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Environmental and floristic differences between three contrasting study areas in an alpine ecosystem: Hardangervidda National Park, Southern Norway

This thesis is worth 60 study points

Summary

Alpine vegetation has been the main focus for many botanists during decades and it has been shown that snow is one of the most important variables explaining vegetation patterns in mountain ecosystems. However, other environmental variables, especially at the local scale, may also have a relevant impact on species abundance and distribution. That is caused by the existence of environmental gradients in alpine ecosystems combined with the existence of microclimates. This study seeks to widen the knowledge on how snow and other environmental variables affect vegetation as well as to infer the impact of the particularities of each study area at the local scale and to model the response of different ecological groups. Thus, the main aims can be summarised as: (1) to interpret the principal environmental gradients reflected by the DCA axes, (2) to interpret the data by the use of Ellenberg indicator values, (3) to model the response of five selected ecological groups by using GLM (4) to test the differences between the three study areas by using Kruskal-Wallis, (5) to group the plots into several plant communities based on their floristic similarities by using TWINSPAN. DCA axis 1 was found to be related to snow cover while DCA axis 2 represented the importance of the local topography and microclimates. Eight different plant communities were sorted by TWINSPAN. Glaimane and Mogen were the most similar sites whereas Stigstuv was slightly more different from them both. It was concluded that local traits at Glaimane and Stigstuv were strong determinants themselves on plant species abundance and distribution.

Contents

1. Introduction

Plant species richness is generally high in alpine areas (Körner, 2003), reflecting the numerous environmental factors that may determine the characteristics of alpine ecosystems and living conditions for plants. Many alpine areas are inhabited by endemisms adapted to the regional peculiarities and that may make these regions biodiversity hotspots (Casazza *et a*l., 2007). Such regional peculiarities often imply that major abiotic environmental factors like topography and microclimates have had, and still have, important evolutionary and ecological effects on vegetation. One important area for its extension and rich alpine biodiversity is Hardangervidda, the largest alpine mountain plateau in the European continent. The core area, protected in 1981 within the Hardangervidda National Park with adjoining conservation areas, comprises a total surface of 7500 km² (60°N, 7° 30′ E) across three counties (Hordaland, Telemark and Buskerud) in south-central Norway (Ryvarden, 2011). The highest point is Sandfloegga with 1721 masl (metres above the sea level) and the mean height is 1200 masl. The whole plateau is above the tree line, around 1100-1400 masl and even higher in the west. There are important environmental gradients across the area, related to altitude and topography. It is especially remarkable for its effects on vegetation the precipitation gradient from west to east of the park, from a more oceanic to a more continental climate with 1400 mm per year in the oceanic area and 700 mm in the continental area (Falldorf *et al.,* 2014). The oceanic climate is associated with a longer growing season and therefore vascular plants tend to be much more abundant than lichens in the west (Sundstøl & Odland, 2017). In fact, the overall vegetation is more abundant in the west since the temperature oscillations are narrower and the precipitation is higher (Kallio *et al*., 1975). In the east, the vegetation is sparser and open, windy heaths are more common, especially if the layer of snow is thin and the bedrock is poor. Therefore, the two main factors explaining plant biodiversity and species composition differences are altitude and distance from the (west) coast (Fig.1).

Many environmental factors determine that plant species richness is generally high in alpine areas (Körner, 2003). These factors are not constant, but vary in different ways. For this reason, it is very interesting both from an evolutionary and ecological point of view to analyse how plant species composition and richness may vary along environmental gradients (Bhattarai, 2017, Doebeli & Dickmann, 2003).

Interactions between species as well as between species and their environment are scale-dependent and so is it species richness (Bruun *et al.*, 2006). Therefore the scale should be taken into consideration in alpine flora studies. For example, on smaller spatial scales, local topography and microclimates have important effects on vegetation, and wind and gravity have an effect on soil formation influencing where plants can easily develop (Bruun *et al.*, 2006). Locally, the presence and duration of the snow layer is particularly relevant.

The local vegetation characteristics in alpine ecosystems are usually dependent on snow accumulation and persistence, which again depend on the climate and the local topography (Reinhardt, 2013). In winter, snow tends to accumulate in the sheltered depressions of the terrain (snowbeds), whereas it is blown away by the wind on the exposed tops of the hills (ridges). That is how the presence of hills results in gradients from more exposed snow-poor sites to more sheltered snowbeds, and thereby constitutes valuable study sites for determining the effect of the snow layer on alpine vegetation (Prakash, 2017). Aspect is important as well, mainly because there may be temperature differences between north-facing and south-facing slopes in sympatric areas. On the one hand, north-facing slopes can profit from early sunlight and cloudy afternoons, which means that they may achieve higher temperature in the morning compared to the south-facing slope. On the other hand, south-facing slopes receive a higher number of total hours of sunlight, so these sites are often more favourable for vegetation establishment and growth (Oke, 1978). However, such ecological effects may not always be straightforward. The slope determines how direct the solar radiation is on vegetation; more direct exposition to sunlight may obviously facilitate the surpassing of temperature thresholds. Nevertheless, the opposite may happen if shadow sites are created (Oke, 1978). For all this, topography, in combination with wind and precipitation, determines how the snow is distributed and accumulated throughout the landscape, so the terrain characteristics need to be taken into account when studying vegetation patterns (Essery & Pomeroy, 2004). What is more, the characteristics of the terrain may even have an impact on the evolution of freezing resistance adaptations since snowbed species will not usually develop such strategies because they are protected by the snow layer (Körner, 2016).

Assuming that plant species are in equilibrium with their environment, there is clear relationship between the species distribution and the environmental variables (Guisan *et al*., 1998). Species show a particular response to these variables. Therefore, knowing these variables makes it possible to infer causal relationships and even predict the distribution and abundance of each species and/or ecological plant groups, given certain environmental conditions. For this purpose, a convenient and practical procedure is to assign each of a number of selected environmental variables into their correspondent category based on their value in the field. That is, the environmental variables are expressed in ranks which reflect their value under certain conditions and they may be aggregated into simpler indicators used to predict the plants' response. The Ellenberg indicator values are considered straight-forward and precise enough to express ecological differences between study areas (Odland, 2009). Commonly, the environmental values are measured in the field and then the values obtained are ranked and standardised from 1 to 9 in a way that they can be applied to infer the response of the species to that particular environmental variable. For example, with regard to snow, plant species are classified into a Snow Indicator (SI) category, from "chianophilous", high Snow Indicator (SI), values close to 9, where the snow layer remains until late July, to "chianophobous", low SI values, close to 1 (Odland & Munkejord, 2009). In most practices, the indicator values are compared by first calculating their weighted average (WA) and then comparing the obtained values between the different floristic communities (Diekmann, 2003). The response to an environmental variable, expressed and classified 1 - 9 via a corresponding category, may vary between species, and it gives information about tolerance and optimum (in relation to the studied environmental variable). Thus, indicator values were considered a practical tool and used in the present study to find the significant environmental variables explaining plant species distribution and abundance. The following environmental variables were considered in this study: slope, aspect, stones, study area, WAR (Weighted Average Reaction value), WAL (Weighted Average Light value), WASI (Weighted Average Snow Indicator value), WAK (Weighted Average continentality value), WAFF (Weighted Average soil moisture value) and WAN (Weighted Average Nitrogen value).

Because responses depend on autoecology, interspecific interactions, physiology, etc. (Whittaker, 1967), a number of different plant species representing different ecological groups were selected for this study, with a particular focus on responses to

snow. Concretely, the ecological groups defined were: Lichens (L), shrubs (S), mosses (M), graminoids (G) and herbs (H). In general, lichens would show a negative linear response with a maximum in the exposed ridges and decreasing towards the snowbed (Prakash, 2017). Since lichens lack proper roots, their abundance is not expected to increase towards the moist and richer snowbed soil. Vascular plants, on the other hand, are likely less abundant in the ridges but would increase towards the snowbed up to a certain point, and then decrease again where the soil becomes too moist for them. However, some species may show a higher snow tolerance and become relatively more abundant towards the snowbeds, especially herbs and graminoids, since shrubs may struggle if covered by snow (Marchand, 1996).

The typical snowbed communities tolerate a thick snow layer lasting until summer, and include several herbs, graminoids and many mosses, among others (Schöb *et al.*, 2009). The snow layer protects these plants from the wind and the excessively low temperatures. Nevertheless, the length of the growing season is very short under these conditions and the snowbed species must be able to develop in a short period of time thanks to the moisture provided by the late melting of the snow (Björk & Molau, 2007). For all that, one of the main objectives of the present study was to test if field observations matched the expected pattern, which would be:

   i) most lichen found at the top of the exposed ridges,

   ii) most mosses in or near the snowbeds,

   iii) few or no shrubs in the snowbeds and

   iv) herbs and graminoids would dominate in the middle of the transect, that is, at intermediate levels of snow.

In addition, the three study areas chosen were compared to look for possible differences between the selected regions. The characteristics of each area were described by several Ellenberg values and used to interpret the vegetation trends. Thanks to the microclimates existing in the three study areas, it would be possible to find the same vegetation communities in all the study areas despite their overall different floristic composition. Thus, one last goal was be to classify the sampled plots into different floristic communities based on their similarities by the use of TWINSPAN© (Hill, 1989).

2. Methods

Three study areas were selected, representing different geographical locations and climates (Fig.1): Stigstuv (in the north); Mogen (in the east, right of the image) and Glaimane (in the south, bottom of the image).

Figure 1. *Above, geographic location of Hardangervidda. Below, geographic location of the three study areas within Hardangervidda Nasjonalpark. The study areas are encircled in black.*

The three different study areas were chosen so as to include the location within the national park as another variable having effect on vegetation abundance and distribution since different sites provide different conditions for growth and development.

The first study area (Stigstuv) was mostly flat but containing hills where the mentioned snow gradient was easy to observe. Lichens were found at the top of the hills whereas black-mosses dominated the snowbeds, as expected. This study area was more exposed to the wind and it was thus drier and less vegetated than the other two.

In the second study area (Glaimane), the species were similar to those in Stigstuv, but the specimens were usually taller. Both *Juniperus comunis* (recorded but not included in the cover estimation) and *Betula nana* were more abundant giving a more "tree-like appearance" to the landscape. The climate was slightly more humid than Stigstuv at some sites, mainly due to the presence of lakes and other water bodies, so plant species might benefit from the higher humidity. The distribution of the ecological groups matched the expectations as well.

The appearance of the third study area (Mogen) was more similar to Glaimane than to Stigstuv, with even more abundant *Betula nana*. The climate was also more humind than in Stigstuv and the vegetation was even taller than in Glaimane. The snowbeds were usually occupied by rocks instead of mosses. Otherwise, the distribution pattern was as expected.

These differences can be visually appreciated below (Fig.3).
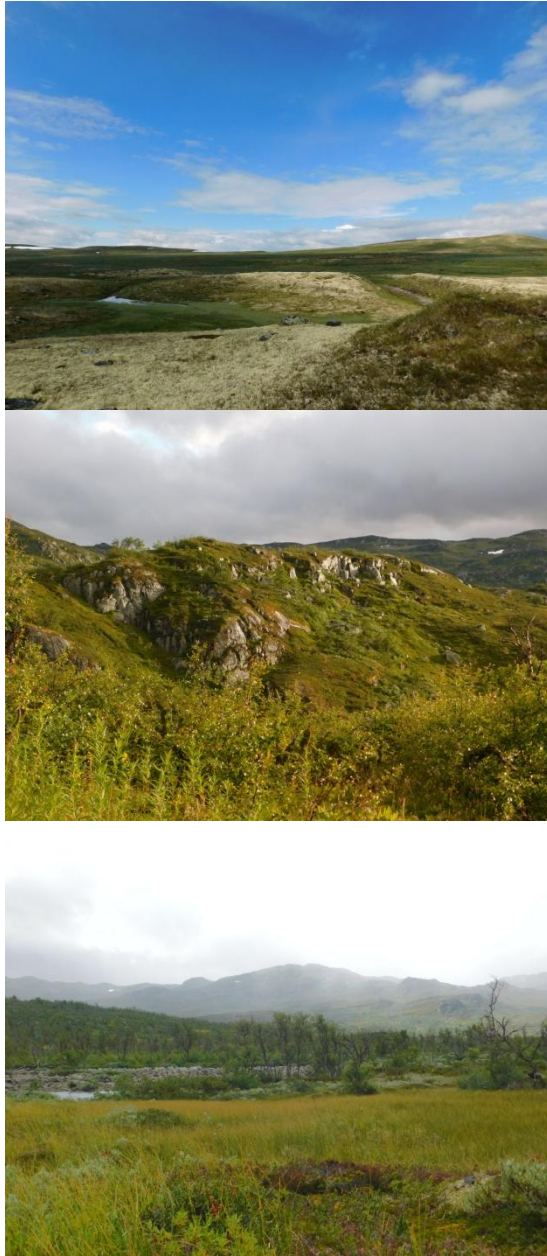
Figure 3. *Landscape differences between the three study areas. From top to bottom: Stigstuv, Glaimane and Mogen.*

The fieldwork was carried out from the 24th July to the 20th August, and divided into three short trips, one to each of the study areas. The fieldwork had to be completed during the short summer season to make sure the sampling sites would be mostly free of snow. Otherwise, visual estimation of cover would have been impossible.

During the first trip, guide and identification of plant species by Ole Reidar Vetaas prepared me for my future independent task.

For each area, the first step was to look for suitable study sites, i.e. sites with an obvious snow gradient. Thus, the study areas consisted of hills with exposed ridges free or almost free of snow and where the snow accumulated on the bottom (snowbeds). This can be observed in the Figure 4, where the existence of several genera of lichens (*Cetraria, Alectoria* and *Cladonia*), on the bottom of the image, indicated the presence of the exposed ridge.

Figure 4. *Establishment of the transect from the top (dominated by lichens) to the bottom (dominated by mosses) of a hill in Stigstuv.*

In order to be suitable, the hills had to be at least 16 m long with no more than 35-40° slope (because that could facilitate the presence of local snowbeds) and at least 100 m separated from each other (Prakash, 2017). Transects were then established and measured, and each transect represented one sampling site (Fig.4). Between four and eight plots should be sampled per transect, approximately (Prakash, 2017). In total, 19 transects were analysed (seven in Stigstuv; nine in Glaimane, and three in Mogen), which made a total of 100 2 x 2 = 4 m^2 plots, and 400 1 m^2 subplots (see Appendix, Table 1).

Figure 5. *Cover estimation of one subplot in Glaimane.*

Depending on the height of the ridge = length of the transect, each transect contained from four to seven 2x2 m plots and each plot was subdivided into four 1x1 m subplots (Fig.6, 7) (Prakash, 2017). Due to the topography, not all transects had the same number of plots. The plots had to be homogenous (no variation in the spatial distribution nor in the relative abundance of at least the major plant species nor in the ecological conditions), and separated 2 m from the neighbour plot. Altitude and aspect were measured for each transect, while slope was measured for each plot. The aspect was transformed based on Goldsmith, 1973 with modifications; the category "flat" corresponded to 5 instead of 0. Since altitude was near the same for all three study areas, i.e. no variation, it was not considered an environmental variable to be included in the statistical analysis. The aspect, altitude and coordinates (at the top) of each transect were recorded by GPS (Garmin 64S). The slope was measured with a clinometer for each of the plots. The plant species included in this study were those considered representative (usually present at least in one or more of the subdivisions of the gradient) as well as easy to identify, and made a total of 38 species (see Appendix, Table 2). Regarding mosses, the species were not identified, only the overall cover was estimated for that ecological group.

These criteria described the method preferred and it is important to note that it was not a destructive method since it was based on visual estimation, so none of the individuals was damaged during the sampling.
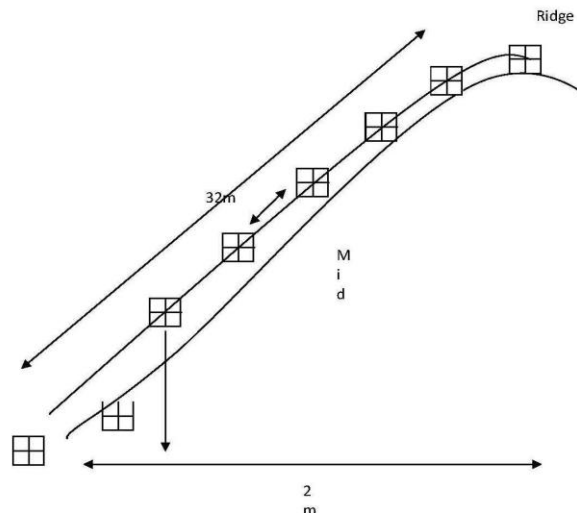
Figure 6. *Schematic representation of a transect, from the ridge to the snowbed, here with a total length of 32 m. The larger squares represent the 2 x 2 m plots and the smaller squares, the 1 x1 m subplots.*
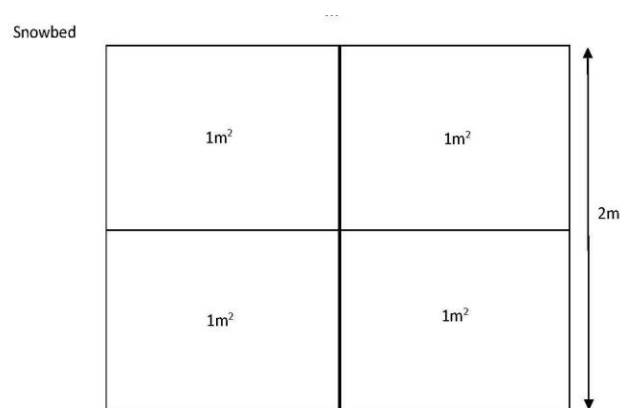
Figure 7. *Schematic representation of a plot (2 x 2 m) and its four subplots (1 x 1 m).*

Plant species cover was visually estimated on a scale from 1% to 91% and no species covered more than 91% of the plot. That scale was chosen so as to represent with accuracy the species' cover even if only one or few individuals were present in the subplot. In addition to plant species, the cover of stones was noted down too because they may take up much space in the plot and in that case the plot should be moved 2 m further.

Data analysis

Once the data were collected, they were written into an Excel file and analysed with the programme Canoco 5© (Ter Braak & Šmilauer, 2002) so as to reflect the main gradients determining floristic composition and abundance (Odland & Munkejord, 2008).

Several ordination methods, both direct (CCA) and indirect (DCA and PCA), were applied to interpret the environmental gradients. Direct ordination shows how species respond to certain environmental factors, while indirect ordination examines first the variation within the dataset, independently of the environmental data. A second stage of the indirect methods, applied once the main source of variation is established, allows correlating the environmental data with the vegetation data to find possible environmental gradients.

DCA (Detrended Correspondence Analysis) is an indirect method which displays the gradients explaining the variation in the species data (Odland & Munkejord, 2008) and thus it was applied to study the distribution of the species along the environmental gradients.

PCA (Principal Components Analysis) is another indirect method that develops ordination axes that represent with the maximum accuracy as possible a linear relationship with the species data (Begon *et al*., 1988).

In addition, a Kruskal-Wallis test was applied to look for possible differences between the three study areas. For that purpose, all data was pooled together per site and then compared to the other sites. The programme used was R© 3.2.5 (Venables & Smith, 2012).

Finally, the programme TWINSPAN© (Hill, 1989) was used to classify the plots into plant communities based on their floristic similarities. A description of the communities found along the gradients is a good overview of the alpine vegetation pattern (Odland, 2005). Since the data needs to be ranked because the programme does not work with percentages (of cover) six cut levels (squared IV-values: 0, 10, 20, 40, 60) and four indicators were selected. The programme consists of an algorithm that splits the groups following a dichotomy pattern. That is, in each step, each group is subdivided into two subgroups according to their floristic similarities. The algorithm is

based on ordination methods and it starts with the first DCA axis. The first DCA axis is divided into two and so it continues (Roleček *et al*., 2009). The groups are identified by a binomial notation (e.g. T-0 will be divided into T-00 and T-01 and so on). Each group or cluster is defined by certain dominant species which will be different between the groups and these species can be used to name the groups. It is a way of simplifying huge amount of data and finding vegetation patterns.

3. Results

The outliers obtained in the different analyses were eliminated, so 98 plots and 392 subplots were included in the end.

First of all, DCA was applied to show the distribution of all species and samples along the main gradients explaining the variation in the floristic data (Fig.8, 9, respectively). The results are shown in the figure below (Table 1), where the four DCA axes can be observed. The longest one was the DCA axis 1 (Eigenvalue = 0.5; variance explained= 12.99%), followed by the DCA axis 2 (Table 1).

Table 1. *DCA results.*

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5050	0.2939	0.2282	0.1408
Explained variation (cumulative)	12.99	20.54	26.41	30.03
Gradient length	4.30	3.34	2.67	2.58
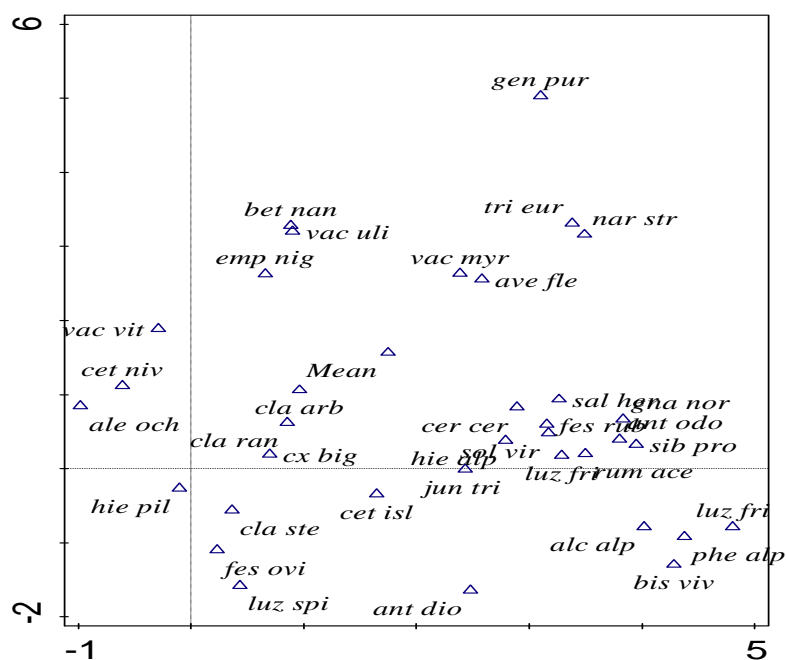
Figure 8. *Species distribution along the two main DCA axes.*
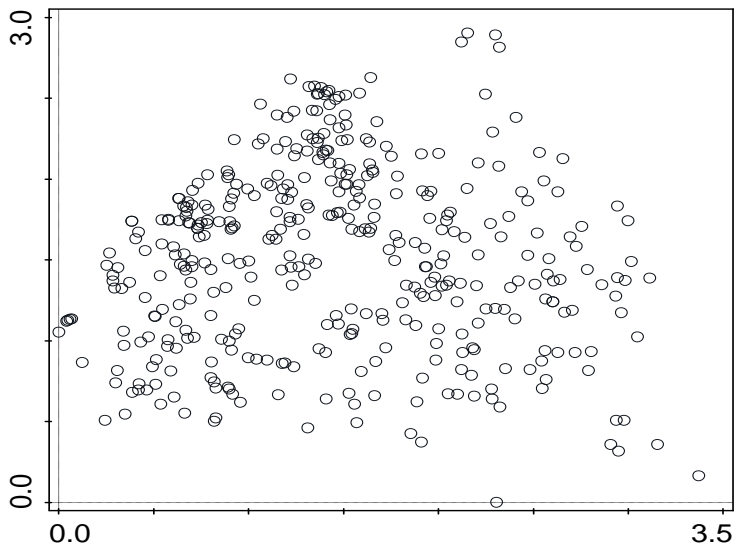
Figure 9. *Samples distribution along the two main DCA axes.*

The first or principal DCA axis is the longest, the one which explained the most variation in the data. Therefore the main axis was the horizontal one (Fig.9). Situated on the left side of this axis, species like *C.nivalis*, *V.vitis-idea* and *A.ochroleuca* were found (Fig.8). That is, mostly chianophobous species. Indeed, most lichens were located on this part of the graph, only *C.islandica* surpassed the central values of this axis (Fig.8). On the contrary, most of the species on the right side of the DCA axis 1 were herbs and graminoids, like *B.vivipara*, *L.frigidea*, *G.norvegicum*, *A.alpinum*, *A.odoratum*, *S.procumbens* and *P.alpinum*, more resistant to the presence of snow. In addition, there were no shrubs on the right side of the DCA axis 1, except *S.herbacea* (Fig.8). Due to the interdependence between the relative position of the species (Fig.8) and the environmental variables represented by each DCA axis, the DCA axes can be interpreted based on the ecology of these plant groups (Odland, 2005). Thereby, the main DCA axis would be related to the snow layer.

The secondary DCA axis was the vertical one, with species such as *G.purpurea*, *V.uliginosum, N.stricta* and *B.nana* on the top and *C.stellaris, L.spicata* and *F.ovina* on the bottom (Fig.8). That could imply that the axis 2 would be related to continentality since these species located on the top can thrive in areas with a lower winter temperatures and more wind whereas those located at the bottom would be found where the atmospheric humidity was higher. However, moisture may not the only explanation since some of the species located at the bottom may also grow in dry environments. For

a more accurate interpretation, all environmental variables should be plotted in the graph (Fig. 10).

In order to infer how the rest of the environmental variables (besides snow and continentality/atmospheric moisture) contribute to the variation in floristic abundance and composition, these variables were then introduced as "supplementary" in the PCA (Table 2). Considering the environmental variables as "supplementary" implies that they were not involved in the analysis above but included afterwards into the ordination method. Thus, it is possible to see how they are related to the main DCA axes. The results of the test are shown in Table 2 and its correspondent graph is shown in Fig.10.

Table 2. *PCA results with environmental data as supplementary data.*

Total variation is 3.88869, supplementary variables account for 33.4% (adjusted explained variation is 31.6%)

| Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5050	0.2939	0.2282	0.1408
Explained variation (cumulative)	12.99	20.54	26.41	30.03
Gradient length	4.30	3.34	2.67	2.58
Pseudo-canonical correlation (suppl.)	0.9466	0.8648	0.6160	0.7001
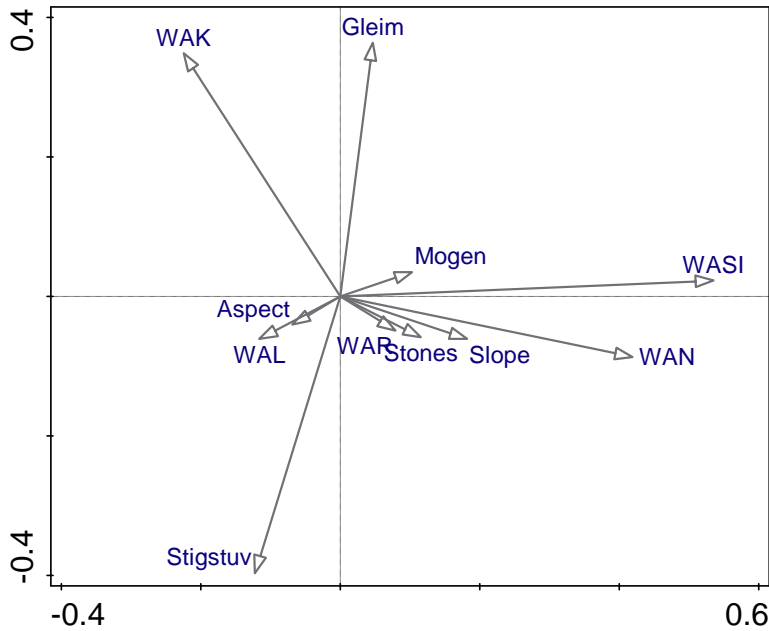
Figure 10. *PCA results using environmental variables as supplementary data.*

Based on figure 10, it can be stated that WASI was correlated to the horizontal DCA axis whereas WAK, Glaimane and Stigstuv were correlated to the vertical axis. That is in accordance with the interpretation based on the species distribution along the DCA axis (Fig.7). The strong effect of the local topography, combined with WAK, explained the distribution patterns along the vertical DCA axis (Fig. 10). The variables represented by the longest arrows explained the most variation and therefore the most relevant ones were: WASI, WAN, Stigstuv, Glaimane and WAK. The rest of the variables showed much shorter arrows and thus less significant effects. Since they showed contrary directions, Stigstuv had an opposite effect than Glaimane, and the same applies to the relationship between WAL and WAFF. WASI and WAN pointed to the same direction in the graph, so they will both increase (or decrease) under the same conditions up to a certain point.

In total, these environmental variables explained 33.4% of the total variation in the species data (Table 2).

After that, the environmental variables were plotted together with the species data to see more clearly how they were related between them as well as to the DCA axes

(Fig.11). In the next figure (Fig.12), the samples together with the environmental variables were plotted.
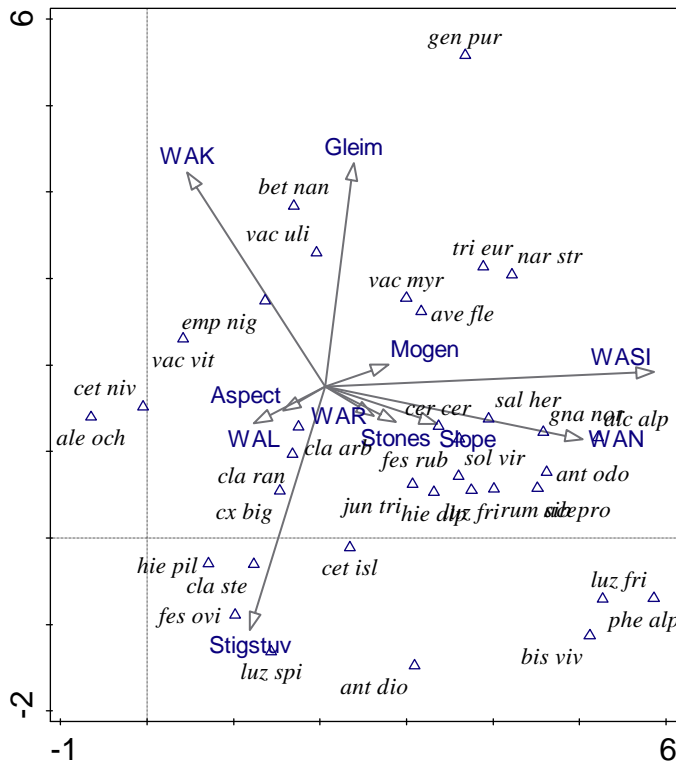

Figure 11. *Spatial ordination of the species and the environmental data (as supplementary data) along the DCA axes.*
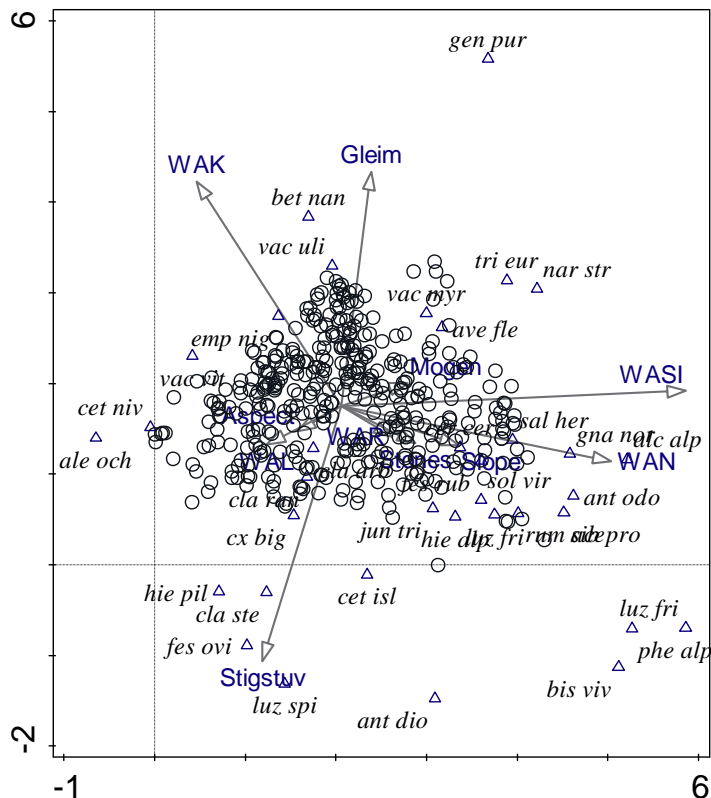
Figure 12. *Spatial ordination of the samples and the environmental data (as supplementary data) along the DCA axes.*

By looking at Fig.11, *E.nigrum, B.nana* and *V.uliginosum* increased with WAK and Glaimane whereas species such as *G.novergicum, A.alpina* and *S.herbacea* increased with WASI. *L.spicata, A.dioica, F.ovina* and *C.stellaris* increased with Stigstuv. Glaimane, rich in *B.nana*, *V.uliginosum* and *V.myrtilus*, showed a very different vegetation pattern from Stigstuv, rich in *C.islandica*, *C.stellaris* and *C.bigelowii*, among others. WASI and WAN followed the same direction and appeared associated to a greater abundance of graminoids and herbs.

Since snow is one of the most important variables in alpine ecosystems (Odland & Munkejord, 2008), as proved by the DCA results (Fig.8), we then studied the relationship between each of the different ecological groups and the WASI using Generalised Linear Models (McCullagh & Nelder 1989) and the results are shown below (Fig.13, 14, 15, 16).
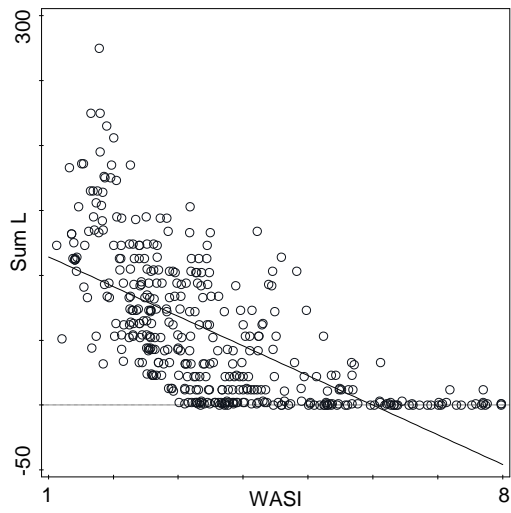
Figure 13. *Relationship between WASI and Sum L.*
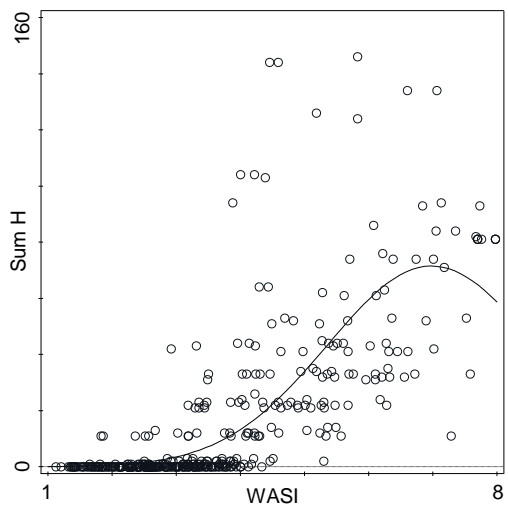
Figure 14. *Relationship between WASI and Sum H.*
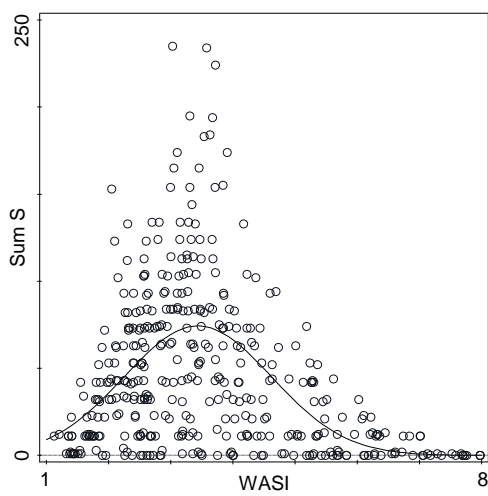
Figure 15. *Relationship between WASI and Sum S.*

Figure 16. *Relationship between WASI and Sum G.*
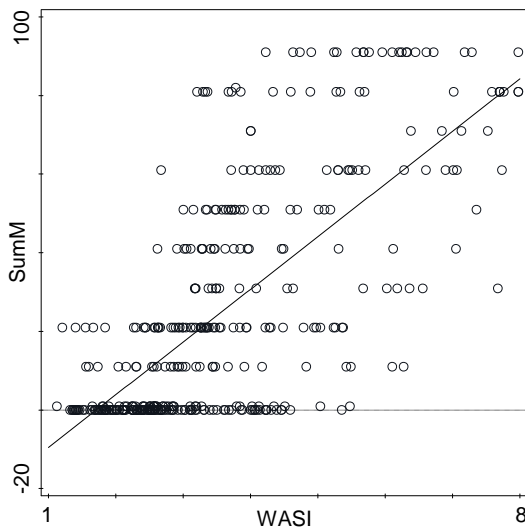
Figure 17. *Relationship between WASI and Sum M.*

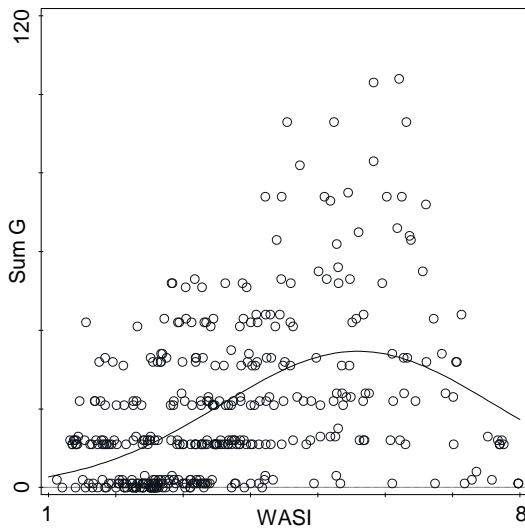Based on the GLM results, the relationship between lichens and WASI was linear and negative, because the slope obtained was negative, which means that lichens became less abundant as the snow layer increased (Fig.13). The opposite is true for mosses, which showed a positive linear correlation with the snow layer and where therefore more abundant when the snow layer was thicker (Fig.17). The abundance of herbs increased with WASI too, until the snow layer became too thick and then it started decreasing (Fig.14). About shrubs, they showed a maximum near the left side of the graph and the curve diminished slightly before reaching the middle of the horizontal

axis (Fig.15). Finally, graminoids showed a very wide curve for all values of WASI, reaching a peak for relatively high WASI values (Fig.16).

The distribution patterns along the main DCA axes can also be plotted using density graphs to make more visual the response within each sample:
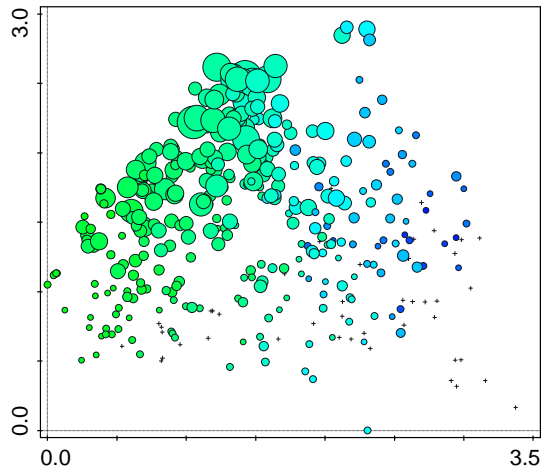
Figure 18. *Density distribution of shrubs along the main DCA axis (snow layer).*
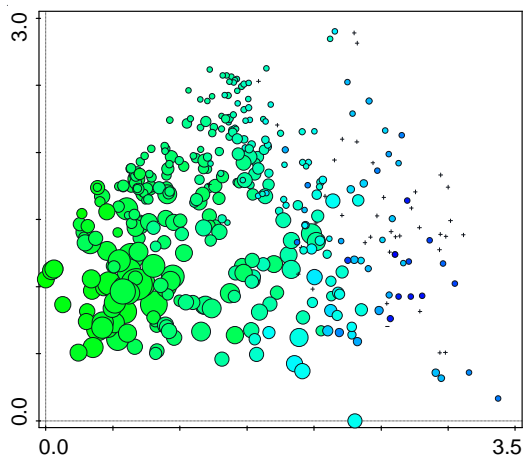
Figure 19. *Density distribution of lichens along the main DCA axis (snow layer).*
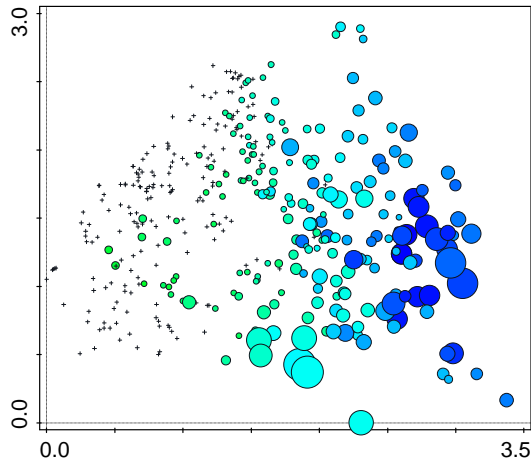
Figure 20. *Density distribution of herbs along the main DCA axis (snow layer).*
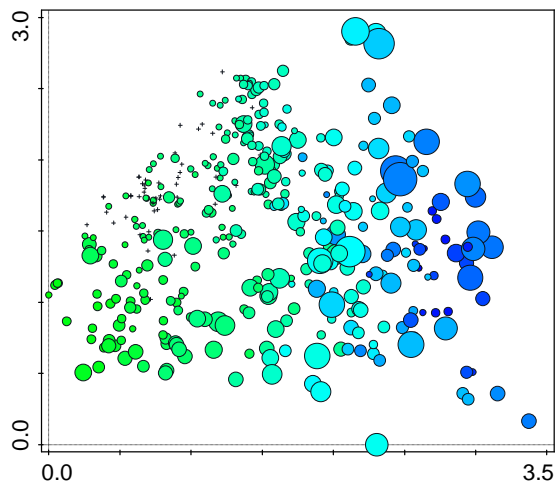
Figure 21. *Density distribution of graminoids along the DCA main axis (snow layer).*
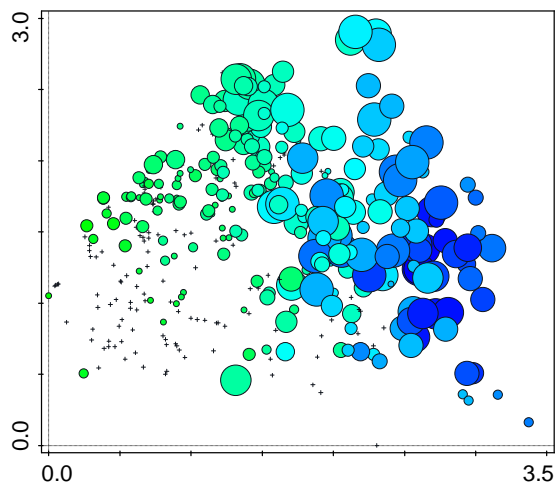
Figure 22. *Density distribution of mosses along the main DCA axis (snow layer).*

The conclusion is the same as for the GLM analysis: lichens and shrubs were more abundant towards the left side of the DCA axis 1 and still quite abundant up until the middle (Fig.19 and 18, respectively), whereas herbs (Fig.20), graminoids (Fig.21) and mosses (Fig.22) were more abundant towards the right side of the DCA axis 1. Mosses dominated the highest values of the snow layer (DCA axis 1). Shrubs (Fig.18) tended to be located closer to the top of the DCA axis 2, the opposite than lichens (Fig.19).

Next, a CCA (Canonical Correspondent Analysis) with forward selection was applied to test the significance of the stated environmental variables and their individual contribution to the total variation in species data. The hypothesis to test was:

H0: The environmental factors have no effect on the species distribution and abundance.

H1: The environmental factors have effect on the species distribution and abundance.

Table 3. *CCA with forward selection and Monte Carlo permutation test (499 permutations).*

Total variation is 3.76162, explanatory variables account for **33.7%** (adjusted explained variation is 31.7%)

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4463	0.2963	0.1297	0.1181
Explained variation (cumulative)	11.86	19.74	23.19	26.33
Pseudo-canonical correlation	0.9635	0.9044	0.8397	0.8520
Explained fitted variation (cumulative)	35.23	58.62	68.86	78.18

Forward Selection Results:

Name	Explains %	Contribution %	pseudo-F	P
WASI	11.6	34.4	50.7	0.002
Stigstuv	6.5	19.2	30.5	0.002
WAR	2.7	7.9	12.9	0.002
WAN	2.6	7.7	12.9	0.002

WAK	2.4	7.2	12.5	0.002
Glaim	2.3	6.8	12.1	0.002
WAL	1.9	5.7	10.4	0.002
WAFF	1.4	4.3	7.9	0.002
Slope	1.2	3.7	7.0	0.002
Aspect	0.6	1.7	3.3	0.002
Stones	0.5	1.5	2.8	0.004

Table 3 shows that all variables were significant except stones (p-value > 0.02). Thus they had an impact on how the species were distributed and how relatively abundant they were along the gradients. Mogen does not appear on Table 3 because there was no more variation for it to explain once the other variables had explained their contribution to the total variation. WASI explained the most variation, followed by Stigstuv (which had the opposite effect as Glaimane), WAR, WAN and WAK.

After that, a Kruskal-Wallis test was applied to look for possible differences in floristic abundance and composition between the three study areas. That test was chosen because the results of the Levene's test for the homogeneity of variances showed that any of the groups was normally distributed (see Appendix, Table 3) and therefore a non-parametric test had to be applied instead. The hypotheses tested were:

H0: The medians of the three groups are equal, that is, there is no influence of the study area on floristic abundance and composition.

H1: The medians of the three groups are different, that is, there is influence of the study area on the floristic abundance and composition.

The results obtained are shown in the tables below (Table 4, 5, 6, 7, 8):

Table 4. *Kruskal-Wallis rank sum test: Sum of G.*

A	B	C
21.0	11.0	21.5

Kruskal-Wallis chi-squared = 39.3548, df = 2, **p-value = 2.846e-09**

Table 5. *Kruskal-Wallis rank sum test: Sum H.*

A	B	C
1	0	11

Kruskal-Wallis chi-squared = 9.262, df = 2, **p-value = 0.009745**

Table 6. *Kruskal-Wallis rank sum test: Sum of L.*

A	B	C
94	22	11

Kruskal-Wallis chi-squared = 122.9812, df = 2, **p-value < 2.2e-16**

Table 7. *Kruskal-Wallis rank sum test: Sum of M.*

A	B	C
0	21	31

Kruskal-Wallis chi-squared = 66.6936, df = 2, **p-value = 3.294e-15**

Table 8. *Kruskal-Wallis rank sum test: Sum of S.*

A	B	C
11.0	63.0	47.5

Kruskal-Wallis chi-squared = 139.5885, df = 2, **p-value < 2.2e-16**

Based on these results, the null hypothesis was rejected, meaning that there were significant differences between the three study areas regarding floristic abundance and composition. Although this test does not specify which groups are different from which, that can be inferred by looking at the medians above. Thus, the study area A (Stigstuv) appeared more different from the other two (Glaimane and Mogen). In fact, Stigstuv

showed a huge lack of mosses and greater abundance of lichens compared to the other two study areas.

Finally, the plots were grouped based on the TWINSPAN© results and the relative position of the species along the axes 1 and 2 in DCA graph. Thus, eight groups were obtained and the main dichotomic subdivision split those communities either domintaed by *C.nivalis* and *V.mirtilus* or *S.herbacea* and *S.virgaurea*. The first group (group 00) was characterised by *Cetraria nivalis* and *Alectoria ochroleuca* and therefore it was called *Cetraria nivalis-Alectoria ochroleuca*-type. The second group (group 01) was *Cladonia arbuscula-Cladonia rangiferina*-type. The third group (group 010) was *Cladonia arbuscula-Empetrum nigrum*-type. The forth group (group 011) was *Empetrum nigrum-Betula nana*-type. The fifth group (group 10) was *Cladonia arbuscula-Salix herbacea*-type. The sixth group (group 100) was *Salix herbacea-Anthoxanthum odoratum*-type. The seventh group (group 110) was *Salix herbacea-Vaccinum myrtillus* type. And the eighth group (group 111) was *Betula nana-Luzula frigidea* type. These denominations are not necessary official, but they simplify the description and understanding of the communities. The main characteristics of each community, based on the mean values of both the environmental values and the species abundance, are described as follows:

The *Cetraria nivalis and Alectoria ochroleuca*-type (group 00) showed mean high values of lichens'abundance (112.5%) and shrubs were the second most abundant ecological group (38.7%). On the contrary, herbs (1%), graminoids (9.7%) and mosses (3.7%) were rare. WASI (1.9) and WAN (2.1) showed small mean values whereas WAK (4.2) was intermediate and WAL value (7) was quite high.

The *Cladonia arbuscula-Cladonia rangiferina*-type (group 01) contained less lichens (85%) and less shrubs (25.9%) than above, but they were still the most dominant groups. On the other hand, herbs (5.3%), graminoids (21.4%) and mosses (10.8%) showed still low abundance, but notably higher than the first community. This group included plots from all the three study areas in an equal measure and both WAL (7.1) and WAN (2.5) showed similar values than the previous group/community whereas WASI (3) was higher and WAK, lower (3.6).

The *Cladonia arbuscula-Empetrum nigrum*-type (group 010) contained more shrubs (69.4%) than lichens (52.4%) even though there were no major changes in WASI (3) compared to the other previous communities, but WAK (4.5) was slightly higher. Again, there was approximately the same number of plots from each study area. The abundance of herbs (1.2%), graminoids (7.6%) and mosses were lower than in the previous community (8.1%), but they were still more abundant than in the first community of this subdivision. WAN (2.4) remained quite similar to the two previous groups and WAL was slightly lower (6.8).

The *Empetrum nigrum-Betula nana*-type (011) represented an abundance of 14.6% lichens and 110.9% shrubs. Mosses were also quite abundant (37%) whereas herbs (0.6%) and graminoids (8.6%) were very scarce. All the plots belonged to either Glaimane or Mogen with no plots from Stigstuv. WAN remained steady (2.3) and WASI was slightly higher (3.3) compared to the other communities from that subdivision, whereas WAL was 7, like in the first group. This community had the highest WAK value (5.2) of all communities.

The *Salix herbacea-Cladonia arbuscula*-type (group 10) showed a great abundance of lichens (75.8%), but not shrubs (12.4%). Herbs (34%) and graminoids (31%) were much more abundant than in the previous subdivision. Mosses showed an abundance of 16%. In this case, no plots belonged to Glaimane and only one of them was located in Mogen. WASI was 4, WAK was 3.3, WAN was 3 and WAL was 6.9.

The *Salix herbacea-Anthoxanthum odoratum*-type (group 100) contained abundant mosses (52%), but few lichens (18%) and shrubs (1.2%). The most dominant ecological group was the herbs (62%) whereas graminoids (24%) were less abundant than in the previous community. There were slightly more plots from Stigstuv although the precedence was fairly equal again. WASI was 6.4 and WAN was 3.6.and WAL was similar to the previous groups (7.1).

The *Salix herbacea-V.myrtillus* type (group 110) contained fairly equal abundance of mosses (54.6%) and shrubs (50%). Graminoids were quite less abundant (28.7%), followed by herbs (24%) and lichens (19.5%). In that case, no plots belonged to Stigstuv and most of them were from Glaimane. WASI (4.6) showed higher values than

in the other communities rich in lichens while WAL (6.4) was lower. WAK was 3.9 and WAN was 2.9.

The *Betula nana-Luzula frigidea*-type (group 111) was notably rich in mosses (57.2%) and graminoids (42.7%), followed by herbs (34.3%). Shrubs represented an abundance of 24.7% and lichens were only 3.4%. No plots were from Stigstuv and there were twice as many plots from Mogen than from Glaimane. WAL (7) was very similar to most of the other communities (7), but WASI (5.8) showed the highest value of all obtained communities. WAN was 3, WAR was 2.6 and WAK 3.5.

4. Discussion

The spatial distribution of the different ecological groups along the two main DCA axes reflected their physiology, tolerance and optimum regarding the presence of snow and local topography (Fig. 7). Both the DCA and the GLM lead to the same conclusion; that herbs, graminoids and shrubs performed a significant unimodal response with different optimal values for the snow conditions while lichens showed a negative linear response and mosses, a positive linear response. When it comes to lichens, the density of the dots was greater on the left side of the DCA axis 1 (Fig. 19), which indicated that this group thrived if the snow layer was thin or absent. The same can be observed in the GLM graph (Fig. 13), where no lichens were found on the right side of the horizontal DCA axis. That means that lichens were more abundant where snow was non-existent or scarce and it explains why they were mostly found on the top of the ridges, where the snow was blown away by the wind. Plus, they were more abundant in Stigstuv than in any of the other study areas, because it was drier and windier, less suitable for the vascular plant species. In fact, lichens are capable of enduring the mechanical stress caused by the wind and they profit from more sunlight by growing on the top of the hills. On the contrary, they were much less abundant in Mogen and Glaimane. Since shrubs and lichens showed similar requisites regarding snow, that may indicate that shrubs were better competitors than lichens in these areas. Shrubs were benefited by the more humid conditions and created shadowed and highly humid sites under the canopy which made more difficult the establishment of lichens.

Regarding mosses, they showed exactly the opposite pattern, they had a positive linear correlation with the snow layer (Fig. 17). Thus, they were more abundant in the snowbeds and almost inexistent on the ridges since they were mostly found on the right side of the DCA axis 1 (Fig. 22). These organisms are highly dependent on humid conditions because they do not possess proper roots and they are not able to regulate their aquatic equilibrium by their own means. Thus they are dependent on the water provided by the snowmelt, and are usually the most dominant group where the snow layer is thickest.

Some graminoids can also tolerate a thick layer of snow (Fig. 21, 16) and many of them were found on the right side of the DCA axis 1 and on the inferior part of the DCA axis 2 (Fig. 7). Whereas few species could grow where snow was absent, some of them grew where it was present for long periods of time and in great quantity, so there were big differences between species within this group. That is why their overall tolerance to snow was wider than for any of the other ecological groups (Fig. 16). However, the average optimum value for snow tolerance was found in the second half of the gradient , where the snow layer was from intermediate to elevated (Fig. 21), meaning that they will be more abundant at the end of the gradient (towards the right side of the DCA axis 1), representing a larger amount of snow. That implies that this ecological group included several chianophilous species.

Like graminoids, herbs were also found to be relatively more abundant where snow was present, that is, on the right side of the DCA axis 1 (Fig. 8, 14, 20). Plus, some species capable of enduring relatively dry conditions (such as *L.spicata* and *F.ovina*) were found in Stigstuv (Fig. 10) while others were more determined by the snow layer (like *N.stricta* and *A.odoratum*). Those were the two clear trends within this group: some species were more determined by the presence of the snow while others depended more on humidity and other microclimatic traits of the different study areas (Fig. 10, 20).

The shrubs were quite abundant at the middle of the DCA axis 1 as well, but the main trend was to be found at the beginning (Fig.15, 18) and they were almost inexistent on the right side of the DCA axis 1 (Fig. 8). However, some dwarf shrubs could grow in the snowbeds or quite close to them (like *Salix herbacea*). That is

because they have deep roots that allow them to endure moisture deficiency before the snowmelt. Some of these species can store carbohydrates in their roots so as to quickly use these resources just after the snowmelt and that is why some of the shrubs species are found after the middle of the gradient towards the snowbeds, closer to the right side of the DCA axis 1 (Fig.15, 17). On the other hand, they tended to be located closer to the top of the DCA axis 2 while lichens did not follow that trend. That indicated that Glaimane represented the ideal moisture and topography conditions for shrubs, so that area was a stronger determinant for shrubs than for lichens, more affected by the presence of snow.

To sum up, the fieldwork observations matched the expected pattern. Whereas Stigstuv appeared to be the richest area in lichens, Glaimane and Mogen contained more mosses and Mogen contained even more mosses than Glaimane because Mogen represented the highest WASI. On the contrary, Stigstuv showed the lowest WASI and that was the main factor explaining the high lichens abundance. Glaimane contained more shrubs than the other two study areas and that explained why it had the same effect than increasing WAK on vegetation (Fig. 7): the drier the climate, the more shrubs. The abundance of herbs and graminoids fluctuated more in the different study areas and it was mostly determined by WAN and WASI. The apparent visual resemblance between Glaimane and Mogen was confirmed by the Kruskal-Wallis results.

These findings were complemented by the TWINSPAN© classification. First of all, the main difference between the two subdivisions was the constant presence of *S.herbacea* in the zones with most snow versus the relative dominance of lichens and shrubs in drier zones.

The *Cetraria nivalis and Alectoria ochroleuca*-type (group 00) included more plots from Stigstuv than any of the other areas, so that indicated that this was a rich area when it comes to lichens. There was a lot of light because of the flat terrain, which did not allow many shadow sites. It also explains the relatively high WAK and the low WASI since that was the study area further west but it contained many exposed sites without snow. Shrubs were the second most abundant ecological group because they do not tolerate much snow either.

The *Cladonia arbuscula-Empetrum nigrum*-type (group 010) represented mostly plots from the beginning of the transect, where WASI was in general still low. The snow conditions were favourable to both lichens and shrubs, that is, mostly plots free from snow, not exactly on the ridges but slightly further away, where slope was higher than 0-10º. That is why shrubs were more abundant than lichens and WAL was lower than on the exposed top. The *Cladonia arbuscula-Cladonia rangiferina*-type (group 01) represented similar conditions to those described, but with higher WAL and WAN, thus facilitating the growth of more herbs and graminoids. This community would follow the previous one in the gradient, with greater slope.

The *Empetrum nigrum-Betula nana*-type (group 011) included some drier plots belonging to Glaimane and Mogen. Shrubs were the most dominant group due to the low WASI and the high WAL. On the other hand, mosses were much more dominant than lichens. That was explained by the dense layer of shrubs, which favoured the retention of moisture near the soil and facilitated mosses' growth. Thus, humidity was still determinant for mosses since they are highly dependent on moisture.

The *Salix herbacea-Cladonia arbuscula*-type (group 10) represented the conditions where the snow layer was slightly thicker in Stigstuv. Despite having sites with relatively high WASI, lichens were still the most dominant group in that study area, so that means that Stigstuv showed a great abundance of that ecological group across the whole landscape. Even where the conditions were not ideal for that group, they were still present. On the contrary, chianophilous species, especially mosses, remained considerably low.

The *Salix herbacea-Anthoxanthum odoratum*-type (group 100), together with the *Betula nana-Luzula frigidea*-type (group 111), were snowbeds communities or at least belonging to the second half of the transect, where snow was more abundant.

The *Betula nana-Luzula frigid*-type (group 111) included plots situated close to the snowbed, mostly in Mogen and some in Glaimane. That is why shrubs were still quite abundant, since they were found across the whole study area, both in Glaimane and Mogen. The *Salix herbacea-V.myrtillus*-type (group 110) showed a similar pattern, but

more representative of Glaimane, where lichens were even less abundant due to the competition with shrubs.

5. Conclusions

Snow was the most determinant factor explaining species abundance and distribution. Herbs could tolerate a considerable amount of snow whereas graminoids showed a very wide tolerance interval for the snow layer, meaning that different species within this group had diverse optimal values regarding the snow layer. In addition, WAN was also a strong determinant for herbs and graminoids. Despite WAN was quite low in the three study areas, those groups rapidly increased with low increases in WAN. On the other hand, the peculiarities of the chosen study areas were also fundamental determinants on the species distribution and composition. Stigstuv included many dry, windy and snow-free sites where lichens and some herbaceous species were the most dominant groups whereas Glaimane included more humid sites where shrubs were better competitors than lichens.

Many authors have claimed that the used of indicator values may not be appropriate outside the area they were determined for and that may explain why WAK was not totally explaining the variation within the DCA axis 2. None of the selected study areas had purely an oceanic climate and therefore the overall peculiarities of the chosen study areas were indeed a better predictor than WAK. Both Stigstuv and Glaimane were found to be strong determinants themselves on vegetation, meaning that the conditions at these areas made them unique zones regarding plant species and composition. In this case, a north-south gradient would be more appropriate than a west-east gradient regarding humidity and climate since all study areas were located in the eastern part of the park.

The main common characteristic to aggregate the plots into vegetation communities was the relative dominance of either lichens and shrubs or herbs and graminoids. That first subdivision related to drier, more exposed to the sun and snow-poorer sites whereas the second subdivision related to humid and snow-rich sites.

Due to climate change, alterations in alpine species distribution and abundance are expected. Therefore further research is recommended, especially regarding lichens and mosses, both inhabiting the two extremes of the snow gradient. It would be interesting to test if snow will be still the most relevant environmental variable for alpine species after changes in snow layer thickness and duration occur.

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Appendix

Materials used

The material used in this work included:

-Tape: To establish and mark the transects.

-Clinometre: To evaluate the slope.

-Notebook, pencil and waterproof sheets: To write down all the fieldwork data.

-GPS Garmin ©: To set the position altitude and aspect of the transects.

-Floras: To identify the plant species.

Glydendals nordiske feltflora (Bo Mosseberg & Lennart Stenberg), Glysendal.

-2x2m sticks: To establish the plots (and subplots).

-Plastic bags: To collect to non-identified species for further interpretation and identification.

Table 1. *Fieldwork data.*

Stigstuv	Glaimane	Mogen
7 transects	9 transects	3 transects
37 plots	48 plots	15 plots
148 subplots	192 subplots	60 subplots

Table 2. *Species selected and their correspondent ecological group.*

Species name	Abbreviation	Ecological group
Alectoria ochroleuca	*ale och*	L
Antennaria dioica	*ant dio*	H
Anthoxanthum odoratum	*ant odo*	G
Avenella flexuosa	*ave fle*	G
Bartsia alpina	*bar alp*	H
Betula nana	*bet nan*	S
Bistorta vivipara	*bis viv*	H
Carex bigelowii	*cx big*	H

Cerastium cerastioides	*cer cer*	H
Cetraria islandica	*cet isl*	L
Cetraria nivalis	*cet niv*	L
Cladonia arbuscula	*cla arb*	L
Cladonia stellaris	*cla ste*	L
Empetrum nigrum ssp *hermaphroditum*	*emp nig*	S
Festuca ovina	*fes ovi*	G
Festuca rubra	*fes rub*	G
Gentiana purpurea	*gen pur*	H
Geum rivale	*geu riv*	H
Gnaphallium norvegicum	*gna nor*	H
Hieracium alpina	*hie alp*	H
Hieracium pilosella	*hie pil*	H
Juncus trifidus	*jun tri*	G
Luzula frigideae	*luz fri*	G
Luzula multiflora ssp frigidea	*luz fri*	G
Luzula spicata	*luz spi*	G
Nardus stricta	*nar str*	G
Phleum alpinum	*phe alp*	G
Ranunculus acris	*ran acr*	H
Rumex acetosa	*rum ace*	H
Salix herbacea	*sal her*	S
Salix laponum	*sal lap*	S
Sibbaldia procumbens	*sib pro*	H
Solidago virgaurea	*sol vir*	H
Trientalis europaea	*tri eur*	H
Vaccinum myrtillus	*vac myr*	S
Vaccinum uliginosum	*vac uli*	S
Vaccinum vitis-videa	*vac vit*	S
Veronica alpina	*ver alp*	H

Table 3. *Results of Levene's test for homogeneity of variances.*

Ecological group	p-value
Graminoids	3.02e-05 ***
Herbs	0.0007901 ***
Lichens	2.058e-07 ***
Mosses	2.771e-06 ***
Shrubs	5.354e-14 ***

Declaration of Master Thesis Authorship

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