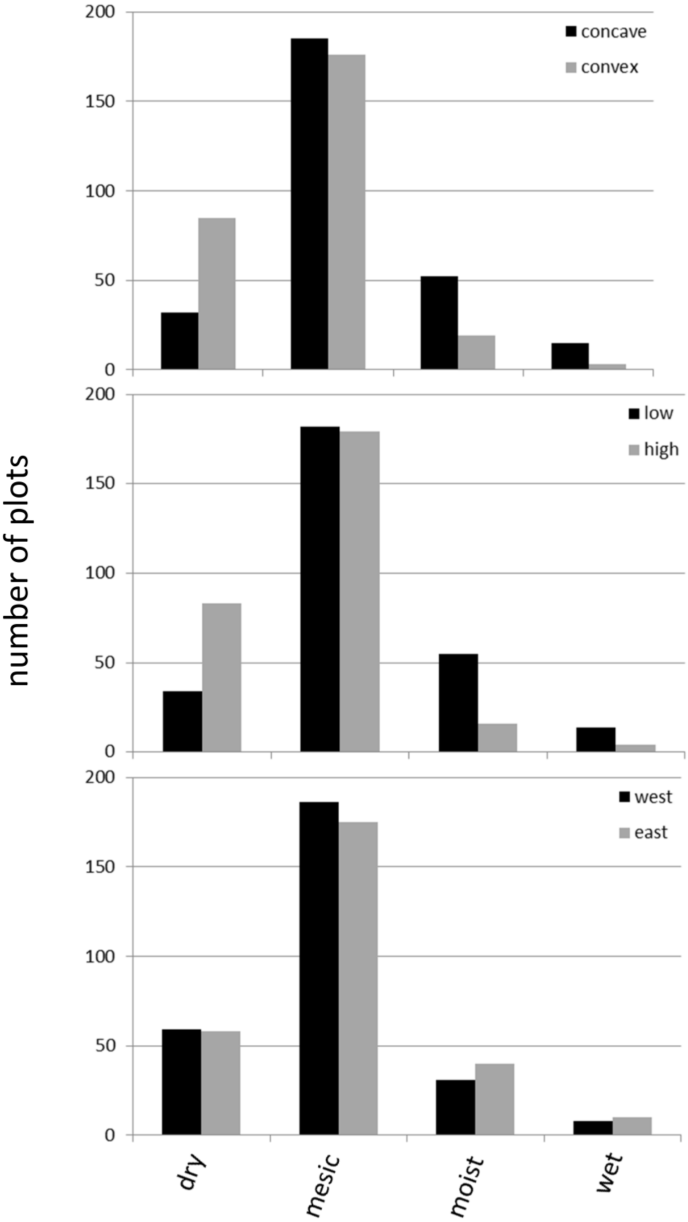
Table S4. Model estimates and effects of landform and grazing on the biomass of selected plant growth forms

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



PAPER III

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

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(*manuscript*)

Authors contributions:

- 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; Olff & 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; Påhlson 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).

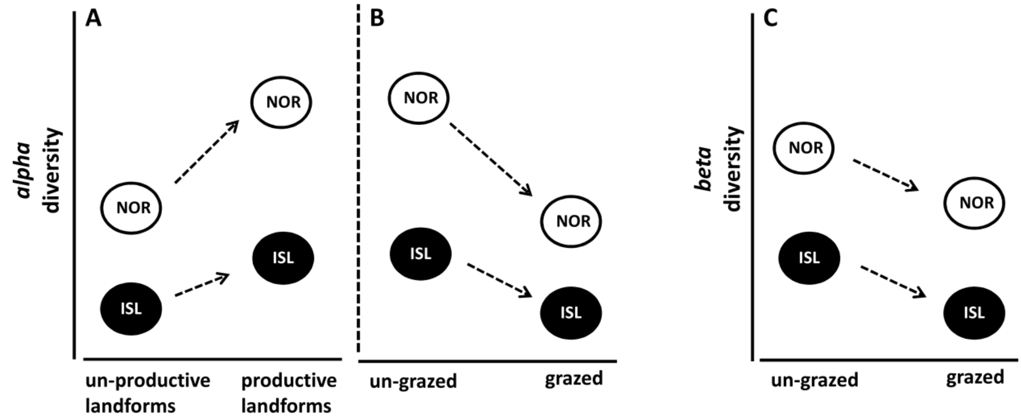

Figure 1.Prior predictions about differences in (A, B) alpha and (C) beta diversity between regions of different species pool size, topographical units of different habitat productivity and contrasting grazing regimes.

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
	Elvevolldalen	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
	Thórgeirsfjördur	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).

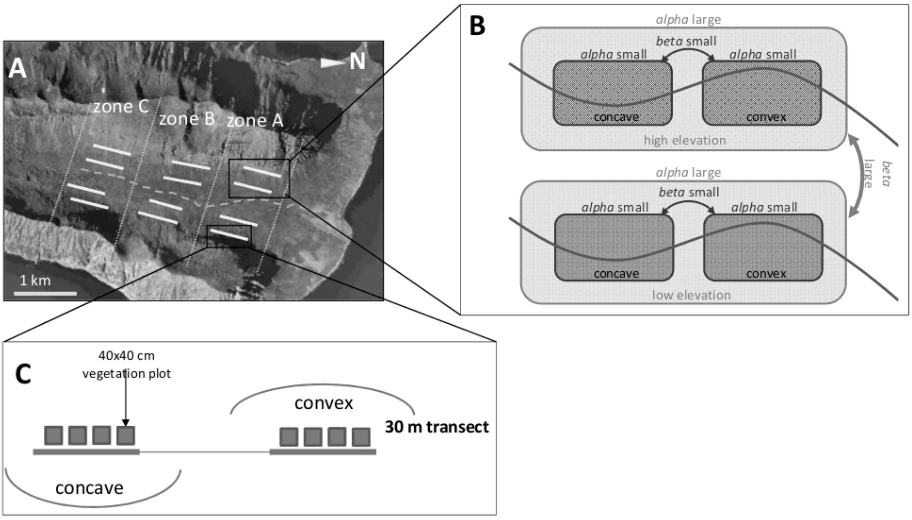

Figure 2. Schematic representation of sampling within each valley and the concept of alpha and beta diversity for the two spatial grain sizes of assessment. (A) Each valley was split into three zones to allow for a spread of sampling units. Within a zone, we sampled vegetation data from each valley side. 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 (g * 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 (grams * 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 form 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

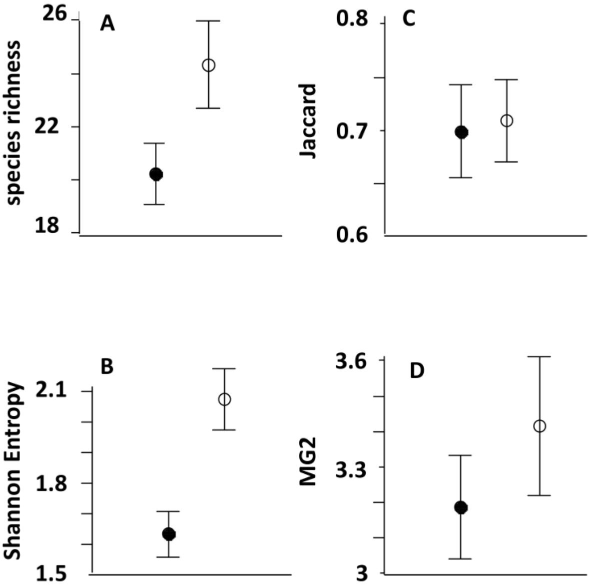

Figure 3. Alpha and beta diversity in both study regions, based on small grain size of analyses. (A) Average species richness and (B) Shannon Entropy within landforms are presented for Norway (open circles) and Iceland (closed circles). (C) Average Jaccard dissimilarity and (D) MG2 distances between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

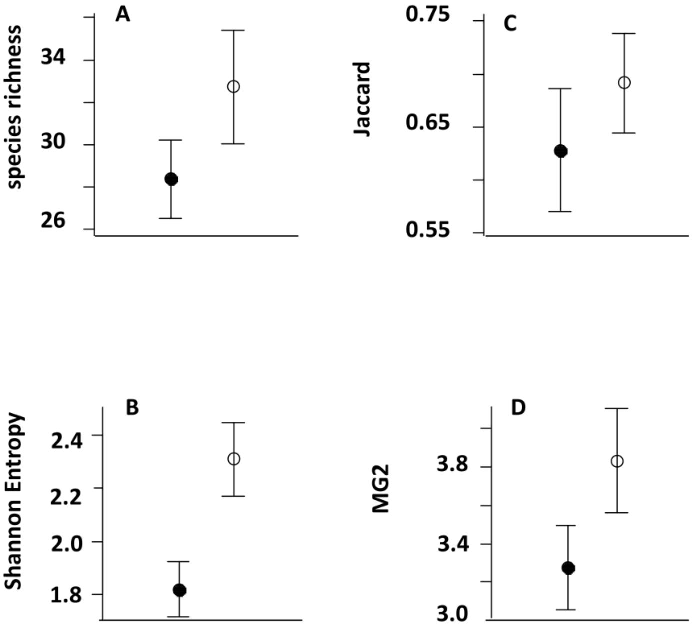

Figure 4. Alpha and beta diversity in both study regions, based on large grain size of analyses. (A) Average species richness and (B) Shannon Entropy within elevations are presented for Norway (open circles) and Iceland (closed circles). (C) Average Jaccard dissimilarity and (D) MG2 distances between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

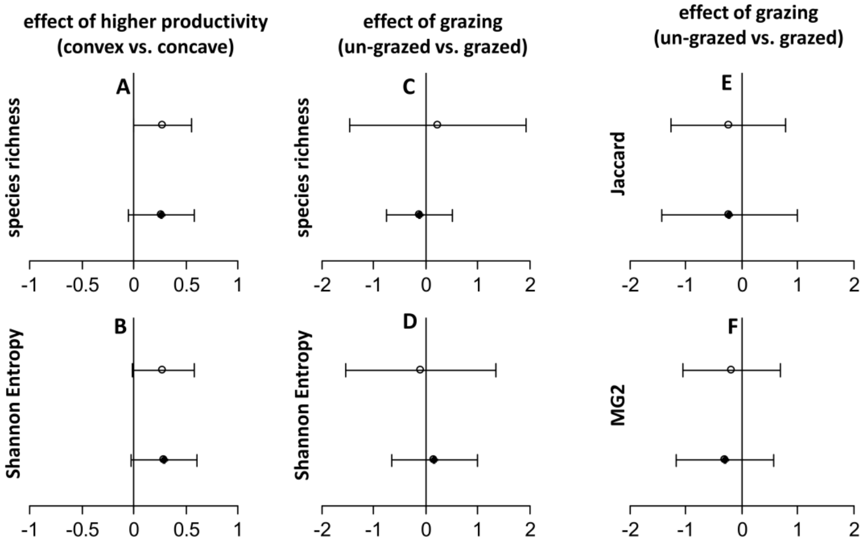

Figure 5. Model estimates representing the effects of landform and grazing on alpha and beta diversity, based on a small grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes. (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).

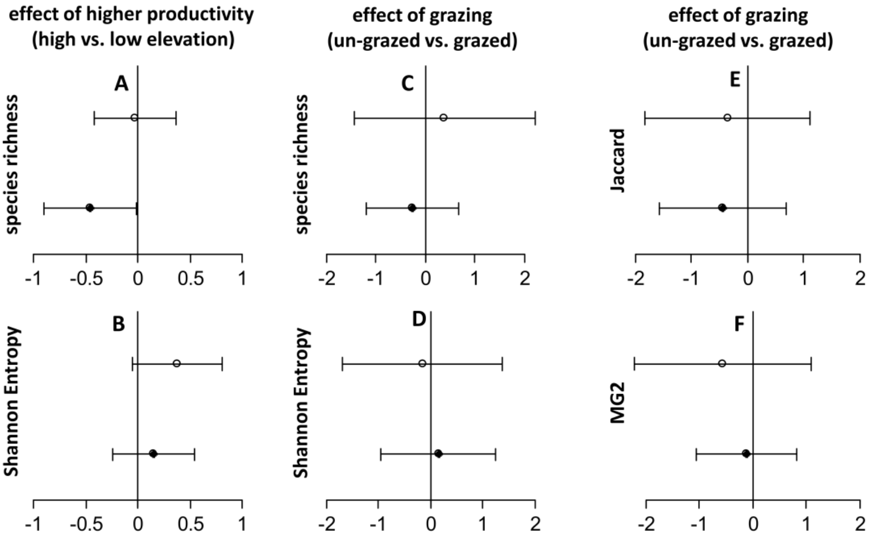

Figure 6. Model estimates representing the effects of elevation and grazing on alpha and beta diversity, based on a large grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes. (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 spool 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 at 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.

Acknowledgements

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References

Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9: 683–693.

Ægisdóttir HH & Thórhallsdóttir TE. 2004. Theories on migration and history of the North-Atlantic flora: a review. Jökull 54: 1-16.

Augustine DJ, McNaughton SJ. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of Wildlife Management 62: 1165–1183.

Baselga A. 2008. Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography 31: 263–271.

Blakemore LC, Searle PL, Daly BK. 1987. Methods for chemical analysis of soil. New Zealand Soil Bureau Report 80.

Bråthen KA, Hagberg O. 2004. More efficient estimation of plant biomass. Journal of Vegetation Science 15: 653–660.

Bråthen KA, Lortie C. 2015. A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. Functional Ecology. doi: 10.1111/1365-2435.12458

Bråthen KA, Ravolainen VT. 2015. Niche construction by growth forms is as strong a predictor of species diversity as environmental gradients. Journal of Ecology 103: 701–713.

Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH. 2007. Induced Shift in Ecosystem Productivity? Extensive scale effects of abundant large herbivores. Ecosystems 10: 773–789

Chaneton EJ, Facelli JM. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. Vegetatio 93: 143–155.

Chase JM, Kraft NJB, Smith KG, Vellend M, Inouye BD. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2: art24.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cornell HV, Lawton JH. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology 61: 1–12.

Dickson TL, Foster BL. 2008. The relative importance of the species pool, productivity and disturbance in regulating grassland plant species richness: a field experiment. Journal of Ecology 96: 937–946.

Eriksson O. 1993. The species-pool hypothesis and plant community diversity. Oikos 68: 371–374.

Eskelinen A, Stark S, Männistö M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. Oecologia 161: 113–23.

Foster BL. 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4: 530–535.

Foster BL, Dickson TL, Murphy CA, Karel IS, Smith VH. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. Journal of Ecology 92: 435–449.

Graham CH, Moritz C, Williams SE. 2006. Habitat history improves prediction of biodiversity in rainforest fauna. Proceedings of the National Academy of Sciences of the United States of America. USA 103: 632–636.

Grime JP. 1973. Competitive exclusion in herbaceous vegetation. Nature 242: 344–347.

Grime JP. 1979. Plant strategies and vegetation processes. Wiley, New York.

Guo H, Wieski K, Lan Z, Pennings SC. 2014. Relative influence of deterministic processes on structuring marsh plant communities varies across an abiotic gradient. Oikos 123: 173–178.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hultén E. 1971. Atlas över växternas utbredning i Norden. Generalstabens litografiska anstalts förlag, Stockholm.

Huston MA. 1979. A general hypothesis of species diversity. The American Naturalist 113: 81–101.

Huston MA. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86: 393–401.

Jóhannesson H, Sæmundsson K. 2009. Geological Map of Iceland - 1: 600 000. Reykjavík: Icelandic Institute of Natural History (1st edition).

Jonasson S. 1988. Evaluation of the point intercept method for the estimation of plant biomass. Oikos 52: 101–106.

Kristinsson H. 2010. Flóra Íslands (The Flora of Iceland). Mál og menning, Reykjavík.

Laycock W. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. Journal of Range Management 44: 427–433.

Lenoir J, Gégout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Grytnes J-A, Virtanen R, Svenning J-C. 2010. Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. Plos One 5: e15734.

Levin SA. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. Ecology 73: 1943–1967.

Lezama F, Baeza S, Altesor A, Cesa A, Chaneton EJ, Paruelo JM. 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. Journal of Vegetation Science 25: 8–21.

Lid J, Lid DT. 2005. Norsk flora. Det Norske Samlaget.

Loreau M, Mouquet N, Holt RD. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecology Letters 6: 673–679.

Michalet R, Brooker RW, Cavieres LA, Kikvidze Z, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? Ecology Letters 9 767–773.

Michalet R, Maalouf J-P, Choler P, Clément B, Rosebery D, Royer J-M, Schöb C, Lortie CJ. 2014. Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. Ecography 37: 1-11.

Milchunas DG, Sala OE, Lauenroth WK. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132: 87–106.

Miller AE, Bowman WD. 2002. Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition by nitrogen form ? Oecologia 130: 609–616.

Mörsdorf MA, Ravolainen VT, Støvern LE, Yoccoz NG, Jónsdóttir IS, Bråthen KA. 2015. Definition of sampling units begets conclusions in ecology: the case of habitats for plant communities. PeerJ 3(3): e815.

Normand S, Vormisto J, Svenning J-C, Grández C, Balslev H. 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. Plant Ecology 186: 161–176.

Olff H, Ritchie ME. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13: 261–265.

Pärtel M, Zobel M. 2007. Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. Journal of Ecology 95: 90–94.

Pärtel M, Zobel M, Liira J, Zobel K. 2000. Species richness limitations in productive and oligotrophic communities. Oikos 90: 191–193.

Påhlsson LE. 1994. Vegetationstyper i Norden. Nordiska ministerrådet, Köpenhamn.

Pinheiro J, Bates B, DebRoy S, Sarkar D. 2004. nlme: Linear and nonlinear mixed effects models. R package 3rd edn.

Qian H, Chen S, Mao L, Ouyang Z. 2013. Drivers of β-diversity along latitudinal gradients revisited. Global Ecology and Biogeography 22: 659–670.

Ravolainen VT, Yoccoz NG, Bråthen KA, Ims RA, Iversen M, González VT. 2010. Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. Ecosystems 13: 157–170.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ricklefs RE. 1987. Community diversity: Relative roles of local and regional processes. Science 235: 167–171.

Ricklefs RE. 2008. Disintegration of the ecological community. The American Naturalist 172: 741–750.

Steindórsson S. 1964. Gróður á Íslandi (Vegetation on Iceland). Almenna bókafélagið.

Svensson JR, Lindegarth M, Jonsson PR, Pavia H. 2012. Disturbance-diversity models: what do they really predict and how are they tested? Proceedings of the Royal Socieity B 279: 2163–2170

Taylor DR, Aarssen LW, Loehle C. 1990. On the Relationship between r/K selection and environmental carrying capacity: A new habitat templet for plant life history strategies. Oikos 58: 239–250.

Tilman D. 1987. The importance of the mechanisms of interspecific competition. The American Naturalist 129: 769–774.

Tilman D, Lehman CL, Thomson KT. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences of the United States of America 94: 1857–1861

Unnsteinsdóttir ER, Hersteinsson P. 2009. Surviving north of the natural range: the importance of density independence in determining population size. Journal of Zoology 277: 232–240.

Wiens JA. 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.

Wohlfarth B, Björck S, Funder S, Houmark-Nielsen M, Ingólfsson Ó, Lunkka J-P, Mangerud J, Saarnisto M, Vorren T. 2008. Quaternary of Norden. Episodes 31: 73–81.

Xiao S, Zobel M., Szava-Kovats R, Pärtel M. 2010. The effects of species pool, dispersal and competition on the diversity-productivity relationship. Global Ecology and Biogeography 19: 343–351.

Zobel K, Liira J. 1997. A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities. Oikos 80: 325–332.

Zobel K. 2001. On the species-pool hypothesis and on the quasi-neutral concept of plant community diversity. Folia Geobotanica 36: 3–8.

Zobel M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12: 266–269.

Zobel M, Pärtel M. 2008. What determines the relationship between plant diversity and habitat productivity? Global Ecology and Biogeography 17: 679–684.

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 ($g*m^{-2}$). Nomenclature follows the Panarctic Flora (http://nhm2.uio.no/paf/)

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

Rumex acetosa	13.52
Rumex acetosella	13.52
Saussurea alpina	13.52
Saxifraga aizoides	13.52
Saxifraga rosacea subsp. rosacea	6.94
Scorzoneroides autumnalis	13.52
Senecio vulgaris	13.52
Sibbaldia procumbens	13.52
Silene acaulis	13.52
Silene dioica	13.52
Solidago virgaurea	13.52
Stellaria graminea	6.94
Stellaria media	6.94
Stellaria nemorum subsp. nemorum	6.94
Succia pratensis	13.52
Taraxacum ssp.	13.52
Thalictrum alpinum	6.94
Tofieldia pusilla	6.94
Trientalis europaea	6.94
Triglochin palustris	6.29
Trollius europaeus	15.34
Urtica dioica	15.34
Valeriana sambucifolia	15.34
Veronica alpina	6.94
Veronica fruticans subsp. fruticans	6.94
Vicia cracca	6.94
Viola biflora	6.94
Viola canina	6.94
Viola palustris subsp. palustris	6.94
Viola riviniana	6.94

grasses

Agrostis ssp.	9.91
Anthoxanthum nipponicum	9.91
Anthoxanthum odoratum	9.91
Avenula pubescens	9.91
Calamagrostis lapponica subsp. lapponica	9.91
Calamagrostis neglecta	9.91
Calamagrostis phragmitoides	9.91
Dactylis glomerata	9.91
Deschampsia alpina	9.91
Deschampsia cespitosa subsp. cespitosa	9.91
Elymus caninus	9.91
Festuca ovina subsp. ovina	6.29
Festuca rubra subsp. richardsonii	6.29
Festuca rubra	6.29
Festuca vivipara	6.29
Hierochloë odorata	9.91
Melica nutans	9.91
Milium effusum var. effusum	9.91
Nardus stricta	79.02
Phleum alpinum subsp. alpinum	9.91
Poa alpina	9.91
Poa glauca	9.91
Poa pratensis	9.91
Trisetum spicatum	9.91

sedges/rushes

Carex atrata	11.62
Carex bigelowii	11.62
Carex brunnescens	11.62
Carex canescens subsp. canescens	11.62
Carex capillaris	11.62
Carex chordorrhiza	11.62
Carex diandra	11.62
Carex echinata subsp. echinata	11.62
Carex flava	11.62
Carex lachenalii	11.62
Carex limosa	11.62
Carex lyngbyei	11.62
Carex nigra	11.62
Carex norvegica	11.62
Carex pallescens	11.62
Carex paupercula	11.62
Carex rariflora	11.62
Carex rostrata	11.62
Carex rupestris	11.62
Carex vaginata	11.62
Eriophorum angustifolium	11.62
Eriophorum scheuchzeri	11.62

Eriophorum vaginatum	11.62
Juncus filiformis	6.29
Juncus trifidus	6.29
Kobresia myosuroides	6.29
Luzula multiflora	11.62
Luzula pilosa	11.62
Luzula spicata subsp. spicata	11.62
Luzula sylvatica	11.62
Trichophorum cespitosum subsp. cespitosum	6.29
deciduous shrubs	
Alnus incana	73.53
Astragalus alpinus	6.94
Betula nana	73.53
Betula pubescens	73.53
Ribes ssp.	73.53
Rubus chamaemorus	13.52
Rubus idaeus	13.52
Rubus saxatilis	73.53
Salix arctica	73.53
Salix caprea subsp. caprea	73.53
Salix herbacea	35.46
Salix lanata	73.53
Salix lapponum	73.53
Salix phylicifolia	73.53
Salix reticulata	73.53
Sorbus aucuparia	73.53
Vaccinium myrtillus	35.46
Vaccinium uliginosum	35.46

evergreen shrubs	
Calluna vulgaris	79.02
Cassiope tetragona subsp. tetragona	79.02
Dryas octopetala	13.52
Empetrum nigrum	79.02
Juniperus communis	79.02
Kalmia procumbens	79.02
Phyllodoce caerulea	79.02
Thymus praecox	6.94
Vaccinium vitis-idaea	35.46
pteridophytes	
Athyrium distentifolium	15.34
Athyrium filix femina	15.34
Botrychium lunaria	13.52
Diphasiastrum alpinum	13.52
Dryopteris expansa	15.34
Dryopteris filix-mas	15.34
Equisetum arvense	6.94
Equisetum fluviatile	6.94
Equisetum hyemale	6.94
Equisetum palustre	6.94
Equisetum pratense	6.94
Equisetum sylvaticum	6.94
Equisetum variegatum	6.94
Gymnocarpium dryopteris	13.52
Huperzia selago	13.52
Lycopodium annotinum	13.52
Matteuccia struthiopteris subsp. struthiopteris	15.34
Phegopteris connectilis	13.52
Polystichum lonchitis	13.52
Selaginella selaginoides	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.

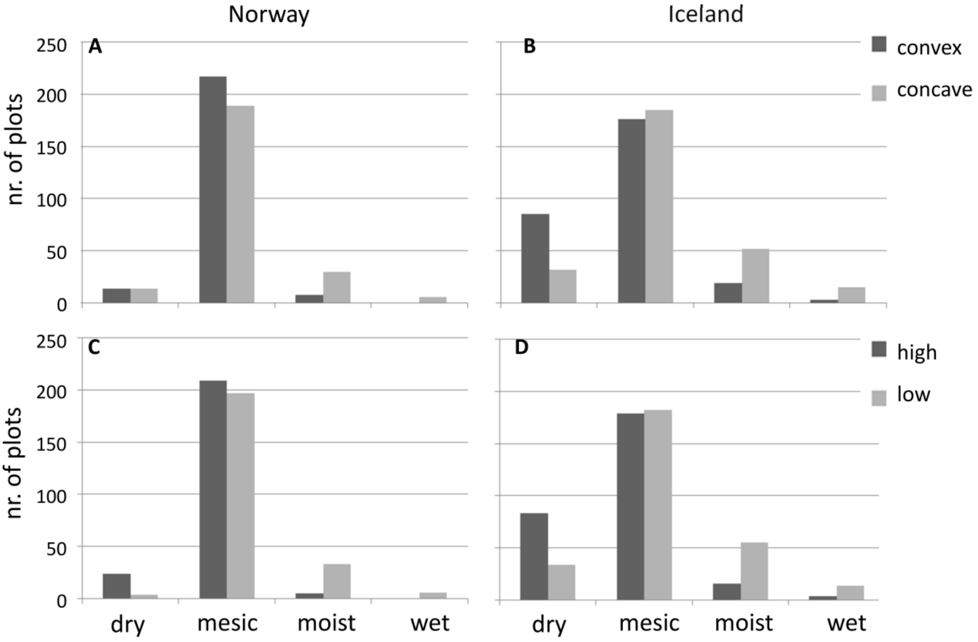


*Figure S2. Average biomass (g*m-2) of plant growth forms for each elevation. Open symbols represent Norway, closed symbols represent Iceland. Error bars are 1 standard error. Observe that y-axes have different dimensions for growth forms due to large discrepancies in biomass.*

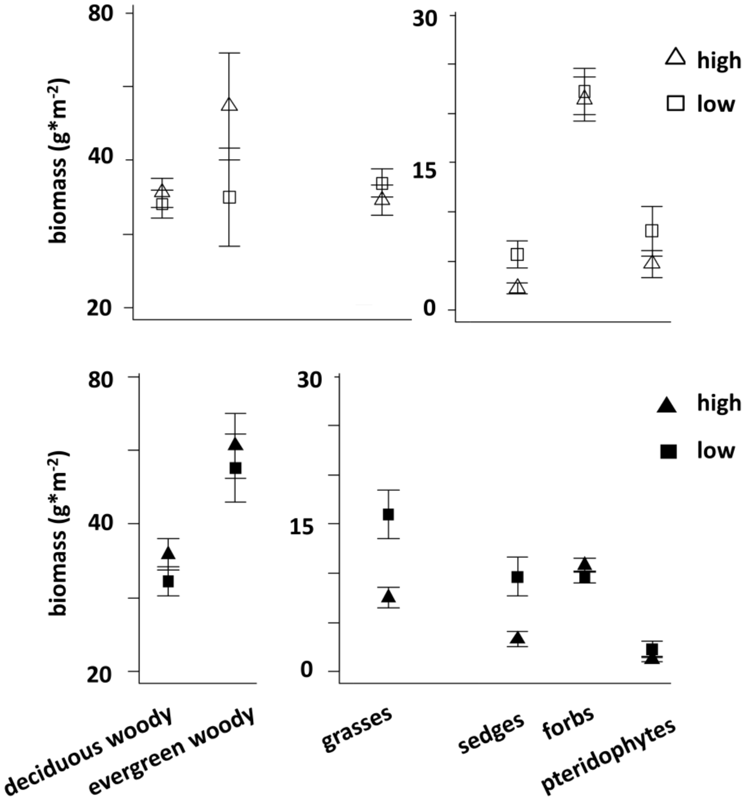
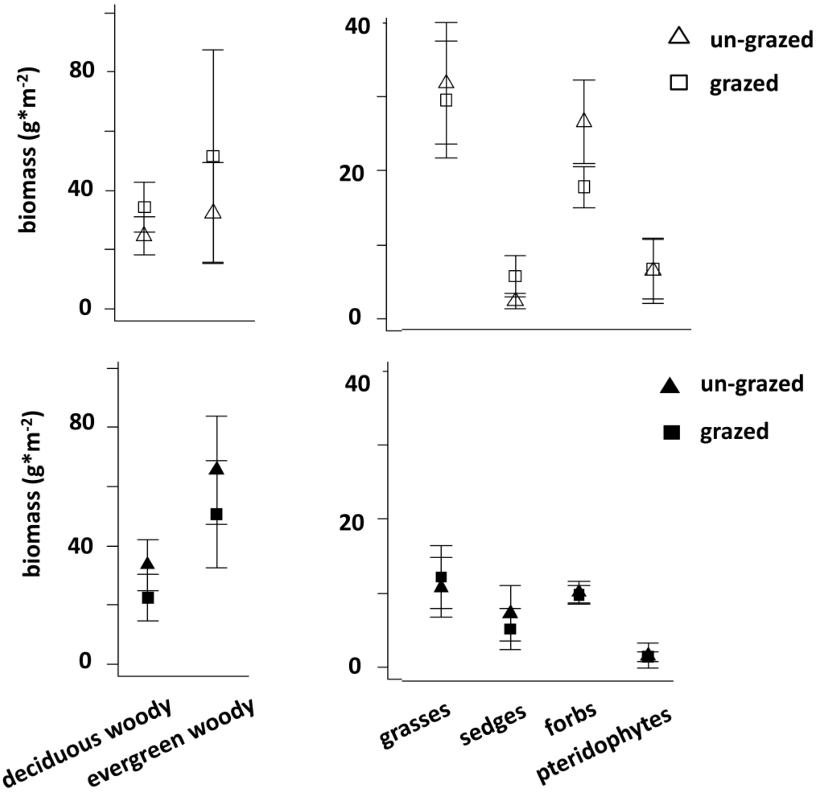


*Figure S3. Average biomass (g*m-2) of plant growth forms for each grazing regime. Open symbols represent Norway, closed symbols represent Iceland. Error bars are 1 standard error. Observe that y-axes have different dimensions for growth forms due to large discrepancies in biomass.*



Háskólaprent ehf.