



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

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Local and regional drivers of diversity in tundra
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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 sauðfjárbreit. 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 endurspegladi 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 beitra 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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List of papers

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 assess 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

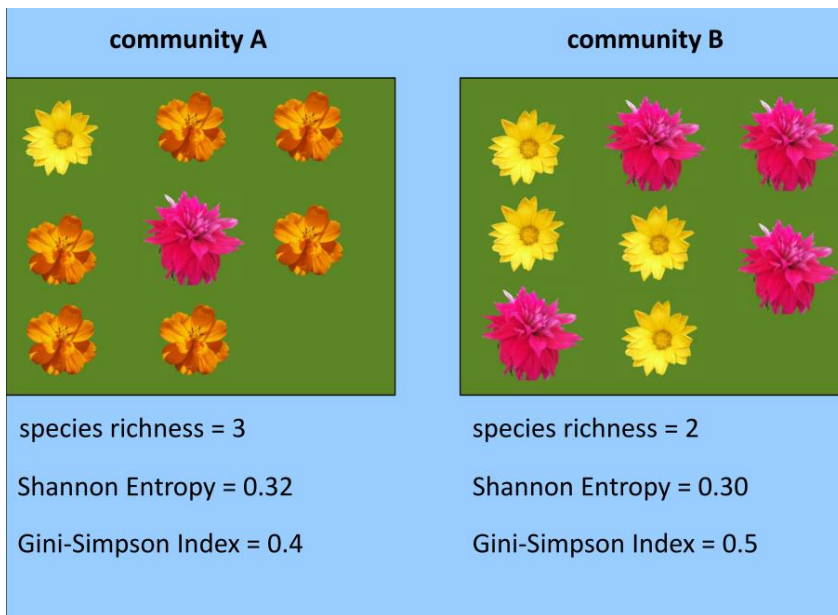


Figure 1.1. Species richness, Shannon Entropy and Gini-Simpson index for two plant communities (inspired by Purvis & Hector 2000). Outcomes of diversity assessments are thereby dependent on the diversity measure used. Community A has one more species than community B (species richness). Also the uncertainty 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	$= (b+c)/(a+b+c)$ <p>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</p>	Proportion of unshared species to the total species number of two communities
Sørensen	$= 2(b+c)/(2a+b+c)$ <p>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</p>	Proportion of unshared species to the average richness of two communities
Bray-Curtis	$= \frac{\sum (\text{abs}(x_{1k} - x_{2k}))}{\sum (x_{1k} + x_{2k})}$ <p>x_{1k}: abundance of species k in community 1 x_{2k}: abundance of species k in community 2</p>	Proportional dissimilarity between communities based on species abundances.
Modified Gower	$= \frac{\sum (w_k (\text{abs}(x'_{1k} - x'_{2k}))}{\sum (w_k)}$ <p>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 $x_{1k} = x_{2k} = 0$, otherwise $w_k = 1$</p>	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; Hédli 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.

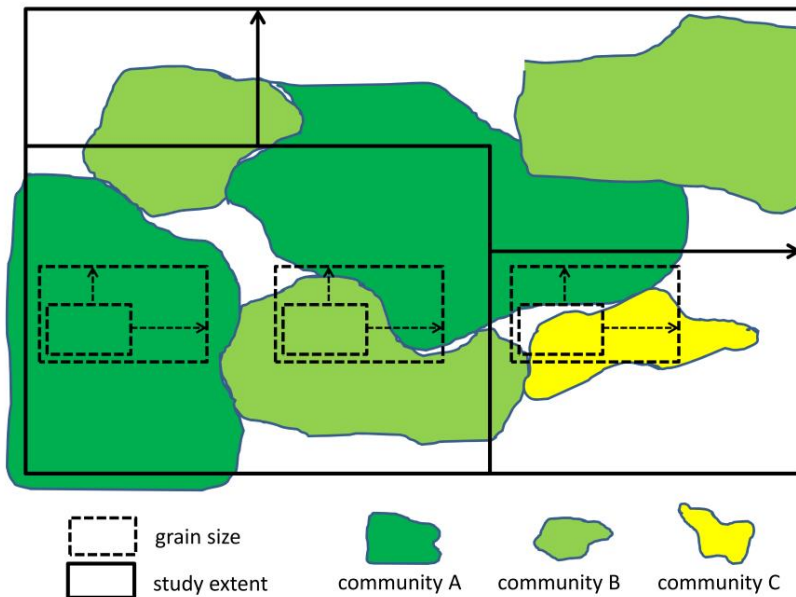


Figure 1.2. Visualizing the effects of grain size and study extent on information that can be retrieved for three communities. Using a small grain size compared to large grain size provides information about variation between communities A and B. Results based on a small study extent can only refer to 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; Olf & 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; Olf & Ritchie 1998). Within tundra regions, grazing by reindeer (*Rangifer tarandus* L.) or sheep (*Ovis 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; Olf & 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).

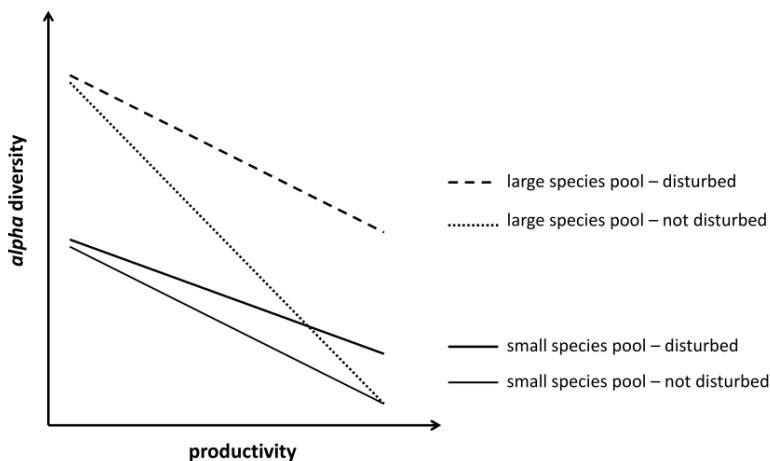


Figure 1.3. The shifting limitation hypothesis, exemplified for a negative linear relationship between *alpha* diversity and productivity. *Alpha* diversity under low productivity is determined by species pool size whereas *alpha* diversity under high productivity is determined by local species interactions. 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.

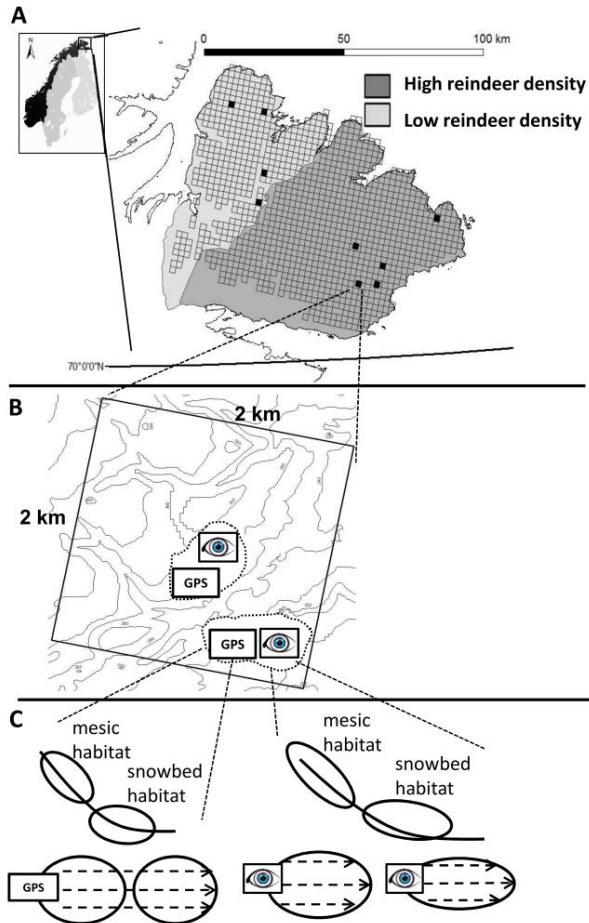


Figure 2.1. The hierarchical nestedness of the sampling design. (A) Shows the geographical location of the sampling region (Varanger peninsula, northern Norway). The shades of gray delimit the districts of contrasting reindeer density. Open squares show 2×2 km landscape areas where major roads, power lines, glaciers and large water bodies have been omitted. Black squares correspond to landscape areas that adhered to all other 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.

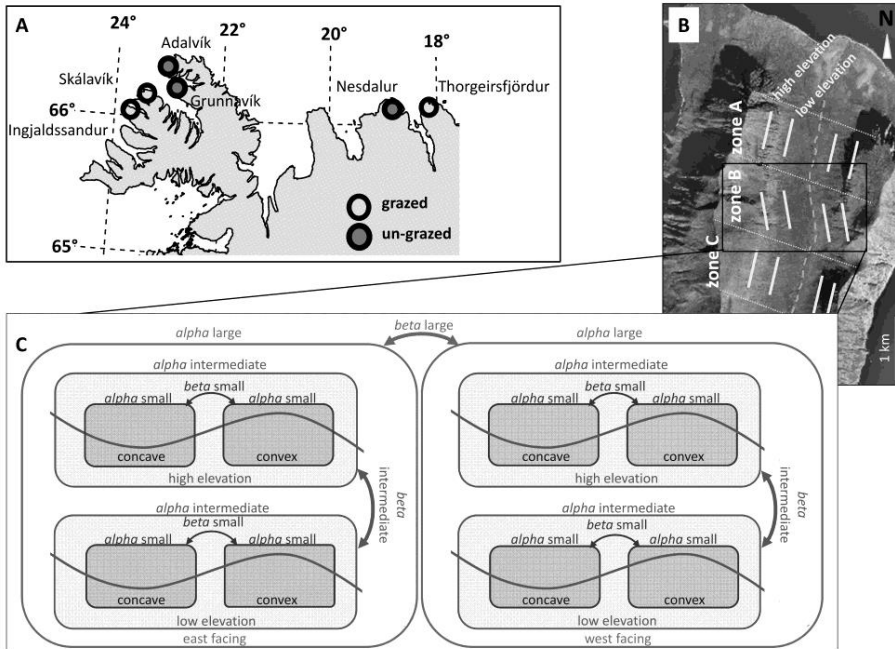


Figure 2.2. (A) Location of sampling sites in grazed and un-grazed valleys in Iceland. (B) Each valley was split up into three zones (zone A, zone B, zone C) to spread sampling throughout the valley. (C) Within each zone, the major topographical contrasts were covered; landform curvature (small grain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

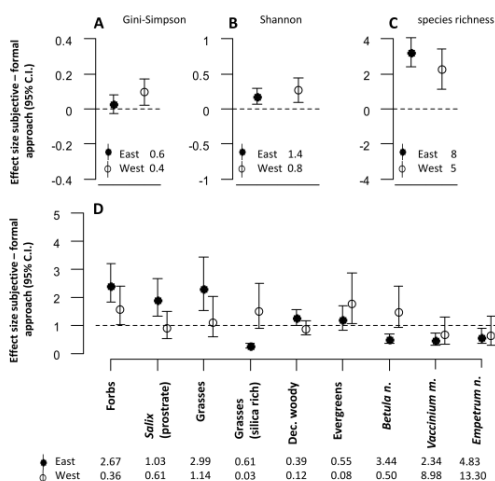


Figure 3.1. Model estimates for the mesic habitat. Effect sizes (mean \pm 95% confidence interval) of the response difference between the subjective and the formal approach of defining sampling units are shown for (A, B, C) estimates of diversity and (D) estimates of biomass of dominant plant species 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.

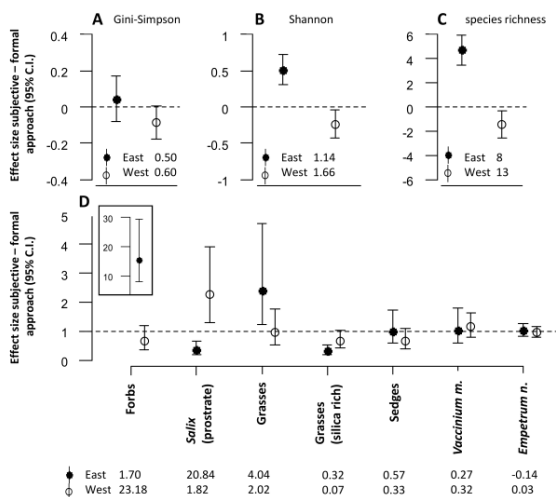


Figure 3.2. Model estimates for the snow bed habitat. All other information as for Figure 3.1.

“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).

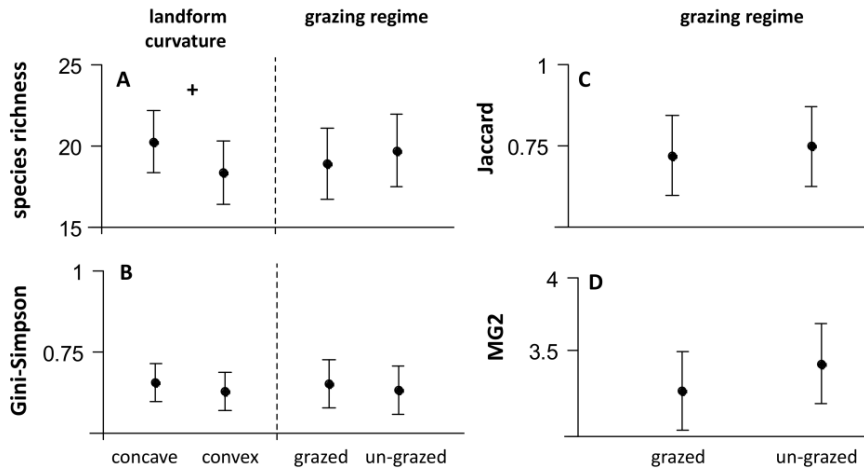


Figure 3.3. Plant diversity in Icelandic tundra within (*alfa*) and between (*beta*) plant communities, using a small spatial grain size. (A, B) *Alfa* diversity (species richness and Gini-Simpson) is presented given the influence of landform curvature and grazing regime. (C, D) *Beta* diversity (Jaccard 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).

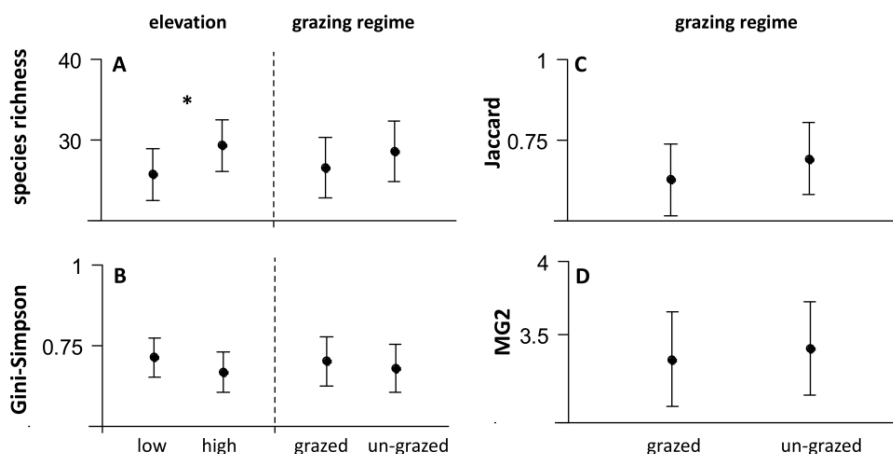


Figure 3.4. Plant diversity in Icelandic tundra within (*alpha*) and between (*beta*) plant communities, using an intermediate spatial grain size. (A, B) *Alpha* diversity (species richness and Gini-Simpson) is presented given the influence of elevation and grazing regime. (C, D) *Beta* diversity (Jaccard dissimilarity and Modified Gower distance MG2), which was calculated between different elevations, is presented given the influence of grazing. *Alpha* 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).

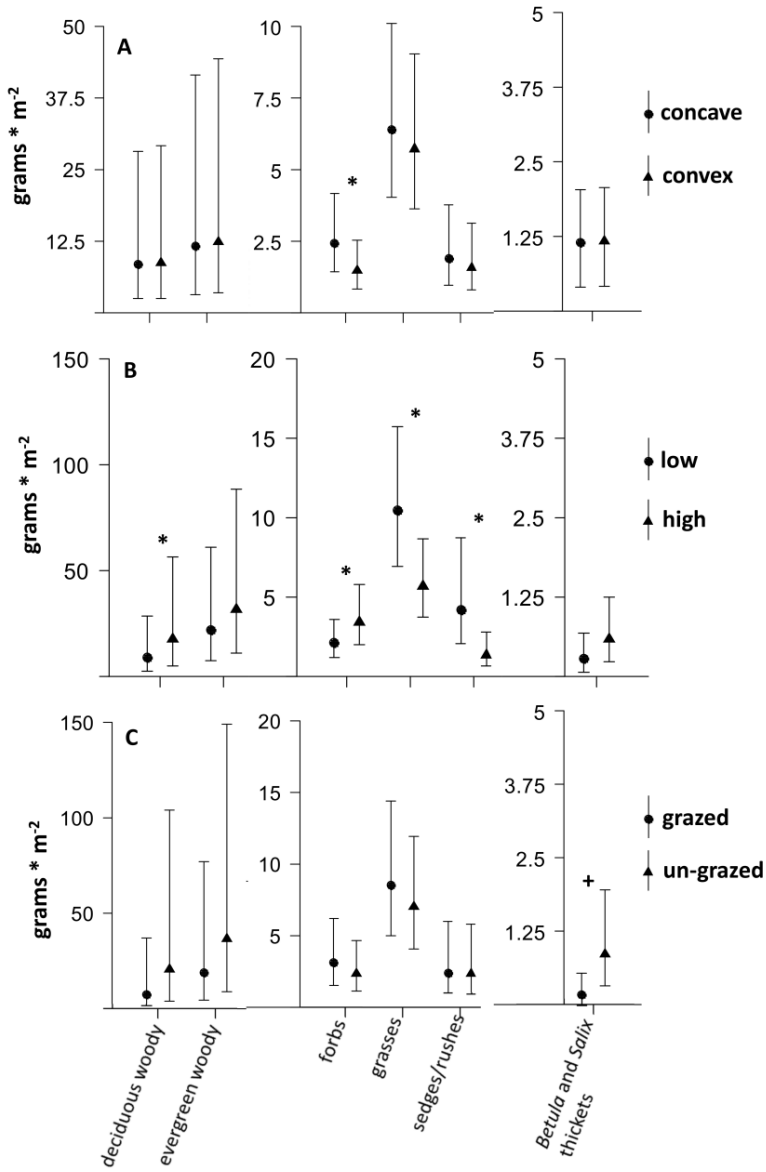


Figure 3.5. Model estimates of biomass of plant growth forms in contrasting landforms, elevations and grazing regimes. The symbols represent geometric means that were derived via back transforming model estimates [g/m²]. “*” indicates statistically significant effects on a 5% significance level, whereas “+” 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 pool 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 heterogeneity 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 pool 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 opposed 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.

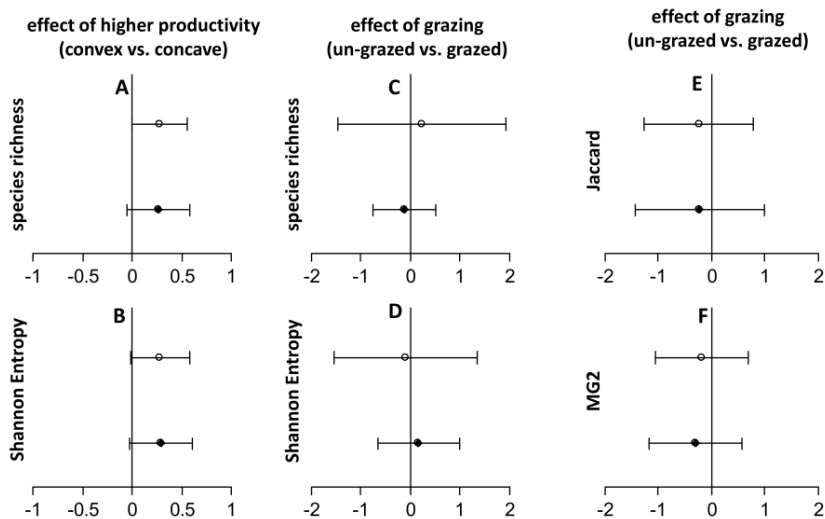


Figure 3.6. Model estimates representing the effects of landform and grazing on alpha and beta diversity, based on a small grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes.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

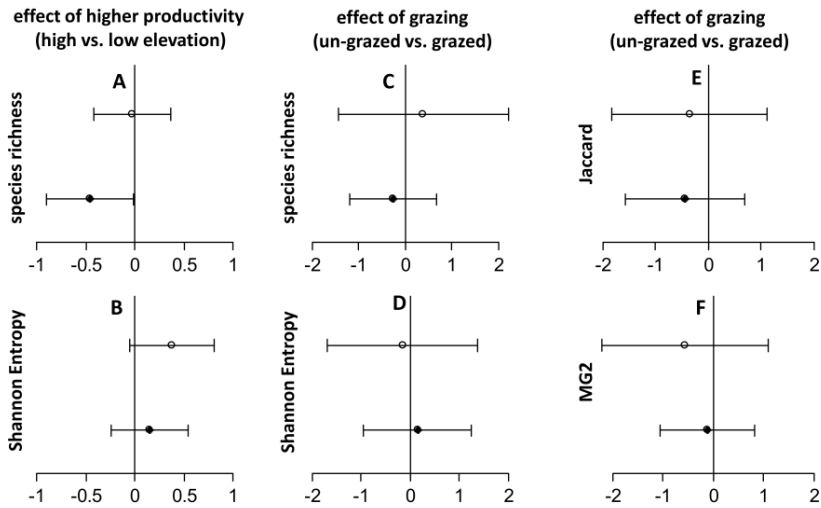


Figure 3.7. Model estimates representing the effects of elevation and grazing on alpha and beta diversity, based on a large grain size. Open circles represent effect sizes for Norway and closed circles represent effect sizes for Iceland. Error bars represent the 95% confidence intervals of effect sizes.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

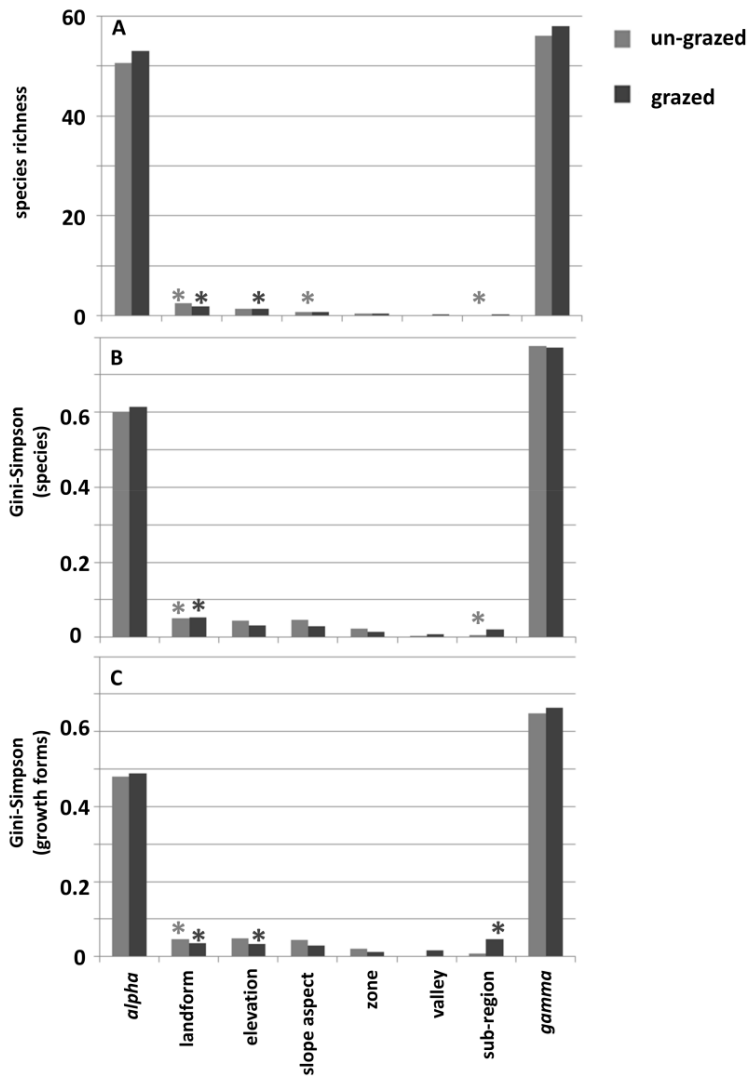


Figure 4.1. Additive diversity partitioning of the Icelandic dataset across all spatial hierarchies of the sampling design. “*” indicates statistically significant turnover components of the respective spatial scale for either un-grazed (light gray) or grazed (dark gray) valleys. Statistical significance 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).

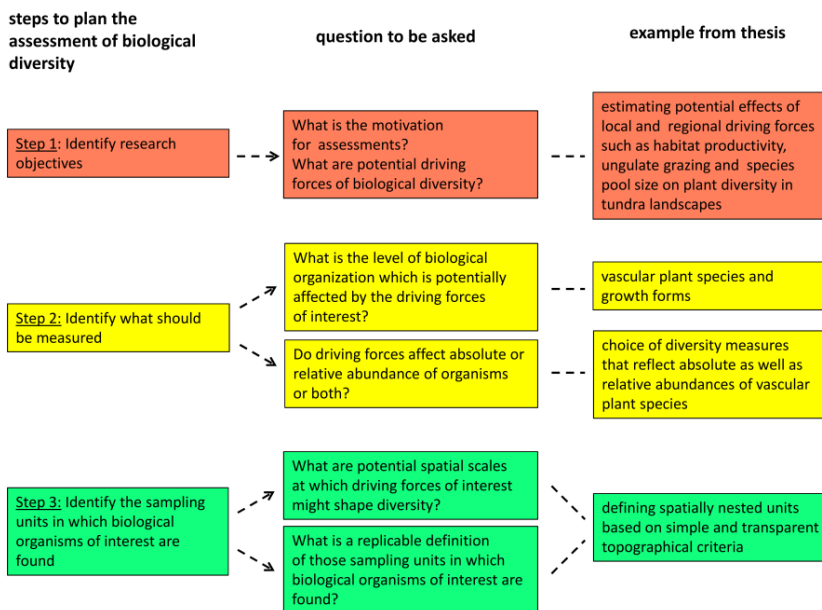


Figure 4.2. Important steps to the assessment of biological diversity

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.

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