Impact of Nitrogen Deposition on Species Richness and Species Composition of Ombrotrophic Mires in Western Norway

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Front page: Sunset at Havmyran, Hitra. Photo: Mari Jokerud

From left to right:*Sphagnum pulchrum, S. angustifolium, S. fallax, S. subnitens* and *S. compactum*. Photo Mari Jokerud

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ABSTRACT

There is almost no research on ombrotrophic mire vegetation and the possible impact of atmospheric nitrogen deposition on species richness and composition in Norway. It is important to detect whether N deposition is impacting this system since this vegetation type is listed as 'vulnerable' in the Norwegian Red List and since it has low 'critical loads' for nitrogen. Findings from European research show that deposition of N reduces biodiversity in nutrient poor ecosystems, including ombrotrophic mires. Increased N deposition favours faster growing and larger species, leading to competitive exclusion of plants adapted to low N deposition. As a result, N-sensitive vegetation has declined in European peatlands, heathlands and grasslands since the mid-20th century.

The aim of this thesis is to assess changes in species richness and species composition in vascular plants and bryophytes, and to determine whether nitrogen deposition impacts species richness and species composition on ombrotrophic mires in Western Norway. This is investigated over time by performing resample and over space by performing a gradient survey. Two resample surveys were performed, in an southern locality which has been subjected to relatively high levels of N deposition (58°31'40" N, 8°46'43" E and 1357 mgN/m^2/year) and a northern locality where N deposition levels have been lower (63°28'53" N, 8°37'19"E and 269 mgN/m^2/year) and the gradient was performed between the southern and northern locality. The combination of the two different approaches also allows comparison between different approaches.

Changes in occurrence and relative frequency of occurrence over time were investigated using to assess whether species richness had changed. Relative changes in species environmental optima were calculated with Ellenberg environmental indicator values in order to detect which environmental variables that could explain possible changes in species composition. Linear multiple regression model and backward selection was used to assess which environmental gradient that best explains species richness patterns in the gradient study.

The findings from both surveys suggest that nitrogen deposition is impacting the mire vegetation in the south where nitrogen deposition is highest and also above the suggested critical load (500-1000 mgN/m^2/yr). The southern locality showed decreased species richness and alteration of species composition which are most likely caused by increased N deposition. The northern resampling locality showed changes in terms of increased species richness and alteration of species composition but these changes are probably related to natural succession. The gradient survey support the finding that that N deposition decrease species richness on southern ombrotrophic mires

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1. INTRODUCTION

1.1 NITROGEN DEPOSITION AS A GLOBAL THREAT

During the last century, and especially the last fifty years, the use of fossil fuels and the Haber-Bosch process to produce agricultural fertilizers have greatly increased global food production and improved our standard of living. However this development is not without costs as the release of reactive nitrogen to the environment has increased tremendously, posing a major global threat to biodiversity (Bobbink et al., 2010, Galloway et al., 2008, Sala et al., 2000, Sutton et al., 2011). Reactive nitrogen is defined in Sutton et al., (2011) as all forms of nitrogen except di-nitrogen (N_2) which is abundant in the atmosphere. Reactive nitrogen is released to the environment in two forms, reduced (ammonia (NH_3), hydrazine (NH_2NH_2) and diimide (HNNH)) originating primarily from is fertilizers, and oxidized (nitrogen dioxide (NO), nitrous acid (HNO_2), nitrogen dioxide (NO_2) and nitric acid (HNO_3)) originating primarily from combustion of fossil fuel from energy, transport and industry (Sutton et al., 2011). Other sources of reactive nitrogen are biomass burning and soil emissions (Fowler et al., 2005, Galloway et al., 2004).

Current nitrogen emission scenaria suggest increased rates of atmospheric nitrogen deposition on a global scale by 2050 (Galloway et al., 2008). Europe covers 3% of world continental areas and accounted for 14 % of the global oxidized nitrogen (NO_x) emissions in 2000, 3/4 of which is deposited within mainland Europe. There are strong nitrogen deposition gradients in Europe where north-west mainland Europe receives the highest loads of total N deposition (>3000 kg/N/km^{-2}/yr^{-1}) decreasing towards the coastal and peripheral areas so that, for example, in northern parts of Scandinavia deposition is largely below 500 /N/km^{-2}/yr^{-1}. Global change drivers do not operate in isolation, so climate change with increased air temperatures and changed precipitation patterns is likely to affect the biogeochemical nitrogen cycle in north-western Europe significantly (De Wit et al., 2007, Hole and Engardt, 2008).

The European Union have implemented several directives related to nitrogen emissions and concentrations (2008/50EC, 2008/1/EC and 2001/81/EC) (Sutton et al., 2011).

1.3 THE EFFECT OF ATMOSPHERIC NITROGEN DEPOSITION ON PLANT COMMUNITIES

Phoenix et al. (2006) suggests that air pollution may pose a far greater threat to global biodiversity than previously recognised, and atmospheric nitrogen deposition is recognized as one of the major threats. European research show that deposition of atmospheric nitrogen reduces biodiversity in nutrient poor ecosystems (Berendse et al., 2001, Sutton et al., 2011). Elevated nitrogen deposition favours faster growing and bigger species (often nitrophilous), leading to competitive exclusion of plants adapted to low nitrogen availability (Bergamini and Pauli, 2001, Bobbink et al., 1998, Stevens et al., 2004, Sutton et al., 2011). As a result, nitrogen-sensitive vegetation has declined in European peatlands, heathlands, grasslands, and forests since the mid-20th century (Stevens et al., 2004, Sutton et al., 2011). One of the first studies that documented a statistical relationship between increase in nitrogen deposition and decrease in species richness was Stevens et al., 2004, who found a negative linear the relationship. This does not support the idea of 'critical loads', which is defined as "a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified Sensitive elements of the environment do not occur according to present knowledge" (Nilsson and Grennfelt, 1988). However a more detailed study published in 2010 found a curvilinear relationship and this might indicate that critical load of nitrogen deposition actually does exist (Stevens et al., 2010).

Ombrotrophic mires are particular sensitive to nitrogen deposition because they are nutrient and species poor ecosystems (Aarrestad and Stabbetorp, 2010, Bobbink et al., 2003). Ombrotrophic mires accumulate peat and thereby shift the source of nutrients from water from inorganic soils and bedrock to rainwater (Moen, 1998, Rydin et al., 2006). The vegetation has low species richness mostly consisting of *Sphagnum* species, graminiods, dwarf shrubs and some herbs (Aarrestad and Stabbetorp, 2010). Ombrotrophic mires are vulnerable to nitrogen deposition and are anticipated to have critical loads between 500 and 1000 mgN/m^2/year, so that even in Norway this threshold has been exceeded to some degree and for most of Europe it has been severely exceeded (Aarrestad and Stabbetorp, 2010, Sutton et al., 2011). The effects of increased nitrogen deposition on ombrotrophic mires are considered to be an increase in vascular plant cover, change in moss flora, nitrogen saturation in *Sphagnum*, nitrogen accumulation in peat and peat water (Berendse et al., 2001, Bergamini and Pauli, 2001, Bobbink et al., 2003, Gunnarsson et al., 2004, Nordbakken et al., 2003). Research on ombrotrophic mires have indicated that ombrotrophic vegetation has declined and nitrophilous species has increased due to nitrogen deposition, and hummocks are anticipated to be more affected since the deposition is 40 % higher here than in hollows (Aarrestad and Stabbetorp,

2010, Bobbink et al., 2003, Bobbink et al., 1998). This makes ombrotrophic mires particularly interesting to study in a Nitrogen deposition effects context.

Field experiments have commonly been used to assess changes in the vegetation of ombrotrophic mires due to nitrogen deposition. They often focus on either species specific changes or changes in vegetation. Berendse et al. (2001) proposes three different phases of nitrogen pollution in *Sphagnum* bogs: (i) at low deposition levels N is still limiting *Sphagnum* growth, so that N addition leads to increased peat moss growth. (ii) At intermediate deposition, N no longer limits *Sphagnum* growth, but the *Sphagnum* layer has not yet reached its maximum organic N content. Here low growing species e.g. *Drosera rotundifolia, Polytrichum strictum* and *Sphagnum* can increase in frequency because all these species easily and efficient take up nutrients and will therefore absorb most of the increased N deposition up to the critical load (Aarrestad and Stabbetorp, 2010, Berendse et al., 2001, Mitchell et al., 2002, Nordbakken et al., 2003, Rydin et al., 2006). This leads to increased Sphagnum growth and very little nitrogen will pass through the Sphagnum filter down to the roots of vascular plants (Berendse et al., 2001, Nordbakken et al., 2003, Rydin et al., 2006). (iii) At high deposition, the *Sphagnum* layer has reached its maximum organic N content, so that additional N input will reach the soil solution. This is because above the critical load Sphagnum is N saturated and growth will not increase, nitrogen will then be available for vascular plants through their roots (Berendse et al., 2001, Nordbakken et al., 2003, Rydin et al., 2006). The result of this is that mosses will become P limited or co-limited by P and K (Aerts et al., 1992, Bragazza et al., 2004, Gunnarsson and Rydin, 2000), and large productive species will increase while bryophytes and other low growing species will decline caused by reduced light availability (Berendse et al., 2001, Bergamini and Pauli, 2001). *Drosera rotundifolia* for instance decreased and the survivorship of the plants after 4 years of receiving nitrogen above the critical load was significantly reduced, this was probably a result of intensified competition for light because *Eriophorum* spp. and *Andromeda polifolia* increased (Redbo-Torstensson, 1994). Berendse et al. (2001) propose that the bogs that have reached phase 3 will eventually change into grassland or heathland ecosystems.

Gradient studies have also been used in order to determine whether nitrogen deposition is impacting mires. For example, a gradient study from 2004 examined fifteen mires across Europe with a natural gradient of bulk atmospheric nitrogen deposition (Bragazza et al., 2004). The survey found that the hummocks appear to be more sensitive to increased atmospheric nitrogen deposition because stem volume density of *Sphagnum* in hummocks decreases at higher N deposition which

has a negative impact on water transport through the *Sphagnum* stem and in turn makes the hummocks less firm. They also suggest a critical load of N deposition of ca 1000 $mgN/m^2/year^{-1}$, above this limit the *Sphagnum* plants shifts from being N-limited to be K+P co-limited (Bragazza et al., 2004).

A third common approach in assessing environmental change effects is resampling studies, and a resampling of a Swedish mire was made in 2008 by (Kapfer et al., 2011), 54 years after the original survey was carried out. Trees and dwarf shrubs were found to have increased in frequency while the typical mire species had declined or disappeared. This was attributed to effects of increased temperature and nutrient availability (Kapfer et al., 2011).

1.4 AIM

The aim of this thesis it to assess changes in species richness and species composition in vascular plants and bryophytes, and to determine whether nitrogen deposition impacts species richness and species composition on ombrotrophic mires in Western Norway. This will be investigated (i) time using a resampling approach, (ii) over space using a gradient approach, and the use of these tow methods also allows (iii) a comparison of the results and conclusions obtained by the two approaches:

(i) For the resampling survey I selected two sites, one in a low deposition area receiving atmospheric Nitrogen deposition below the critical load (<500 $mgN/m^2/yr$) and the other in a high deposition area receiving atmospheric Nitrogen deposition above the critical load (1000 $mgN/m^2/yr$). Here I will investigate species richness and composition and compare the results between the two sites. I predict that the site in the high deposition area will have greater changes than the site in the low deposition area in terms of significant reduction of species richness and alteration of species composition. These changes are expected to be related to the species' nitrogen tolerance.

(ii) For the gradient study I aimed at sampling 20 ombrotrophic mires along a latitudinal gradient along the west coast of Norway. The sites in southern Norway receive nitrogen deposition above the critical load of 1000 $mgN/m^2/yr$ and this gradually declines towards the northern most parts of Western Norway receiving nitrogen deposition below the critical load of 500 $mgN/m^2/yr$). Other explanatory factors were kept as constant as possible. Based on biogeographical patterns alone

species richness would be expected to decline northwards, but I expect that atmospheric nitrogen deposition has impacted species richness in the southernmost sites so that the sites in southern Norway will have lower species richness than the sites further north.

(iii) I will also compare the results of the two approaches. The gradient study is expected to reflect the resampling study by showing decline in species richness from north to south to north as the resampling survey is expected to show a decline in species richness and alteration of species composition in the southern site.

2. INVESTIGATED SITES

This thesis consists of a resampling of two historical surveys and a gradient study, both conducted in ombrotrophic mire vegetation. One of the historical surveys is at Austre Moland located in a high-deposition area receiving an average of 1357 mgN/m^2/year, while Hitra is located in a low-deposition area receiving an average of 269 mgN/m^2/year (Figure 1a). The historical phytosociological survey from Austre Moland was collected by Arne Pedersen in 1967 as his post-graduate thesis in biology (Pedersen, 1973), the historical phytosociological survey from Hitra was conducted by Arnfinn Skogen in 1964 and is unpublished (Skogen, 1964). The gradient study consists of 21 localities from southern Norway along the western coast of Norway and up to Hitra.

The nitrogen deposition in Norway has been relatively constant over recent decades (Aarrestad and Stabbetorp, 2010). The nitrogen deposition gradient within Norway is large, low deposition areas receive less than 500 mg N/m^2year^{-1} while the high deposition areas receive more than 1600 mgN/m^2year^1. The highest loads of nitrogen deposition are in south and south-west Norway and it decreases with latitude and altitude (Figure 1a). According to Aarrestad and Stabbetorp (2010) 14 % of Norway's area has received nitrogen deposition exceeding the critical load for Norwegian vegetation types, this is based on the period from 2002 to 2006. This makes Norway a good place to study how nitrogen deposition affects species richness and species composition since nitrogen deposition is both above and below the critical load for several ecosystems.

Hole and Engardt (2008) anticipates that Norway in the future will experience a moderate increase in nitrogen deposition of about 10 %. However, due to increased precipitation resulting from climate change (at least 50 % increase of the precipitation during the period 2071-2100 compared to period 1961-1990), the west coast of Norway is predicted to experience a large increase in total nitrogen deposition in the future (10-20 % increase in the period 2021-2050 and a 20-40 % increase in 2071-2100 compared to current N deposition). This study also predicts that deposition of oxidized nitrogen will increase more than reduced nitrogen, and most of the oxidized nitrogen is long transported from the continent of Europe (Aarrestad and Stabbetorp, 2010, Hole and Engardt, 2008).

2.1 HITRA

2.1.1 Site selection and investigated areas

The mire complex Havmyran is an area in the municipality of Hitra, mid Norway at latitude of 63°28'53" N and a longitude of 8°37'19"E (Figure 1a). The elevation is approximately 60 m above sea level (a.s.l.) The study site consists of three mires on Havmyrane; Øvre Laksåvatnet, Stjernegjølen and Litlbrattåvatnet, all Atlantic ombrotrophic mires consisting mostly of ombrotrophic hummock, lawn and some lawn areas (Figure 1c). The bedrock at these mires are the plutonic rock tonalite which has a high content of silicon oxide (SiO_2) since it consists of quartz and plagioclase and this makes the soil nutrient poor since it is acidic due to the high silicon oxide (Gjelle and Sigmond, 1995, Leknes, 1999, Schou Jensen et al., 2011).

2.1.2 Climate and nitrogen deposition

The climate on Hitra is oceanic with mild winters consisting of average normal winter temperature (December – February) of -0.2^{o}C and average normal summer temperature (June – August) of 12.3^{o}C (Figure 2c, Norwegian Meteorological Institute, 2011). From 1944 to 2010 average summer temperatures have increased slightly from 12.8 to 13.6^{o}C, however it showed a decreasing trend until 1980s (11.9^{o}C, Figure 2b, Norwegian Meteorological Institute, 2011). The average winter temperature has been fluctuating and is currently 1.5^{o}C). Mean annual temperatures have increased with 0.2 from 6.1 to 6.3^{o}C also with some fluctuations (Figure 2a, Norwegian Meteorological Institute, 2011). In Moen et al., (1998) Hitra is classified as belonging to the strongly oceanic section (O3h) and the average precipitation on Hitra from 1978 to 2006 is 1199 mm (Aas et al., 2008).

Total nitrogen deposition on Hitra has been low but fluctuating, with an average of 269 mgN/m^2/yr a little more than 50% of which is reduced nitrogen. A minimum was in 1988-1992 with 160 mgN/m^2/yr but it has since increased to 372 mgN/m^2/yr. The increase the last decade could be due to Tjeldbergodden industrial complex which has been built on the main land just across the fjord of Hitra and it was officially inaugurated on 5 June 1997. Tjeldbergodden has four components; a gas receiving terminal plus plants for methanol, air separation and gas liquefaction. The amount of nitrogen oxides released from here is just under 400 tonnes per year (Statoil, 2007). Slightly more than half of the nitrogen deposition consists of reduced nitrogen (Table 1).

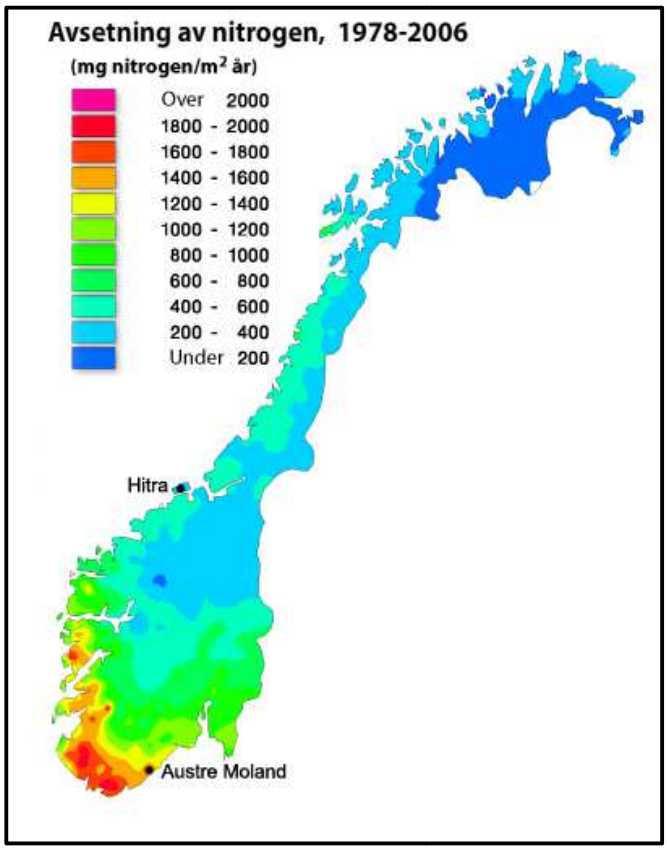
Table 1. Precipitation and nitrogen deposition history at Hitra from 1978 to 2006. Data source: (Aas et al., 2008).

Site	Year	Average precipitation amount (mm)	Total N (oxi) deposition (mg N/m^2/yr)	Total N (red) deposition (mg N/m^2/yr)	Total N (red+oxi) deposition (mg N/m^2/yr)
Hitra	1978-1982	1 144	135	199	335
Hitra	1983-1987	NA	NA	NA	NA
Hitra	1988-1992	1 310	80	80	160
Hitra	1992-1996	1 158	105	117	222
Hitra	1997-2001	1 112	100	157	257
Hitra	2002-2006	1 272	150	222	372
Average	**1978-2006**	**1 199**	**114**	**155**	**269**

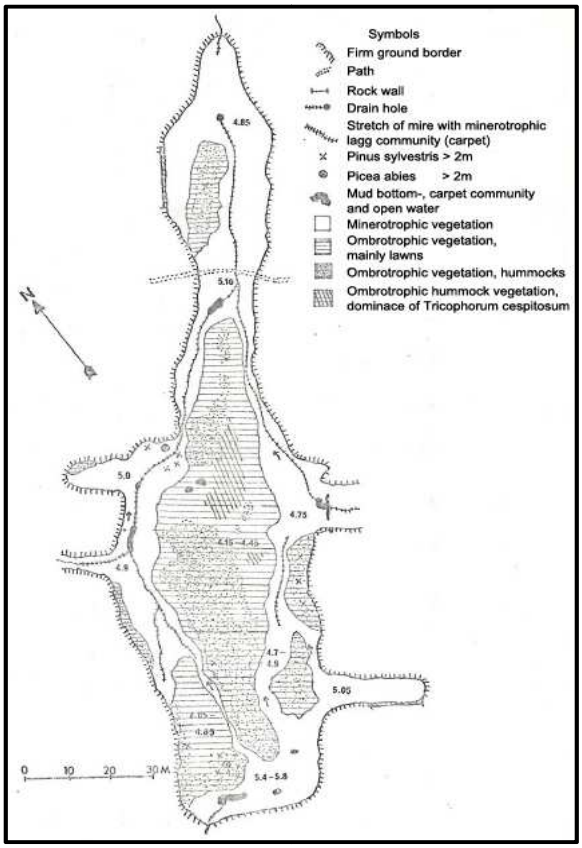
2.1.3 Vegetation

Havmyran on Hitra consist of ombrotrophic and minerotrophic mires, where Atlantic ombrotrophic mires dominates the flat and large mire areas while minerotrophic mires is often located between ombrotrophic mires and in the transition between small rock cliffs and ombrotrophic mires (Aarrestad et al., 1996). The ombrotrophic vegetation is characterized by *Andromeda polifolia, Calluna vulgaris, Erica tetralix, Rubus chamaemorus, Pleurozium schreberi, Racomitrium lanuginosum Sphagnum austinii* and *S. capillifolium* on the hummocks. The lawn vegetation is less homogenous and dominated by *Narthecium ossifragum, Carex spp., Eriophorum angustifolium, E. vaginatum, Trichophorum cespitosum, Sphagnum papillosum* and *S. tenellum*. The minerotrophic vegetation is more species rich than the ombrotrophic vegetation. It is characterized by same species as in the ombrotrophic lawn and more nutrient demanding species such as *Euphrasia* spp., *Molinia caerulea, Potentilla erecta, Selaginella selaginoides, Campylium stellatum* and *Sphagnum subnitens.*

a)



b)



c)

d)

Figure 1. a) Nitrogen deposition in Norway from 1978 to 2006, (Norwegian Institute for Air Research, 2009). b) Vegetation map of Lauvmyra in Austre Moland, numbers states pH for different mire vegetation (Pedersen, 1973). c) Arial photography of the mire areas at Hitra. Top left: Overview Hitra, top right: The mires around Øvre Laksådals-vatnet, bottom left: The mires around Stjernegjølen, bottom right: the mires to the right of Litlbrattåvatnet. d) Arial photography of the mire in Austre Moland with yellow points as plot location (Norwegian Mapping Authority et al., 2005).

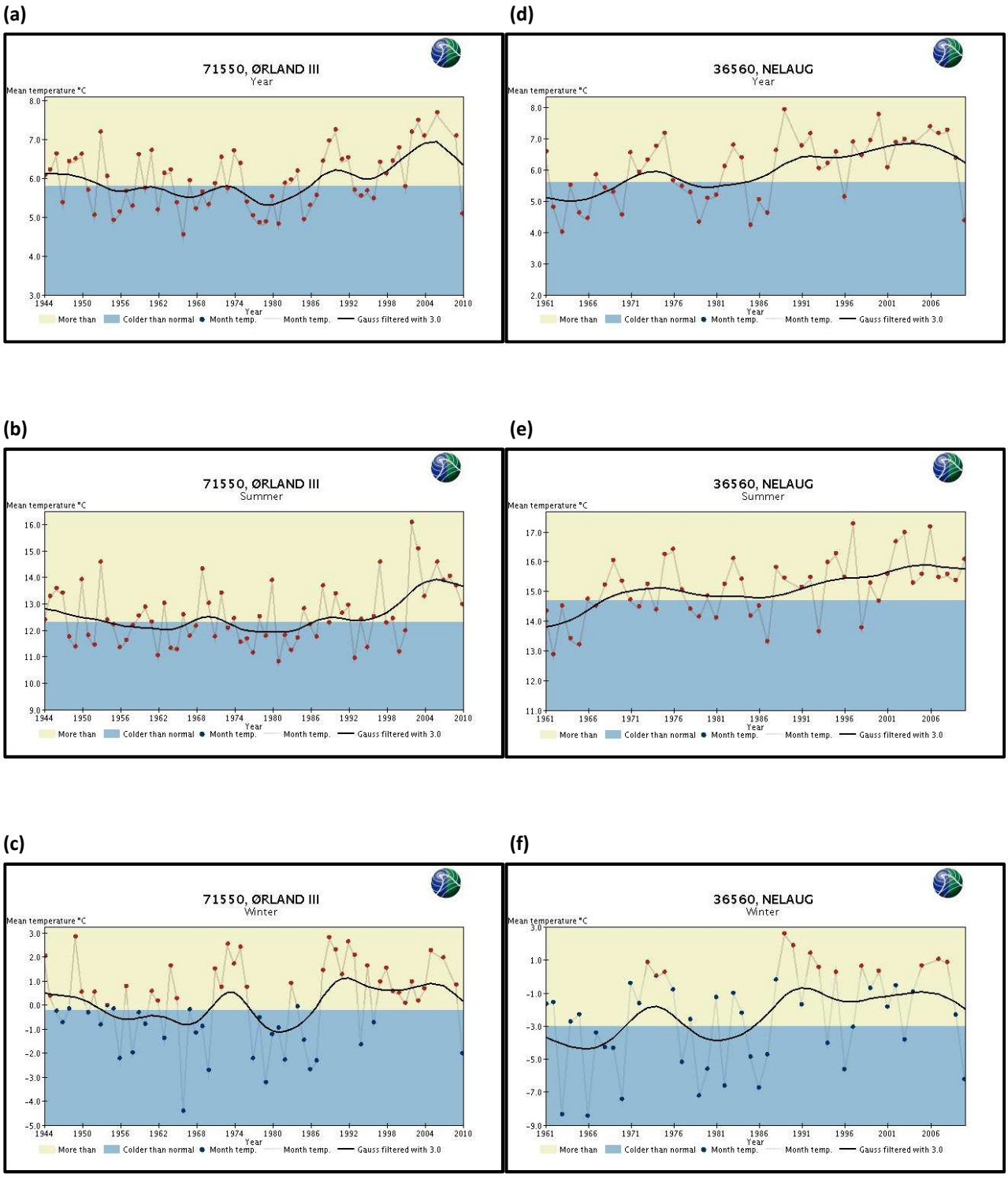


Figure 2. Mean year (a), summer (b) winter (c) year temperatures at Ørlandet, app. 53 km NE of Hitra.
Mean year (d), summer (e) winter (f) year temperatures at Nerlaug, app. 16.5 km NW of Austre Moland.
These maps were provided by (Norwegian Meteorological Institute, 2011).
The distance was measured by using a distance tool at (Norwegian Mapping Authority et al., 2005).

2.2 AUSTRE MOLAND

2.2.1 Site selection and investigated areas

The mire Lauvmyra in Austre Moland is in the municipality of Arendal, southern Norway at latitude of 58°31'40" N and a longitude of 8°46'43" E (Figure 1a). The elevation is approximately 100 m above sea level (a.s.l.). The area of the mire is approximately 4320 m^2, length is 155 meter, width at the widest 50 m and width at the narrowest is 10 m (Figure 1b and d). This is an ombro-minerotrophic mire complex with the ombrotrophic hummocks and lawns in the middle and minerotrophic lawns until the pine forest border. The bedrock at this mire is quartzite which has a high content of silicon oxide (SiO_2) and it is a hard metamorphic rock which is formed from metamorphism of sandstone. This makes the soil nutrient poor since it is acidic due to the high silicon oxide and it is not easily disintegrated (Gjelle and Sigmond, 1995, Leknes, 1999, Schou Jensen et al., 2011).

2.2.2 Climate and nitrogen deposition

Austre Moland has a weak oceanic climate with relatively mild winters with mean winter temperature (December – February) of ca. -3^oC and relative cool summers with mean summer temperature (June to August) of 14.7^oC (Figure 2e and f, Norwegian Meteorological Institute, 2011). From 1961 to 2010 both mean summer and mean winter temperature has increased, from 13.8 to 15.7^oC and from -3.7 to -2.0^oC, respectively. Mean annual temperature have increased in the same time period with 0.9 from 5.1 to 6.2^oC however with some fluctuations (Figure 2d, Norwegian Meteorological Institute, 2011). In Moen et al. (1998) Austre Moland is classified as belonging to the oceanic section (O2) and average precipitation from 1978 to 2006 is 1185 mm (Table 2, Aas et al., 2008). Total nitrogen deposition in Austre Moland has decreased a little since the peak in 1988-1992 and the average N deposition from 1978 to 2006 is 1357 $mgN/m^2/yr$. Both total oxidized and reduced nitrogen have decreased since the peak period. Slightly more than half of the nitrogen deposition consists of oxidized nitrogen (Table 2).

Table 2. Precipitation and nitrogen deposition history at Austre Moland from 1978 to 2006.
Data source: (Aas et al., 2008).

Site	Year	Average precipitation amount (mm)	Total N (oxi) deposition (mg N/m^2/yr)	Total N (red) deposition (mg N/m^2/yr)	Total N (red+oxi) deposition (mg N/m^2/yr)
AA	1978-1982	1104	750	649	1398
AA	1983-1987	NA	NA	NA	NA
AA	1988-1992	1165	830	670	1500
AA	1992-1996	1064	738	542	1280
AA	1997-2001	1354	786	604	1391
AA	2002-2006	1238	678	536	1214
Average	**1978-2006**	**1185**	**756**	**600**	**1357**

2.2.3 Vegetation

Arne Pedersen characterises Lauvmyra in Austre Moland as an ombro-minerotrophic mire complex, with ombrotrophic and minerotrophic vegetation covering roughly equal areas (Figure 1b). The ombrotrophic areas with both hummocks and lawns are mostly confined to the central parts where the mire has its highest elevation. The ombrotrophic vegetation is dominated by *Myrica gale*, *Betula pubescens*, *Erica tetralix* and *Calluna vulgaris* in the shrub layer while *Narthecium ossifragum* and *Eriophorum vaginatum* in turns dominates the field layer. *Sphagnum magellanicum* often dominates the bottom layer but occasionally there are small hummocks with *Sphagnum capillifolium* and *Sphagnum fuscum*. In some areas *Trichophorum cespitosum* dominates and then the shrub species are less abundant (Pedersen, 1973).

The minerotrophic vegetation is less homogenous than the ombrotrophic vegetation. In the south end of the mire there is an transition zone which is species poor, it consist mostly of *Carex rostrata* and *Menyanthes trifoliata* in the field layer with *Sphagnum pulchrum* dominating the bottom layer. In the western parts of the mire *Carex lasiocarpa* dominates but *Carex nigra, Carex rostrata, Menyanthes trifoliata, Myrica gale*, *Peucedanum palustre* and *Viola palustre* are also abundant. The bottom layer is still dominated by *Sphagnum pulchrum* although *Sphagnum imbricatum* dominates some areas. In the northern part of the mire there is a minerotrophic lawn vegetation with dominance of *Erica tetralix, Narthecium ossifragum, Potentilla erecta* and *Sphagnum imbricatum*. Lauvmyra receives nutrients from several small streams from south, west and east which divide the mire into several parts. As a result of Lauvmyras relatively complex hydrology and strong nutrient gradients, *Sphagnum* diversity is high with a total of 21 species recorded (Pedersen, 1973).

2.3 GRADIENT SURVEY

2.3.1 Site selection

The nitrogen deposition gradient in Norway runs south-to-north, and parallels strong bioclimatic gradients (Fig. 1a). In order to avoid covariance between deposition and climate variables in the dataset, all sites were selected to be within approximately the same climate regime; Specifically, all sites were selected to have average temperature during growing season (June-September) between 10 and 13^{o}C and an average precipitation per year between 1300 and 2500 mm (see Chapter 3.3 for details). In order to have an equally distribution of sites along the nitrogen gradient within approximately the same climate regime; four nitrogen deposition categories were selected: 0-500, 500-1000, 1000-1500, >1500 mgN/m^2/yr. Five sites were sampled within the first category, seven in the second category, four in the third category and four in the fourth category. The gradient study consists of 20 ombrotrophic mires from southern Norway along the western coast of Norway and up to Hitra.

2.3.2 Climate and environmental gradients

The climate of these sites are classified in Moen et al. (1998) as belonging to the oceanic section and the sites are almost equally divided between the clearly (O2) and strongly (O3) oceanic section. Average growing season temperature (June – September) varies between 9.53 and 14.9 ^{o}C (Table 3, Norwegian Meteorological Institute, 2011). Average precipitation varies between 1103 and 2813 mm between 1978 and 2006 and average nitrogen deposition has varied between 269 to 1750 mgN/m^2/yr (Table 3, Aas et al,. 2008).

2.3.3 Vegetation.

All sites in the gradient study are of ombrotrophic mires. The hummock and lawn vegetation is species poor and share a number of species *Andromeda polifolia, Erica tetralix, Oxycoccus palustris, Drosera rotundifolia, Narthecium ossifragum, Eriophorum vaginatum, Sphagnum capillifolium, Sphagnum magellanicum* and *Sphagnum papillosum*. On the hummocks *Calluna vulgaris, Sphagnum capillifolium* and *Sphagnum magellanicum* tends to be more abundant, while *Narthecium ossifragum, Carex spp., Eriophorum vaginatum, Trichophorum cespitosum Sphagnum papillosum* and *Sphagnum tenellum* tends to be more abundant in the lawn vegetation.

Table 3. Average precipitation and nitrogen deposition per year for the different localities in the gradient study from 1978 to 2006 (Aas et al., 2008). Average growing season temperature from 1961 to 1990 (Norwegian Meteorological Institute, 2011). Coordinates provided by sampled GPS data.

No.	Site	Latitude	Longitude	Precipitation	Temperature	Nitrogen
1	Fjosbumura	58.57	8.57	1103	13.15	1027
2	Storemyr ved Tveitvatnet	58.47	8.10	1349	12.75	1346
3	Store Bjormyr	58.30	8.48	1185	14.09	1357
4	Myr i Bjørnestølheia	58.13	7.41	1698	13.11	1750
5	Dyrlimyra	58.15	6.54	1755	11.77	1706
6	Bervamyr	58.31	6.45	1988	11.5	1679
7	Måmyra	59.10	6.12	2191	10.05	1540
8	Myrer S for Mosvatnet	59.23	6.26	2303	9.53	1320
9	Håmyrane	60.39	6.28	1951	10.8	852
10	Myr ved Vestrevatn	60.34	5.33	2342	11.19	990
11	Myrområdet langs Lona	61.17	5.10	2628	12.22	886
12	Myr ved Kleppstølsvatn	61.31	5.50	2813	9.97	870
13	Myr SØ for Lonene	61.36	5.41	2813	10.88	870
14	Store myran	61.49	5.35	2313	10.17	584
15	Myr S for Otervatn	61.54	5.25	2313	11.4	584
16	Gåsmyra	62.17	6.38	1742	12.08	484
17	Djupmyra	62.37	7.1	1384	12.04	336
18	Myr ved Sletta	63.00	7.58	1469	11.41	366
19	Rødmyran	63.03	8.14	1643	11.91	397
20	Havmyrene	63.28	8.37	1199	11.44	269

3. MATERIAL AND METHODS

3.1 HISTORICAL SURVEY METHODS

3.1.1 Hitra

The historical dataset from Hitra belongs to Arnfinn Skogen (UiB) who carried out the vegetation survey on Havmyran in 1964. His aim was to do a phytosociological survey of the vegetation on Havmyran on Hitra (A. Skogen, pers comm.) He performed vegetation analyses with 0.25 m^2 plots and used Hult-Sernander-du Ritz 5-grade scale to estimate abundance of the species. Stjernegjølen was sampled from 25.08 – 03.09.1964 and Øvre Laksådalsvatnet 04.09 - 05.09.1965 and the mire west of Litlbrattåvatnet 22.08.1964. Skogen aimed to sample plots from same vegetation type e.g. different hummock and lawn vegetation associations and his vegetation types are listed in table 4.

3.1.2 Austre Moland

The main aim for Pedersen's (1973) study was to do a phytosociological survey of the *Sphagnum* flora in Austre Moland. He used "synedrier" when sampling plots, a "synedrie" is defined as a vegetation type with one dominant *Sphagnum* species and its associated homogeneous vegetation (Pedersen, 1973). I will refer to these as *Sphagnum* associations (Table 5). A total of 118 plots by 0.25 m^2 were sampled from Lauvmyra during the summer of 1968 and he used Hult-Sernander-Du Rietz 6-grade scale to estimate abundance of the species.

Table 4. An overview of the different vegetation types on Hitra (Skogen, 1964).

Locality	Area	Vegetation type
Stjernegjølen	III a)	Calluna – Rubus
	III b)	Calluna – Narthecium – vegetation in ombrotrophic environment
	III c)	Narthecium – Trichophorum – Carex – *Sphagnum* mire in minerotrophic environment
	III d)	Calluna – Eriophorum – Racomitrium – Cladonia – vegetation in ombrotrophic environment
	III e)	Narthecium – Trichophorum – Carex – *Sphagnum* mire in minerotrophic environment
	III h)	*Sphagnum* – Carex rostrata
	III i)	*Sphagnum* – Trichophorum - Eriophorum
	III j)	*Sphagnum* – Trichophorum - Eriophorum
	III k)	Calluna – Eriophorum – Racomitrium – Cladonia – vegetation in ombrotrophic environment
	III l)	Calluna – Narthecium – vegetation in ombrotrophic environment
Øvre Laksådalsvatnet	VIII a)	Calluna – Eriophorum – Racomitrium – Cladonia – vegetation in ombrotrophic environment
	VIII b)	Narthecium – Trichophorum – Carex – *Sphagnum* mire in minerotrophic environment
	VIII d)	Narthecium – Trichophorum – *Sphagnum* – Calluna – vegetation in minerotrophic environment
	VIII e)	Narthecium – Trichophorum – *Sphagnum* – Calluna – vegetation in minerotrophic environment
Myren vest for Litlbrattåvatnet	I a	Narthecium – Calluna – *Sphagnum* – vegetation in minerotrophic environment
	II b)	Calluna – Racomitrium – Cladonia – minerotrophic mire

Table 5. An overview of the different vegetation types at Austre Moland (Pedersen, 1973).

***Sphagnum* associations**	**Type**
Sphagnum imbricatum	Menyanthes trifoliata
	Eriophorum vaginatum – Molinia caerulea
	Narthecium ossifragum
	Potentilla erecta
Sphagnum magellanicum	Eriophorum vaginatum
	Narthecium ossifragum
Sphagnum papillosum	Narthecium ossifragum
	Eriophorum vaginatum – Molinia caerulea
Sphagnum subsecundum	Carex rostrata –Sarmentypnum exannulatum
Sphagnum inundatum	Small drainage channel with slow running water
Sphagnum tenellum	Rhynchospora alba – Trichophorum cespitosum
Sphagnum pulchrum	Menyanthes trifoliata
	Carex rostrata
	Viola palustris – Carex nigra
Sphagnum fallax	Eriophorum vaginatum
Sphagnum angustifolium	Vaccinium
	Eriophorum vaginatum
Sphagnum flexuosum	Viola palustris – Carex nigra
Sphagnum subnitens	Menyanthes trifoliata
	Potentilla erecta
Sphagnum nemoreum	Ombrotrophic mire areas
Sphagnum rubellum	Eriophorum vaginatum – Potentilla erecta
Sphagnum warnstorfii	Viola palustris – Carex nigra
Sphagnum fuscum	Hummocks on overgrown mire areas
Sphagnum russowii	
Sphagnum girgensohnii	Vaccinium – Potentilla erecta

3.2 SURVEY METHOD 2010

3.2.1 Hitra

Arnfinn Skogen's original field notes were used to relocate the localities (Figure 3a). Arnfinn Skogen's focus was to detect different vegetation types on Havmyran e.g. different hummock and lawn vegetation associations, and we used the same approach when choosing plot locations. The first field work was conducted with two assistants from 28.08 to 04.09.2009 and consists of Øvre Laksådalsvatnet (VIII) and "Myren rett vest for Litle Brattåvatnet" (II). From 19 – 24.08.2010 the field work at Stjernegjølen (III) was conducted. During the field work a piece of wood was found in area III with 'III a' carved into it (Figure 3b) suggesting that even if there were no permanent plots we had properly located the original sample area. Some extra field work was conducted from 14-15.08.11 to get a total amount of 103 plots of 0.25m^2.

3.2.2 Austre Moland

When choosing location of the different plots I tried to sample the same number of plots in the different *Sphagnum* associations as Arne Pedersen, while at the same time aiming to cover most parts of the mire. The main focus was on the *Sphagnum* species and the main species they were associated with in 1968. In total 113 plots by 0.25m^2 were sampled during eleven days of field work from 23.06 to 03.07.2011 with one assistant.

3.2.3 Gradient study

In each site five hummock and five lawn vegetation plots by 0.25m^2 were sampled, 210 plots in total. First the mire was quickly surveyed in order to get an overview of the different hummock and lawn vegetation. Then the hummocks and lawns with the most frequent *Sphagnum* species for the site were selected and then the less frequent *Sphagnum* species. For instance, if the hummocks consisted of mainly *Sphagnum capillifolium* and *S. magellanicum* they were surveyed in two plots each and the less occurring *Sphagnum fuscum* was survey in one plot. The field work was conducted from 04.07 to 08.08.2010, and in order to resample this survey all plots were given coordinates with a GPS.

3.2.4 Sampling method

To estimate abundance of both vascular plants and bryophytes I used %-cover, which later was converted to Hult-Sernander-du Ritz 5-grade scale of abundance for the resampling study (Figure 3c). The different *Sphagnum* species was collected in separate bags for each plot and the other bryophytes was sampled in one bag. If no liverworts were found in a plot extra *Sphagnum* was sampled in order to search for liverworts when examining the *Sphagnum* under a magnifying glass in the laboratory. Vascular plants that could not be identified in field were sampled in a plant press for further identification. pH was measured during the field work in 2010 with a Wissenschaftlich-Technische Werkstätten GmbH (WTW) model pH3110. In the gradient survey pH was measured in 14 of 20 sites because the some of the mires were too dry during sampling and sometimes it was raining too heavily. In order to resample this survey all plots were given coordinates with a GPS.

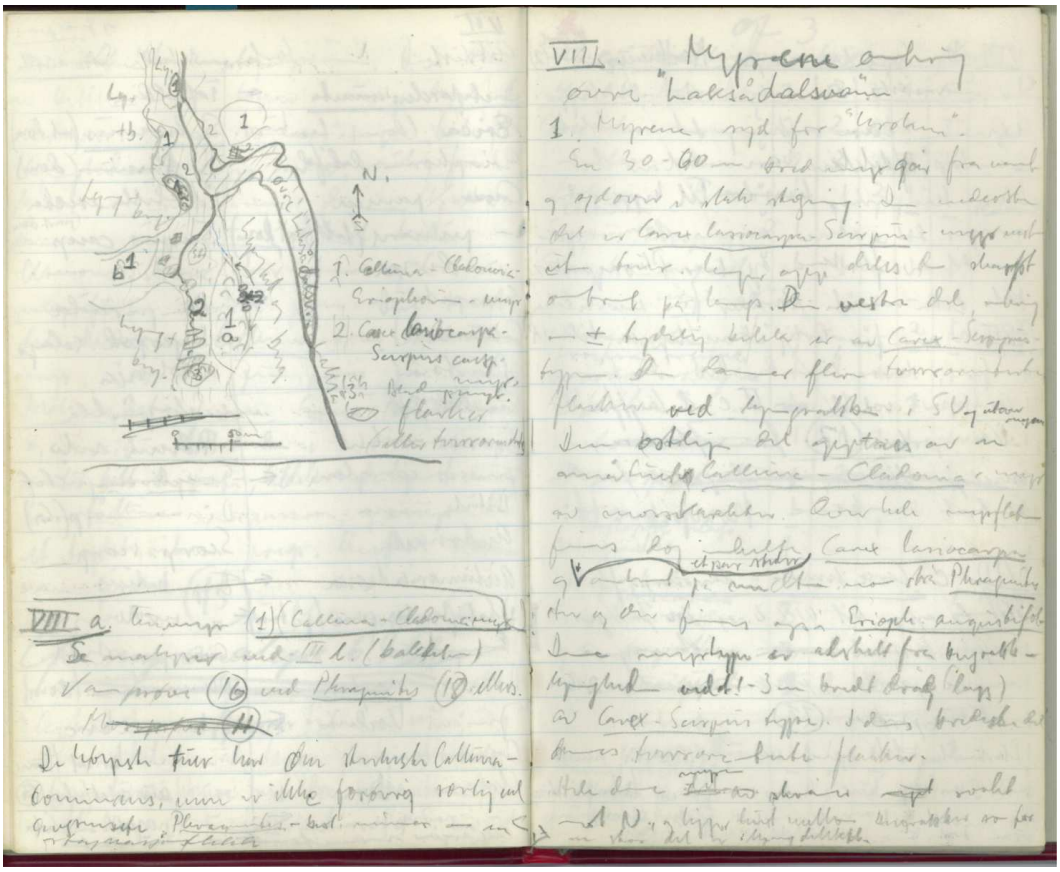
3.2.5 Nomenclature and species determination

When determining species in field Lid and Lid (2007) was used for vascular plants, while Atherton et al. (2010) was used for bryophytes. In the laboratory at the University of Bergen Lid and Lid (2007) was used to determine difficult vascular plants. All bryophytes was double checked and properly determined in the laboratory at University of Bergen for the resampling survey. Smith and Smith (2004) was used to determine *Sphagnum*, acrocarps and pleurocarps while Damsholt et al. (2009) was used to determine liverworts, a total of 1198 individual of bryophytes was determined. However there was not enough time to determine bryophytes in the laboratory for the gradient study so all determination of *Sphagnum*, acrocarps and pleurocarps is based on field determination and these are the only bryophytes in this dataset. It was decided to use field determination of these bryophytes since most of the species are easy to identify e.g. the difficult *Sphagnum* section *Subsecunda* and the *recurvum*-complexs were almost not present. The nomenclature for vascular plants follows Lid and Lid (2007) and Artsdatabaken for bryophytes.

In order to have a reliable resampling dataset for the statistical analyses it was necessary to merge species that were difficult to identify reliably. *Sphagnum capillifolium* and *S. rubellum* was treated together as *Sphagnum capillifolium*, all the *Sphagnum* in section *Subsecunda* (*S. inundatum, S. subsecundum, S. auriculatum, S. platyphyllum, S. contortum*) have been merged to *S. subsecunda*. *Odontoschisma* spp. consists of *O. denudatum, O. elongatum and O. sphagni*. *Riccardia* spp. consists of *R. latifrons, R. multifida, R. sinuata* and *Aneura pinguis. Scapania* spp. consists of *S.*

and *S. irrigua* and *S. nemorea*. Some speceis were only identified to genus; *Dicranum* spp., *Cephalozia* spp. and *Pohlia* spp.

a)



(b)

(c)

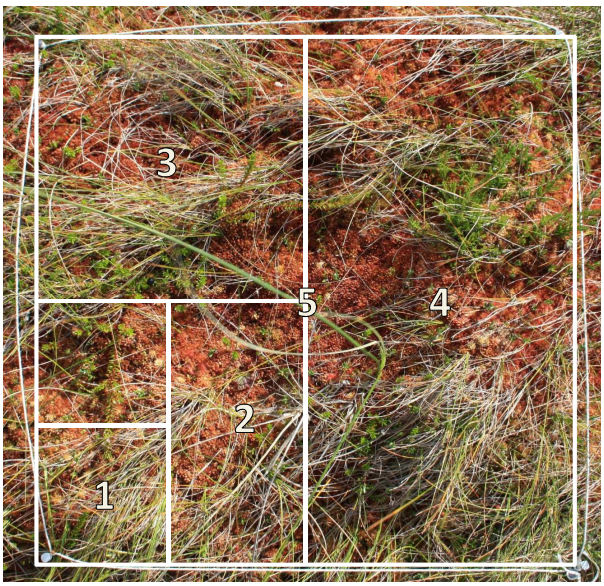


Figure 3 (a) Arnfinn Skogen's field notebook with a description of the locality Øvre Laksådalsvatnet.
(b) Arnfinn Skogen's marking of locality Stjernegjølen III a.
(c) Illustration of Hult-Sernander-Du Rietz 5-grade scale of abundance.

3.3 GRADIENT SURVEY

3.3.1 Locality selection

The Norwegian mire reserve plan was carried out with intentions to map most of the Norwegian mires so the government could establish mire reserves. This work resulted in a series of reports (Flatberg, 1976, Moen, 1975, Moen, 1983, Moen and Olsen, 1983, Moen and Pedersen, 1981) which contain description of mire type, flora, vegetation, conservation values, land and meters above sea level for a number of localities. These reports were used to find appropriate sites for the thesis. Some of the reports also contained a list of species on all the mires, these lists was used to be ensure that only ombrotrophic mires were included in the survey.

3.3.2 Geographic information system (GIS)

The N deposition gradient in Norway runs south-to-north, and parallels strong bioclimatic gradients. In order to avoid covariance between deposition and climate variables in the dataset, all localities were selected to be within approximately the same climate regime; average temperature during growing season (June-September) between 10 to 13^{o}C and an average precipitation per year between 1300 to 2500 mm. Temperature and precipitation maps were used to in order to find these areas (Norwegian Meteorological Institute). This was done in a geographic information system (GIS) computer program, everything was performed in ESRI., 2009. First step was to use the Raster Calculator in the Spatial Analyst toolbox to calculate mean growing season temperature by using the June, July, August and September layers. Then use the Reclassify tool in the Spatial Analyst toolbox to specify the suitable areas which were decided to be between 10 to 13 ^{o}C, and do the same with the average precipitation per year layer where the suitable areas were decided to be between 1300 to 2500 mm. The next step was to calculate the suitable areas for both temperature and precipitation and this was done with the Raster Calculator. Potential localities were plotted into the map and if they were within the suitable areas or borderline then it was accepted (Figure 4a, b and c). Ombrotrophic mires is not classified by species that are present, but by the absence of species that are typical for more nutrient rich mires and (Fremstad, 1997) was used to select these species that could be useful indicators of minerotrophic conditions. If any of these species were present in a potential site it was not selected.

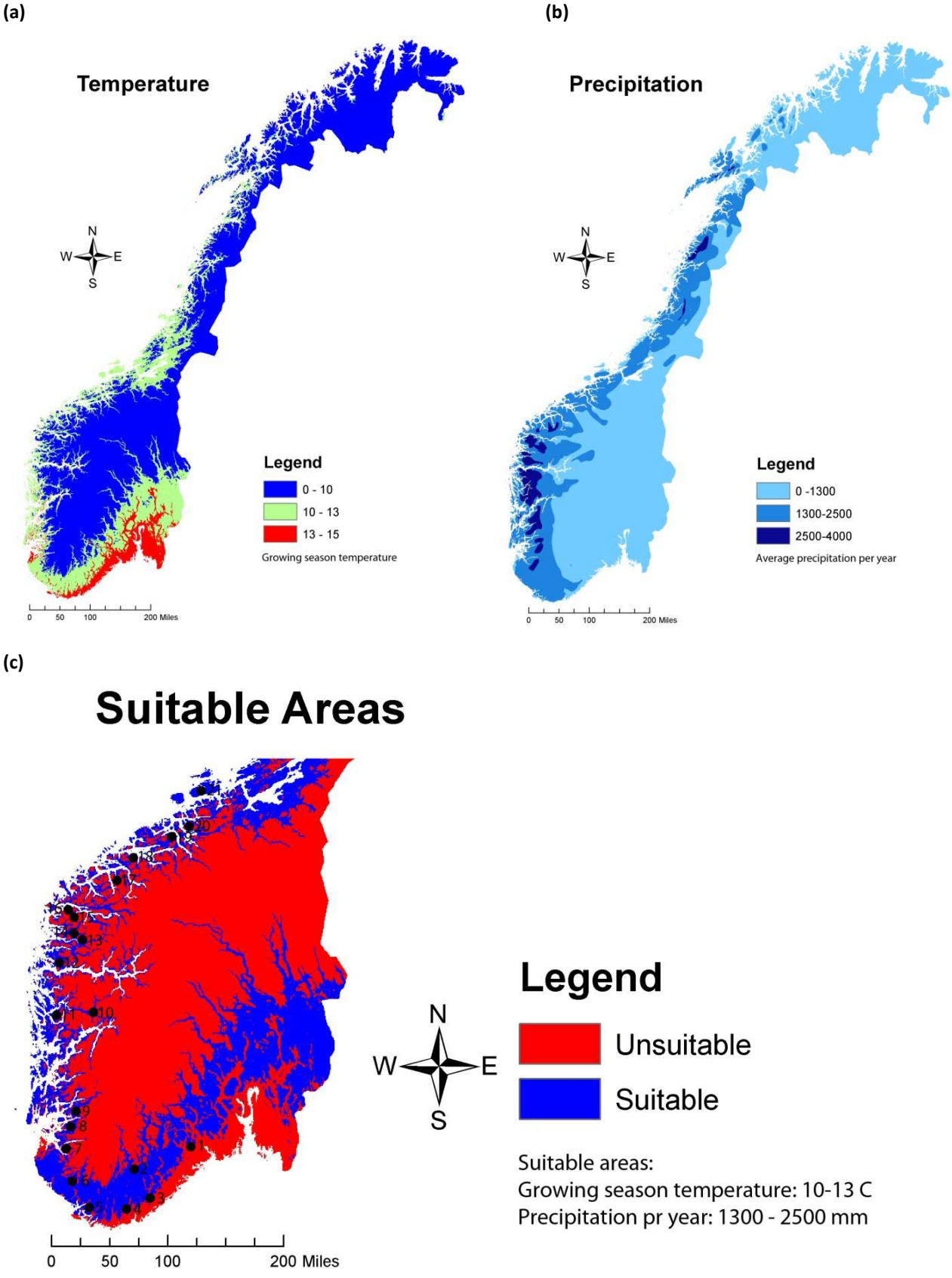


Figure 4. (a) Average growing season temperature made with ArcGIS.
(b) Average precipitation per year made with ArcGIS
(c) Suitable areas map created based on figure a and b in ArcGIS as described in the text.
Data source: Norwegian Meteorological Institute.

3.4 STATISTICS

The aim for this master thesis is to assess changes in species richness and composition in vascular plants and bryophytes over time (resampling survey) and space (gradient survey) and determine whether any changes are caused by nitrogen deposition. All the statistical analyses was performed by using R, version R 2.13.1 (R Development Core Team, 2011), and R package *vegan*, version 2.0-0 for ordination and classification (Oksanen et al., 2011).

3.4.1 Area selection

After the fieldwork on Hitra it was discovered that some of the sampling areas were not identical to the areas sampled in the original survey. However the sampling was based on the same vegetation type as in the original survey and the two surveys could therefore be compared to find which areas from the 1965 survey which were most similar in species composition to the 2010 survey. In order to find the areas from the original dataset that had the most similar species composition to the resurvey dataset a correspondence analysis (CA) was used. CA assumes a unimodal relationship of species along a gradient and since it is an indirect gradient analysis (CA) the explanatory variables underlying the observed gradients are not known environmental variables but theoretical latent variables. Ordination is designed to best explain the variation in species composition (Telford, 2010). A CA plot show the samples as points along the two axes based on the species composition, so that points close to each other represent floristically similar plots and vice versa. The main aim of the CA here was to identify potential outliers and large discrepancies in the species composition between the two surveys in the same area as this may have a large influence on the subsequent analyses. Since I knew that some of my plots were incorrectly located in my survey I choose to compare those in a CA plot with the ones I thought I had resampled and some other plots that Skogen had sampled in the same area. A Clear outliers and areas that were not overlapping between the two surveys (possibly due to selecting wrong area in the resurvey) were removed prior to further analyses.

The same correspondence analysis (CA) was also performed on the Austre Moland dataset to assess whether the different *Sphagnum* associations from the original dataset and the resurvey dataset were similar.

3.3.2 Changes in species richness and frequency

In order to assess changes in species richness, species occurrence (%) and relative frequency of species occurrence (%) over time was calculated for the original survey and the resurvey in each area. Species occurrence (%) was calculated by dividing the number of times a species occurred with total number of plots. If one vegetation type is sampled more in one of the surveys this could impact the species richness data, and a restricted permutation test (999 permutations) was therefore used to test if the species occurrence changes were significant. The randomizing of Austre Moland dataset was restricted to be within the different *Sphagnum* associations and the randomizations for the Hitra dataset were restricted to be within the different areas. Only species that occurred in more than 10 plots of the total data set were analysed, which resulted in analyzing 64 species for Hitra and 50 species for Austre Moland. Different experience in the field may result in significant changes in species occurrence, especially for inconspicuous species or species that may be confused with other species. To account for this potential bias I calculated relative frequency of species occurrence (%) for the original survey and the resurvey in addition to the original species occurrences. This was calculated by dividing the number of times a species occurred with total number of individuals in each survey. The same permutation test that was used in species occurrence (%) was performed to test if the relative frequency of occurrence (%) changes were significant.

3.3.3 Changes in species optimum for environmental gradients

I order to indirectly assess how species have changed in relation to the most important environmental variables, changes in species optimum for Ellenberg environmental indicator values were used for Austre Moland and Hitra (Kapfer et al., 2011). Hills version of Ellenbergs environmental indicator values was used to estimate each species realized optimum value in the original and resurvey for light, soil moisture, pH and nutrients while Ellenbergs version was used for temperature. This was done for both vascular species and mosses (Ellenberg et al., 1991, Hill et al., 2007, Hill et al., 2000). Then the Ellenberg value for co-occurring species of a focus species from the original survey was compared with the resurvey. These values were compared in order to detect significant changes in species optimum and in what direction e.g. if precipitation has decreased and the mire becomes drier some species will be more abundant and some will be outcompeted by the species that are more adapted to drier conditions, while some species will persist because they have a wide tolerance or they might just react more slowly to the changes (Kapfer et al., 2011). We will then observe that species will occur together with species with other

preferences for moisture in the resurvey than in the original survey. This was also done to get an indication of which species that responded to the different environmental variables, since species respond individualistic to environmental changes and thereby change their associates and whether these changes are randomly in relation to the different gradients (Kapfer et al., 2011).

There were four main steps to calculate the relative changes of each species realized optimum value (Kapfer et al. 2011): (i) estimate sample scores for each indicator value for both surveys; (ii) standardize the two data sets so that there is a similar distribution of the sample scores for both surveys; (iii) estimate changes in realized species scores (species optimum); and (iv) test if the changes are random or not with a restricted permutation test with 1000 permutations and the critical *P*-value was set to 0.05. Only species that occurred in five or more plots in both surveys was used to calculate relative changes of each species realized optimum value. This resulted in a reduction of the total number of species from 75 to 52 for Hitra and from 69 to 38 for Austre Moland.

3.3.4 Changes in species richness along the latitudinal gradient

A one Sample t-test was used to compare mean number of species per site and to test if the species richness for all sites in the gradient survey were significantly different. Since only pH was measured during field work and was done in 14 of 20 sites, average Ellenberg environmental indicator values were used in order to assess if these environmental variables could explain possible changes in species richness along the latitudinal gradient. Hills version of Ellenbergs environmental indicator values was used to calculate average value in each site for light, soil moisture, pH and nutrients while Ellenbergs version was used for temperature, this was done for both vascular species and mosses (Ellenberg et al., 1991, Hill et al., 2007, Hill et al., 2000). Then a correlation test was performed to assess if there was a changes in species richness along the latitudinal gradient and whether this were correlated with the environmental variables. If some of the environmental variables had a high correlation then it is difficult to assess which one is explaining the changes along the latitudinal gradient.

Linear multiple regression model was selected in order to examine the relationship between total, vascular plant and bryophyte species richness and the environmental variables. First I wanted to find out which of the two variables nitrogen and sulphur (since they were highly correlated) with interactions with the other variables (precipitation and temperature) that best explained the change in the different species richness. This was done by using Akaike's information criterion (AIC) to

compare the two models and the model with the lowest AIC for species richness and was therefore selected for further analysis. A normal distribution was assumed and found appropriate when inspecting the diagnostic plots (q-q plots and trends in residual variation with the estimated mean) for the models. I also wanted to test if log-transformed nitrogen and precipitation better explained the data, this was also done by using AIC to decide which one that should be used. Then backward selection with the appropriate approach was used to detect which variable(s) that best explained the changes in total, vascular plant and bryophyte species richness along the latitudinal gradient.

Linear multiple regression model was also used to examine the relationship between total, vascular plant and bryophyte species richness and the average Ellenberg indicator values for each site. First I wanted to find out which of the two variables nitrogen and pH (since they were highly correlated) with interactions with the other variables (light, temperature and soil moisture) that best explained the change in the different species richness. This was done by using Akaike's information criterion (AIC) to compare the two models and the model with pH had the lowest AIC for species richness and was therefore selected for further analysis. Again a normal distribution was assumed. Then backward selection with the appropriate approach was used to detect which variable(s) that best explained the changes in total, vascular plant and bryophyte species richness along the latitudinal gradient.

3.5 UNCERTAINTIES

Uncertainties might be incorrect determination of species, but since I have sampled all bryophytes and also vascular plant that I was uncertain of in the field this might have been reduced. However determination of bryophytes in the gradient survey is based on field determinations so the probability of incorrect determination is higher than in the resampling survey. When I was doing field work alone I had the possibility to call both of my supervisors at all times if I encountered problems. Since I used estimate % cover as sampling method it may be a couple of percentages off, but since I did all of the estimations it will be consistent. All pH-measurement were done in the field so there are no risks for contamination, which is a risk if soil is sampled. However the pH is influenced by the weather prior to the sampling day.

4. RESULTS

4.1. AREA SELECTION

4.1.1 Hitra

In the correspondence analysis (CA) the areas in the original survey that were most similar to the areas in the resurvey based on species composition was III l, VIII e, VIII f, I a and II b. Area III f, III g and III h had no obvious analogues in the 2010 data and were therefore removed from the 1965 data set (Figure 5). After these plots were removed, the two surveys had similar distribution in species composition in the correspondence analysis (CA) plot, indicating that the sampling of the resurvey in 2010 is acceptable (Appendix 1, figure A1.1.a and b).

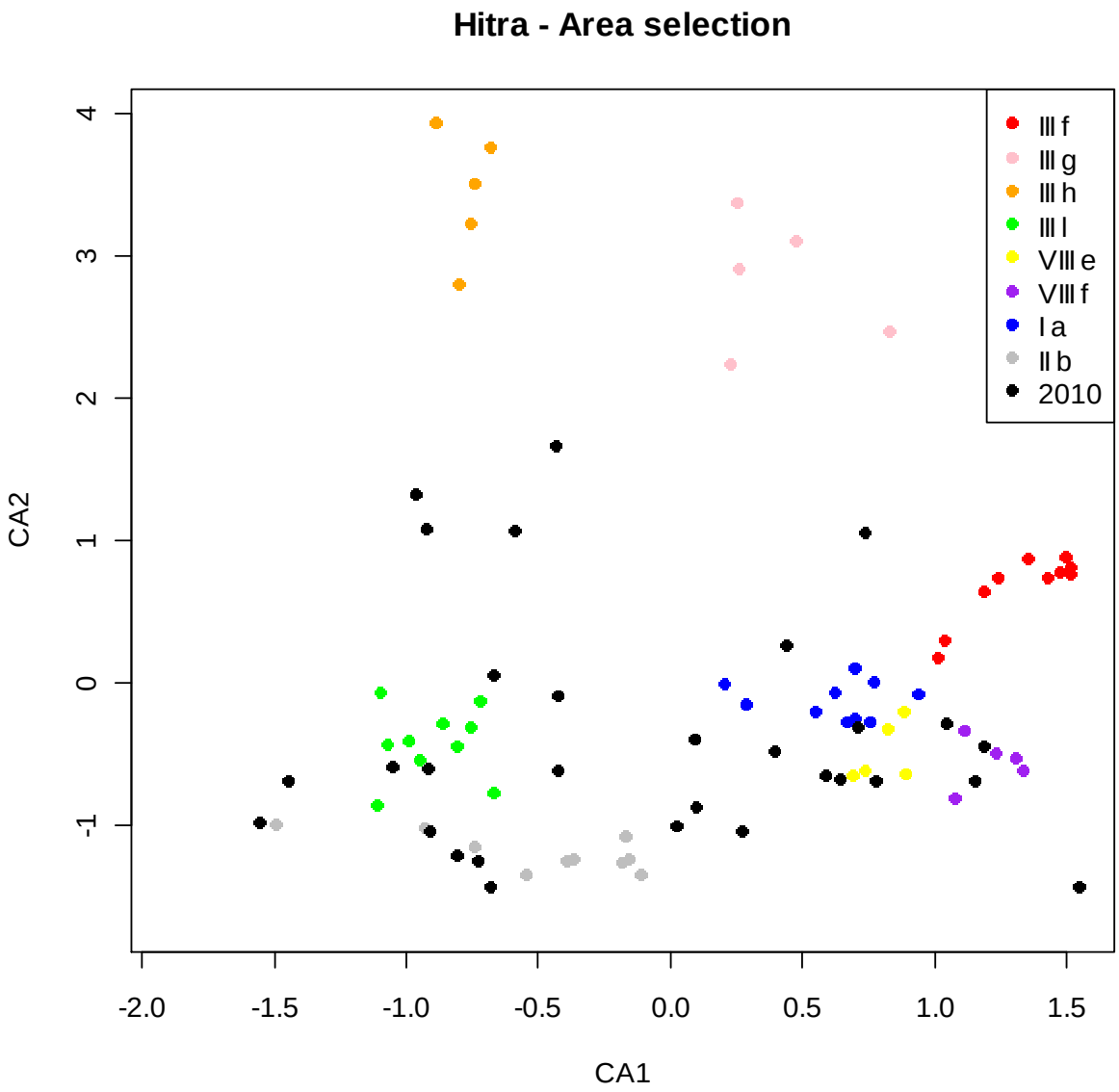


Figure 5. Correspondence analysis visualizing distribution of all the plots at Hitra based on the species composition of each plot. Black circles represent the resample survey from 2010 and coloured circles represent the different areas in the original survey from 1965.

4.1.2 Austre Moland

In the correspondence analysis (CA) plots from both surveys have quite similar distribution in the ordination plot, indicating that the resurvey in 2010 successfully captured the vegetation types and gradients sampled in the original data (Appendix 1, figure A1.2). However *Sphagnum angustifolium, S. capillifolium* and *S. girgensohnii* associations plots have systematically different distribution along the first axis over time (Appendix 1, figure A1.3.a). There is also a somewhat uneven sampling of the associations over time as for instance *Sphagnum subsecundum* had nine plots in the original survey while only one was sampled in the resurvey, *Sphagnum subnitens* consisted of 8 plots in 1968 and only one plot in 2010 and *Sphagnum fallax* had two sampled plots in 1968 and in 2010 it had six plots (Appendix 1, figure A1.3.b,).

4.2. CHANGES IN SPECIES RICHNESS AND FREQUENCY

4.2.1 Hitra

In the original survey a total of 84 species were recorded and in the resurvey there was 101 recorded species (Table 6 and Appendix 1, table A1). Number of species that were present in both resurveys was 75, and number of species that only were present in the original survey was nine and species that were unique to the resurvey were 26. Mean species number per plot has decreased significantly from 18.99 in the original survey to 15.43 in the resurvey (P=0.001). The new species are: *Avenella flexuosa, Arctostaphylos uva-ursi, Arctous alpines, Bartsia alpina, Drosera intermedia, Carex pulicaris, Carex vaginata, Equisetum palustre, Lotus corniculatus, Lycopodium annotium, Pedicularis palustris, Pedicularis sylvatica, Pinus sylvestris (juv.), Schoenus ferrugineus, Solidago virgaurea, Dicranum leioneuron, D. majus, D. polysetum, Sarmentypnum exannulatum, Sphagnum cf. fallax, S. palustre, S. pulchrum, Barbilophozia hatchery* and *Gymnocolea inflata*.

Only species that occurred in more than ten plots for both surveys were tested for changes which resulted in 64 tested species of total 75 species (Table 7). Of these 25 (40%) showed a significant change, 23 decreased and only two (*Erica tetralix* and *Sphagnum fuscum*) showed an increase in occurrence between the two surveys. Species that showed a decrease in occurrence were mostly lawn and hollow species according to (Fremstad, 1997); *Carex dioica, C. lasiocarpa, C. limosa, C. panacea, C. pauciflora, Pinguicula vulgaris, Tofieldia pusilla, Rhynchospora alba, Trichophorum cespitosum, Cladopodiella fluitans, Sphagnum majus, S. papillosum, S. subsecundum* and *S. tenellum*. Species that decreased which is not confined to any particular area of the mire were *Andromeda polifolia Eriophorum vaginatum, Rubus chamaemorus, Trientalis europea, Cephalozia*

spp., Kurzia pauciflora, Mylia anomala, Sphagnum imbricatum and *Straminergon stramineum*. There was one species that decreased significant in frequency that I did not encounter during my resurvey and it was *Carex limosa*.

Of 64 tested species 21 (33%) showed a significant change, 14 decreased and seven increased in frequency between the two surveys (Table 7). Species that showed a decrease in frequency were mostly the same species that decreased in occurrence, except *Trientalis europea, Trichophorum cespitosum, Cephalozia spp. and Kurzia pauciflora* did not decrease in frequency. There was one species that decreased significant in frequency that I did not encounter during my resurvey and it was *Carex limosa*. The average moisture Ellenberg value for decreasing species was 9.1 and code 9 in Ellenberg is explained as species which are waterlogged either in streams, flushes or on bogs (Hill et al., 2007). Average reaction Ellenberg value which refers to environmental acidity was 3.43 (half of them had an average of 5.3), code 3 in Ellenberg is explained as species on acid substrata, often on base-poor mineral soils or in acid flushes and code 4 is explained as between value 3 and 5 which is species on moderately acid soil (code 6 are species growing on basic soil) (Hill et al., 2007).

Species that increased in frequency were: *Calluna vulgaris, Racomitrium lanuginosum, Erica tetralix, Potentilla erecta, Hypnum cupressiforme, Sphagnum compactum* and *Warnstorfia fluitans*, the first two are hummock species. Half of the species that increased in frequency grow on hummocks. The average moisture Ellenberg value for increasing species was 6.7, and code 6 in Ellenberg is explained as species which is present on moist soil. Average reaction Ellenberg value was 2.33 and code 2 in Ellenberg is explained as between value 1 (indicator of extreme acidity, species are never found on weakly acid or basic substrata) and 3 (species on acid substrata and often on base-poor mineral soils or in acid flushes).

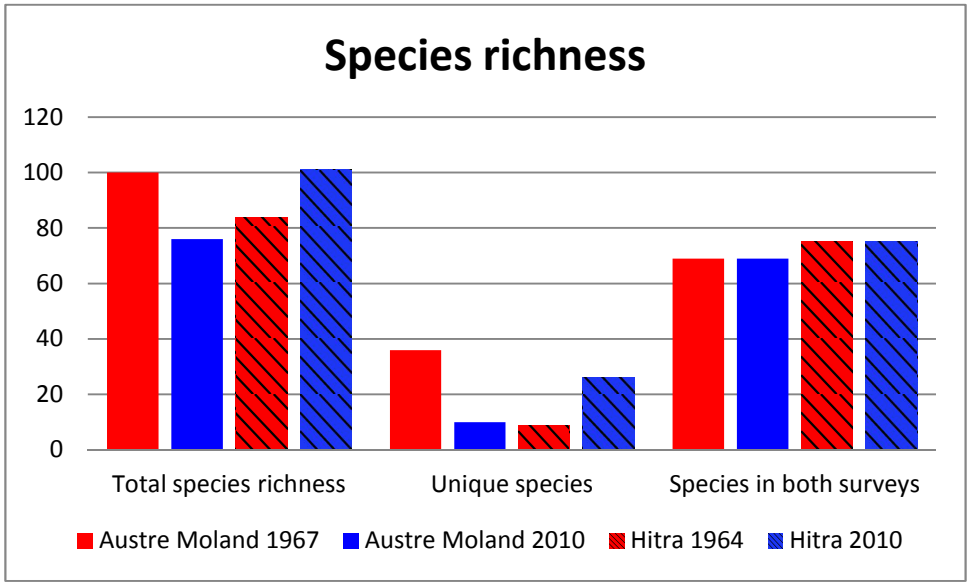
4.2.2 Austre Moland

In the original survey a total of 100 species were recorded and in the resurvey there was 76 recorded species (Table 6 and Appendix1, table A1). Number of species that were present in both resurveys was 69, number of species that were unique to the original survey was 36 and number species that were only present in the resurvey were ten. Mean species number per plot decreased significantly from 15.04 in the original survey to 11.15 in resurvey (P=0.001).

Only species that occurred in more than ten plots for both were tested for changes which resulted in 50 tested species of total 69 species (Table 8). Of these 16 (32%) showed a significant change and 14 of these showed a significant decrease while only two (*Drosera rotundifolia* and *Carex rostrata*) showed an increase in frequency between the two surveys. The species which decreased consisted of hummock, lawn and hollow species, dwarf shrubs (*Andromeda polifolia, Calluna vulgaris, Myrica gale* and *Vaccinium vitis-idaea*), juveniles of tree species (*Betula pubescens* and *Pinus sylvestris*), some sedges (*Carex rostrata, Eriophorum angustifolium* and *Rhynchospora alba*) and some bryophytes (*Straminergon stramineum, Sphagnum flexuosum, Sphagnum subnitens* and *Kurzia pauciflora*). Two decreasing species were not encountered during my resurvey: *Agrostis canina* and *Carex pauciflora*.

Of 50 tested species 21 (42%) showed a significant change, 12 increased and nine decreased in frequency between the two surveys (Table 8). Species that showed an increase in frequency were *Carex rostrata, Drosera rotundifolia, Erica tetralix, Narthecium ossifragum, Molinia caerulea, Myrica gale, Polytrichum strictum, Sphagnum capillifolium, S. imbricatum, S. magellanicum, S. palustre, S. papillosum*. Species that showed a decrease in frequency were more or less the same species that decreased in occurrence *Eriophorum angustifolium, Oxycoccus palustris, Rhynchospora alba, Straminergon stramineum, Sphagnum subnitens* and *Kurzia pauciflora*.

Table 6. Species richness in the original and resurvey of Austre Moland and Hitra.



4.3. CHANGES IN SPECIES OPTIMA

4.3.1 Hitra

Of the 75 species that that occurred in both surveys 52 species was tested for shifts in their optimum value (Table 7). 21 of these species showed a significant change in at least one of the environmental gradients that were investigated and six of the species were vascular plants and 14 were bryophytes. Five species (10%) significantly changed their realized optimum value for light, two in a positive direction and three in a negative direction. All five species (10%) changed in a positive direction for temperature, five of the six species (12%) changed in a negative direction for moisture, nine out of ten (19%) species changed in a negative direction for pH and all three species (6%) changed in a negative direction for nitrogen.

4.3.1 Austre Moland

38 species of the 69 species that occurred in both surveys was tested for shifts in their optimum value (Table 8). Of these, 15 species (9 vascular plants, 6 bryophytes) showed a significant change along at least one of the environmental gradients that were investigated. Five species (13%) significantly changed their realized optimum value for light, one in a positive direction and four in a negative direction. All three species (8%) changed in a negative direction for temperature. Five species (13%) changed for moisture, three in a negative and two in a positive direction. Six species (16%) changed for pH, five in a negative and one in a positive direction. Three species (8%) changed for nitrogen, two in a negative and one in a positive direction.

Table 7. Species occurrence pr plot at Hitra (n=103), relative species occurrence and changes in species optimum for different environmental gradients (indicator values for light L, temperature T, soil moisture M, pH and nutrients N from 1965 to 2010.

*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001, n.s., not significant. Significant change values are printed in bold.

	Species occurrence (%)			Relative species occurrence (%)			Change in species optimum				
							1965-2010				
	1965	2010	Change	1965	2010	Change	L	T	M	pH	N
Andromeda polifolia	92.2	75.7	**-16.5****	4.81	4.86	0.05n.s.	-0.07n.s.	-0.13n.s.	-0.13n.s.	**-0.21****	-0.04n.s.
Betula pubescens juv.	17.5	24.3	6.8n.s.	0.91	1.56	0.65n.s.	-0.37n.s.	0.02n.s.	-0.18n.s.	-0.20n.s.	-0.31n.s.
Calluna vulgaris	73.8	81.6	7.8n.s.	3.85	5.23	**1.39*****	0.15 n.s.	-0.10n.s.	-0.02n.s.	-0.02n.s.	0.09n.s.
Empetrum nirgum	35.9	31.1	-4.9n.s.	1.87	1.99	0.12n.s.	-0.01n.s.	-0.40n.s.	-0.09n.s.	-0.24n.s.	-0.06n.s.
Erica tetralix	36.9	53.4	**16.5****	1.92	3.43	**1.50*****	0.21n.s.	0.19n.s.	0.29n.s.	-0.31n.s.	-0.27n.s.
Oxycoccus palustris	17.5	19.4	1.9n.s.	0.91	1.25	0.33n.s.	0.43n.s.	-0.05n.s.	0.25n.s.	0.08n.s.	0.35n.s.
Rubus chamaemorus	45.6	29.1	**-16.5****	2.38	1.87	-0.51n.s.	-0.06n.s.	0.13n.s.	-0.02n.s.	-0.16n.s.	0.00n.s.
Vaccinium vitis-idaea.	8.7	6.8	-1.9n.s.	0.46	0.44	-0.02n.s.	-0.68n.s.	0.10n.s.	-0.33n.s.	-0.10n.s.	0.37n.s.
Dactylorhiza maculata	7.8	3.9	-3.9n.s.	0.41	0.25	-0.16n.s.					
Drosera longifolia	20.4	16.5	-3.9n.s.	1.06	1.06	0.00n.s.	-0.16n.s.	0.15n.s.	-0.01n.s.	-0.36n.s.	-0.11n.s.
Drosera rotundifolia	70.9	61.2	-9.7n.s.	3.70	3.93	0.23n.s.	0.09n.s.	0.09n.s.	0.02n.s.	-0.21n.s.	-0.11n.s.
Euphrasia spp.	21.4	24.3	2.9n.s.	1.11	1.56	0.44n.s.	**0.41***	**0.59***	0.18n.s.	-0.31n.s.	-0.18n.s.
Menyanthes trifoliata	7.8	2.9	-4.9n.s.	0.41	0.19	-0.22n.s.					
Narthecium ossifragum	64.1	57.3	-6.8n.s.	3.34	3.68	0.33n.s.	**0.34****	**0.26***	0.24n.s.	0.03n.s.	-0.10n.s.
Pinguicula vulgaris	28.2	7.8	**-20.4*****	1.47	0.50	**-0.97****	-0.10n.s.	-0.10n.s.	-0.14n.s.	-0.21n.s.	0.22n.s.
Potentilla erecta	30.1	35.0	4.9n.s.	1.57	2.24	**0.67****	0.15n.s.	0.09n.s.	0.08n.s.	-0.36n.s.	-0.22n.s.
Selaginella selaginoides	13.6	12.6	-1.0n.s.	0.71	0.81	0.10n.s.	0.15n.s.	0.07n.s.	0.11n.s.	**-0.83***	-0.34n.s.
Succisa pratensis	11.7	12.6	1.0n.s.	0.61	0.81	0.20n.s.	0.07n.s.	-0.21n.s.	-0.12n.s.	**-0.75***	**-0.52***
Tofieldia pusilla	10.7	1.0	**-9.7****	0.56	0.06	**-0.49****					
Trientalis europea	12.6	4.9	**-7.8***	0.66	0.31	-0.35n.s.					
Carex dioica	8.7	1.9	**-6.8***	0.46	0.12	**-0.33***					
Carex echinata	6.8	9.7	2.9n.s.	0.35	0.62	0.27n.s.	-0.70n.s.	0.59n.s.	-0.48n.s.	-0.28n.s.	0.03n.s.
Carex lasiocarpa	25.2	12.6	**-12.6****	1.32	0.81	**-0.51***	-0.50n.s.	-0.14n.s.	-0.06n.s.	-0.27n.s.	-0.04n.s.
Carex limosa	12.6	0.0	**-12.6*****	0.66	0.00	**-0.66*****					
Carex panicea	20.4	5.8	**-14.6****	1.06	0.37	**-0.69****	0.02n.s.	0.30n.s.	0.04n.s.	-0.69n.s.	-0.32n.s.
Carex pauciflora	71.8	11.7	**-60.2*****	3.75	0.75	**-3.00*****	-0.16n.s.	0.16n.s.	-0.14n.s.	0.07n.s.	0.01n.s.
Carex rostrata	4.9	6.8	1.9n.s.	0.25	0.44	0.18n.s.					
Eriophorum angustifolium	39.8	32.0	-7.8n.s.	2.08	2.06	-0.02n.s.	-0.11n.s.	-0.03n.s.	0.04n.s.	-0.32n.s.	-0.04n.s.
Eriophorum vaginatum	97.1	74.8	**-22.3*****	5.06	4.80	-0.27n.s.	0.13n.s.	0.04n.s.	0.04n.s.	**-0.18***	-0.13n.s.
Molinia caerulea	45.6	39.8	-5.8n.s.	2.38	2.55	0.17n.s.	-0.19n.s.	0.22n.s.	-0.11n.s.	0.08n.s.	0.21n.s.
Rhynchospora alba	9.7	1.9	**-7.8***	0.51	0.12	**-0.38***					
Trichophorum cespitosum	63.1	47.6	**-15.5****	3.29	3.05	-0.2n.s.	-0.13n.s.	**0.26***	-0.08n.s.	-0.25n.s.	-0.28n.s.
Aulacomnium palustre	16.5	13.6	-2.9n.s.	0.86	0.87	0.0n.s.	-0.22n.s.	0.09n.s.	-0.12n.s.	-0.24n.s.	-0.09n.s.
Campylium stellatum	12.6	12.6	0.0n.s.	0.66	0.81	0.15n.s.	**-0.36***	0.35n.s.	**-0.64***	-0.72n.s.	-0.20n.s.
Dicranum scoparium	11.7	5.8	-5.8n.s.	0.61	0.37	-0.23n.s.	-0.60n.s.	0.52n.s.	-0.33n.s.	0.21n.s.	1.11n.s.
Dicranum spp.	6.8	6.8	0.0n.s.	0.35	0.44	0.08n.s.	0.04n.s.	0.20n.s.	-0.65n.s.	-0.12n.s.	0.04n.s.
Hylocomium splendens	15.5	18.4	2.9n.s.	0.81	1.18	0.37n.s.	0.24n.s.	0.31n.s.	0.02n.s.	**-0.69****	-0.52n.s.
Hypnum cupressiforme	12.6	19.4	6.8n.s.	0.66	1.25	**0.59***	0.03n.s.	-0.22n.s.	-0.18n.s.	0.43n.s.	0.41n.s.
Pleurozium schreberi	38.8	38.8	0.0n.s.	2.03	2.49	0.47n.s.	-0.08n.s.	-0.05n.s.	-0.08n.s.	-0.15n.s.	-0.31n.s.
Pohlia spp.	8.7	8.7	0.0n.s.	0.46	0.56	0.11n.s.	-0.23n.s.	-0.37n.s.	-0.55n.s.	-0.30n.s.	-0.19n.s.

Table 7. (Continued)

	Species occurrence (%)			Relative species occurrence (%)			Change in species optimum				
							1968-2010				
	1968	2010	Change	1968	2010	Change	**L**	T	M	pH	N
Racomitrium lanuginosum	58.3	64.1	5.8n.s.	3.04	4.11	**1.07*** **	-0.09n.s.	-0.28n.s.	-0.20n.s.	0.13n.s.	0.09n.s.
Rhytidiadelphus loreus	5.8	8.7	2.9n.s.	0.30	0.56	0.26n.s.	-0.09n.s.	-0.16n.s.	0.03n.s.	**-0.89*** **	-0.52n.s.
Straminergon stramineum	29.1	9.7	**-19.4*** **	1.52	0.62	**-0.90*** **	-0.04n.s.	-0.41n.s.	-0.42n.s.	**-1.06** **	**-0.71** **
Warnstorfia fluitans	4.9	11.7	6.8n.s.	0.25	0.75	**0.49***					
Sphagnum angustifolium	6.8	6.8	0.0n.s.	0.35	0.44	0.08n.s.	0.73n.s.	0.06n.s.	0.25n.s.	-0.59n.s.	0.29n.s.
Sphagnum capillifolium	68.9	63.1	-5.8n.s.	3.59	4.05	0.45n.s.	-0.21n.s.	-0.09n.s.	**-0.35***	-0.14n.s.	0.10n.s.
Sphagnum compactum	10.7	10.7	0.0n.s.	0.56	0.69	**0.13*** **	-0.34n.s.	0.01n.s.	-0.23n.s.	-0.30n.s.	-0.27n.s.
Sphagnum fuscum	1.0	9.7	**8.7** **	0.05	0.62	0.57n.s.					
Sphagnum imbricatum	26.2	18.4	**-7.8***	1.37	1.18	-0.18n.s.	**-0.57***	-0.22n.s.	**-0.63*** **	0.00n.s.	0.17n.s.
Sphagnum magellanicum	16.5	18.4	1.9n.s.	0.86	1.18	0.32n.s.	-0.29n.s.	0.34n.s.	-0.22n.s.	**0.53** **	0.42n.s.
Sphagnum majus	18.4	3.9	**-14.6*** **	0.96	0.25	**-0.71** **					
Sphagnum papillosum	57.3	40.8	**-16.5** **	2.99	2.62	-0.37n.s.	-0.09n.s.	**0.29***	-0.12n.s.	0.14n.s.	-0.04n.s.
Sphagnum strictum	4.9	5.8	1.0n.s.	0.25	0.37	0.12n.s.					
Sphagnum subnitens	19.4	14.6	-4.9n.s.	1.01	0.93	-0.08n.s.	-0.04n.s.	0.41n.s.	-0.09n.s.	0.22n.s.	0.31n.s.
Sphagnum subsecundum	25.2	10.7	**-14.6*** **	1.32	0.69	**-0.63*** **	-0.18n.s.	0.09n.s.	**-0.22** **	-0.24n.s.	0.02n.s.
Sphagnum tenellum	70.9	39.8	**-31.1*** **	3.70	2.55	**-1.14*** **	-0.05n.s.	**0.38** **	-0.09n.s.	0.08n.s.	-0.07n.s.
Calypogeia sphagnicola	22.3	17.5	-4.9n.s.	1.16	1.12	-0.04n.s.	0.21n.s.	0.03n.s.	0.06n.s.	0.35n.s.	0.32n.s.
Cephalozia spp.	54.4	39.8	**-14.6***	2.84	2.55	-0.28n.s.	0.00n.s.	0.04n.s.	0.02n.s.	0.11n.s.	0.08n.s.
Cladopodiella fluitans	33.0	7.8	**-25.2*** **	1.72	0.50	**-1.22*** **	-0.03n.s.	0.05n.s.	**0.62** **	0.12n.s.	0.19n.s.
Kurzia pauciflora	42.7	30.1	**-12.6***	2.23	1.93	-0.30n.s.	0.18n.s.	0.06n.s.	0.21n.s.	0.00n.s.	-0.09n.s.
Mylia anomala	48.5	16.5	**-32.0*** **	2.53	1.06	**-1.47*** **	**-0.43***	-0.21n.s.	**-0.44** **	-0.09n.s.	0.08n.s.
Odontoschisma spp.	35.9	35.9	0.0n.s.	1.87	2.31	0.43n.s.	-0.17n.s.	0.22n.s.	-0.24n.s.	-0.32n.s.	-0.12n.s.
Ptilidium ciliare	30.1	20.4	-9.7n.s.	1.57	1.31	-0.26n.s.	-0.11n.s.	-0.23n.s.	-0.10n.s.	**-0.37***	-0.18n.s.
Riccardia spp.	21.4	24.3	2.9n.s.	1.11	1.56	0.44n.s.	0.05n.s.	-0.48n.s.	-0.01n.s.	**-1.16** **	**-0.75** **

Table 8. Species occurrence pr plot at Austre Moland (n=113), relative species occurrence and changes in species optimum for different environmental gradients (indicator values for light L, temperature T, soil moisture M, pH and nutrients N from 1965 to 2010.
*P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001, n.s., not significant. Significant change values are printed in bold.

	Species occurrence %			Relative species occurrence (%)			Change in species optimum				
							1968-2010				
	1968	2010	Change	1968	2010	Change	L	T	M	pH	N
Andromeda polifolia	48.7	30.1	**-18.6****	3.24	2.70	-0.54n.s.	0.06n.s.	-0.01n.s.	-0.13n.s.	-0.13n.s.	-0.14n.s
Betula pubescens juv.	15.0	5.3	-9.7n.s.	1.00	0.48	-0.52n.s.	0.25n.s.	**-0.97***	**-0.89*****	-0.21n.s.	-0.46n.s
Calluna vulgaris	30.1	12.4	**-17.7****	2.00	1.11	**-0.89****	0.49n.s.	0.28n.s.	0.19n.s.	-0.37n.s.	-0.58n.s
Erica tetralix	45.1	48.7	3.5n.s.	3.00	4.37	**1.37*****	0.15n.s.	0.11n.s.	0.15n.s.	-0.17n.s.	-0.22n.s
Myrica gale	69.0	63.7	-5.3n.s.	4.59	5.71	**1.13****	0.01n.s.	-0.14n.s.	-0.03n.s.	**-0.32***	-0.22n.s
Oxycoccus palustris	80.5	37.2	**-43.4*****	5.35	3.33	**-2.02*****	0.19n.s.	-0.12n.s.	0.07n.s.	**-0.33****	-0.21n.s
Pinus sylvestris juv.	37.2	19.5	**-17.7***	2.47	1.75	-0.72n.s.	0.09n.s.	-0.03n.s.	-0.05n.s.	-0.10n.s.	-0.10n.s
Vaccinium myrtillus	8.8	4.4	-4.4n.s.	0.59	0.40	-0.19n.s.					
Vaccinium vitis-idaea	8.8	2.7	**-6.2***	0.59	0.24	-0.35n.s.					
Drosera rotundifolia	44.2	59.3	**15.0***	2.94	5.32	**2.38*****	0.09n.s.	0.05n.s.	-0.12n.s.	**-0.32***	-0.19n.s
Menyanthes trifoliata	33.6	32.7	-0.9n.s.	2.24	2.94	0.70n.s.	-0.09n.s.	-0.27n.s.	0.05n.s.	-0.19n.s.	-0.06n.s
Narthecium ossifragum	31.0	34.5	3.5n.s.	2.06	3.10	**1.04***	0.23n.s.	0.34n.s.	**0.50****	-0.03n.s.	0.11n.s
Peucedanum palustre	8.0	5.3	-2.7n.s.	0.53	0.48	-0.05n.s.	**-1.54***	-1.44n.s.	-0.20n.s.	0.53n.s.	**0.89***
Potentilla erecta	30.1	15.0	**-15.0****	2.00	1.35	-0.65n.s.	0.05n.s.	-0.24n.s.	0.05n.s.	-0.02n.s.	0.56n.s.
Trientalis europea	33.6	23.9	-9.7n.s.	2.24	2.14	-0.09n.s.	-0.48n.s.	-0.40n.s.	-0.11n.s.	-0.15n.s.	0.35n.s.
Viola palustris	26.5	17.7	-8.8n.s.	1.76	1.59	-0.18n.s.	**-0.92***	-0.08n.s.	**-0.58***	-0.45n.s.	-0.07n.s.
Agrostis canina	15.9	0.0	**-15.9*****	1.06	0.00	**-1.06*****					
Carex dioica	8.8	2.7	-6.2n.s.	0.59	0.24	-0.35n.s.					
Carex echinata	23.0	16.8	-6.2n.s.	1.53	1.51	-0.02n.s.	-0.38n.s.	-0.46n.s.	0.20n.s.	-0.01n.s.	-0.07n.s.
Carex panicea	23.9	19.5	-4.4n.s.	1.59	1.75	0.16n.s.	-0.41n.s.	-0.35n.s.	-0.33n.s.	-0.05n.s.	-0.10n.s.
Carex pauciflora	27.4	0.0	**-27.4*****	1.82	0.00	**-1.82*****					
Carex paupercula	19.5	9.7	-9.7n.s.	1.29	0.87	-0.42n.s.	0.13n.s.	0.05n.s.	0.07n.s.	-0.18n.s.	-0.29n.s.
Carex rostrata	46.9	59.3	**12.4***	3.12	5.32	**2.20*****	-0.25n.s.	0.11n.s.	0.10n.s.	-0.01n.s.	0.11n.s.
Eriophorum	37.2	13.3	**-23.9*****	2.47	1.19	**-1.28***	0.13n.s.	-0.07n.s.	0.05n.s.	-0.26n.s.	0.04n.s.
Eriophorum vaginatum	50.4	51.3	0.9n.s.	3.35	4.60	1.25n.s.	0.19n.s.	0.10n.s.	**0.32***	-0.10n.s.	-0.15n.s.
Molinia caerulea	48.7	61.1	12.4n.s.	3.24	5.48	**2.24*****	-0.26n.s.	0.17n.s.	0.04n.s.	0.00n.s.	0.06n.s.
Rhynchospora alba	14.2	3.5	**-10.6****	0.94	0.32	**-0.62****					
Trichophorum	19.5	16.8	-2.7n.s.	1.29	1.51	0.21n.s.	0.16n.s.	**-0.45***	0.04n.s.	**-0.55*****	-0.34n.s.
Aulacomnium palustre	22.1	16.8	-5.3n.s.	1.47	1.51	0.04n.s.	0.32n.s.	0.31n.s.	0.27n.s.	-0.12n.s.	-0.18n.s.
Polytrichum strictum	12.4	18.6	6.2n.s.	0.82	1.67	**0.84****	**0.35***	0.23n.s.	0.37n.s.	-0.09n.s.	-0.22n.s.
Sarmentypnum	9.7	4.4	-5.3n.s.	0.65	0.40	-0.25n.s.					
Straminergon	66.4	32.7	**-33.6*****	4.41	2.94	**-1.48*****	-0.06n.s.	-0.26n.s.	0.05n.s.	-0.16n.s.	0.01n.s.
Sphagnum	5.3	8.0	2.7n.s.	0.35	0.71	0.36n.s.	0.33n.s.	0.09n.s.	1.57n.s.	**1.03***	1.02n.s.
Sphagnum capillifolium	54.0	56.6	2.7n.s.	3.59	5.08	**1.49****	0.20n.s.	0.12n.s.	0.18n.s.	-0.17n.s.	**-0.23***
Sphagnum fallax	10.6	14.2	3.5n.s.	0.71	1.27	0.56n.s.	-0.88n.s.	-0.76n.s.	-0.05n.s.	0.39n.s.	0.55n.s.
Sphagnum flexuosum	26.5	12.4	**-14.2***	1.76	1.11	-0.65n.s.	-0.76n.s.	-0.18n.s.	-0.04n.s.	-0.34n.s.	-0.35n.s.
Sphagnum girgensohnii	6.2	4.4	-1.8n.s.	0.41	0.40	-0.01n.s.					
Sphagnum imbricatum	45.1	54.0	8.8n.s.	3.00	4.84	**1.84****	0.07n.s.	0.13n.s.	0.11n.s.	-0.14n.s.	-0.24n.s.

Table 8. (Continued)

	Species occurrence (%)			Relative species occurrence (%)			Change in species optimum				
							1968-2010				
	1968	2010	Change	1968	2010	Change	L	T	M	pH	N
Sphagnum magellanicum	24.8	28.3	3.5n.s.	1.65	2.54	**0.89***	-0.15n.s.	-0.35n.s.	-0.13n.s.	-0.01n.s.	-0.14n.s.
Sphagnum palustre	4.4	12.4	8.0n.s.	0.29	1.11	**0.82****					
Sphagnum papillosum	25.7	38.1	12.4n.s.	1.71	3.41	**1.71*****	**-0.31***	-0.03n.s.	-0.11n.s.	0.18n.s.	0.16n.s.
Sphagnum pulchrum	38.1	32.7	-5.3n.s.	2.53	2.94	0.41n.s.	-0.16n.s.	-0.24n.s.	-0.08n.s.	-0.13n.s.	-0.17n.s.
Sphagnum russowii	7.1	5.3	-1.8n.s.	0.47	0.48	0.01n.s.	-0.92n.s.	**-1.85***	0.13n.s.	0.20n.s.	**1.40****
Sphagnum subnitens	19.5	2.7	**-16.8*****	1.29	0.24	**-1.06****					
Sphagnum subsecundum	12.4	6.2	-6.2n.s.	0.82	0.56	-0.27n.s.	**-0.75*****	-0.65n.s.	0.14n.s.	-0.46n.s.	0.57n.s.
Sphagnum tenellum	12.4	8.0	-4.4n.s.	0.82	0.71	-0.11n.s.	-0.23n.s.	0.52n.s.	-0.19n.s.	0.33n.s.	0.36n.s.
Cephalozia spp.	14.2	10.6	-3.5n.s.	0.94	0.95	0.01n.s.	-0.02n.s.	0.24n.s.	0.05n.s.	-0.17n.s.	0.12n.s.
Cladopodiella fluitans	16.8	10.6	-6.2n.s.	1.12	0.95	-0.17n.s.	-0.08n.s.	-0.31n.s.	**-0.42***	**-0.40***	-0.28n.s.
Kurzia pauciflora	14.2	4.4	**-9.7***	0.94	0.40	**-0.54***					
Odontoschisma spp.	8.8	3.5	-5.3n.s.	0.59	0.32	-0.27n.s.					

4.4. CHANGES IN SPECIES RICHNESS ALONG THE LATITUDINAL GRADIENT

Latitude show a strong correlation with total species richness (Spp), vascular plant species richness (V) and bryophyte species richness (B) (Spp: $r = 0.80$, V: $r = 0.57$ and B: $r = 0.76$), hence number of species increases northwards. Nitrogen and sulphur deposition show a strong negative correlation with species richness (N: $r = -0.76$, S: $r = -0.76$), and these variables were highly intercorrelated (r= -0.99). The significant decrease in bryophytes southwards is also best correlated with nitrogen and sulphur deposition (N: $r = -0.76$, S: $r = -0.75$), it is the same outcome for vascular plants although the correlation is not that strong (N: $r = -0.50$, S: $r = -0.52$). Precipitation and temperature show almost no correlation with species richness, vascular plants or bryophytes (r <-0.25), Appendix 1, table A2).

Since nitrogen and sulphur deposition show a strong negative correlation with species richness and since they were highly correlated the Akaike's information criterion (AIC) were used to compare two linear multiple regression models, the first examined the relationship between total, vascular plant and bryophyte species richness with nitrogen, precipitation and temperature interacted. The second model examined interactions of sulphur, precipitation and temperature as explanatory variable. The model with the lowest AIC value for total, vascular plant and bryophyte species richness was nitrogen and was therefore selected for further analysis (Appendix 1, table A3). In diagnostic plots I looked at the scale-location of this linear multiple regression model and line is not steep enough to be interpreted as Poisson distribution (Appendix 1, figure A4). The results from the

AIC comparison between log transforming nitrogen and precipitation in the regression model and the current models shows very little difference. Even though the log transformed regression model showed a somewhat lower AIC value I use Occam's razor that the simplest statistical model is best and use the regression model without the log transforming (Crawley, 2007).

The result of the backward selection was that nitrogen deposition was the only variable that explains the significant decrease in total species richness southwards, and it shows a significant negative linear relationship (r^2 = -0.5779, $p < 0.001$,). It was the same result for the significant decrease in bryophyte species richness southwards (r^2 = 0.581, $p < 0.001$). Vascular plant species richness shows a weak relationship with nitrogen (r^2 = 0.2482, $p < 0.001$, Figure 7). In the reduced data set (only 14 sites where pH was measured) with pH as an additional environmental variable with the same procedure, pH best explains the decrease in total, vascular plant and bryophyte species richness southwards (Spp: r^2 = 0.6622, V: r^2 = 0.2349, B: r^2 = 0.7583, $p < 0.001$, Figure 8).

Average Ellenberg indicator value for nutrients and pH show a negative correlation with species richness (Nu: r = -0.34, pH: r = -0.43), and these variables were quite high intercorrelated (r= -0.81). Average Ellenberg indicator value for light, temperature and soil moisture show a negative correlation with species richness (L: r = -0.36, Temp: r = -0.56 and Soil: r = -0.48). Since nutrients and pH show a negative correlation with species richness and since they were highly correlated the Akaike's information criterion (AIC) that compared two linear multiple regression models, the first examined the relationship between total, vascular plant and bryophyte species richness were nutrients, precipitation and temperature interacted. The second examined interactions of pH, precipitation and temperature as explanatory variables, the model with the lowest AIC value for species richness and was the one with pH and was therefore selected for further analysis (Appendix 1, table A3). When examining the relationship between total, vascular plant and bryophyte species richness and the average Ellenberg indicator values the backward selection found no relationship.

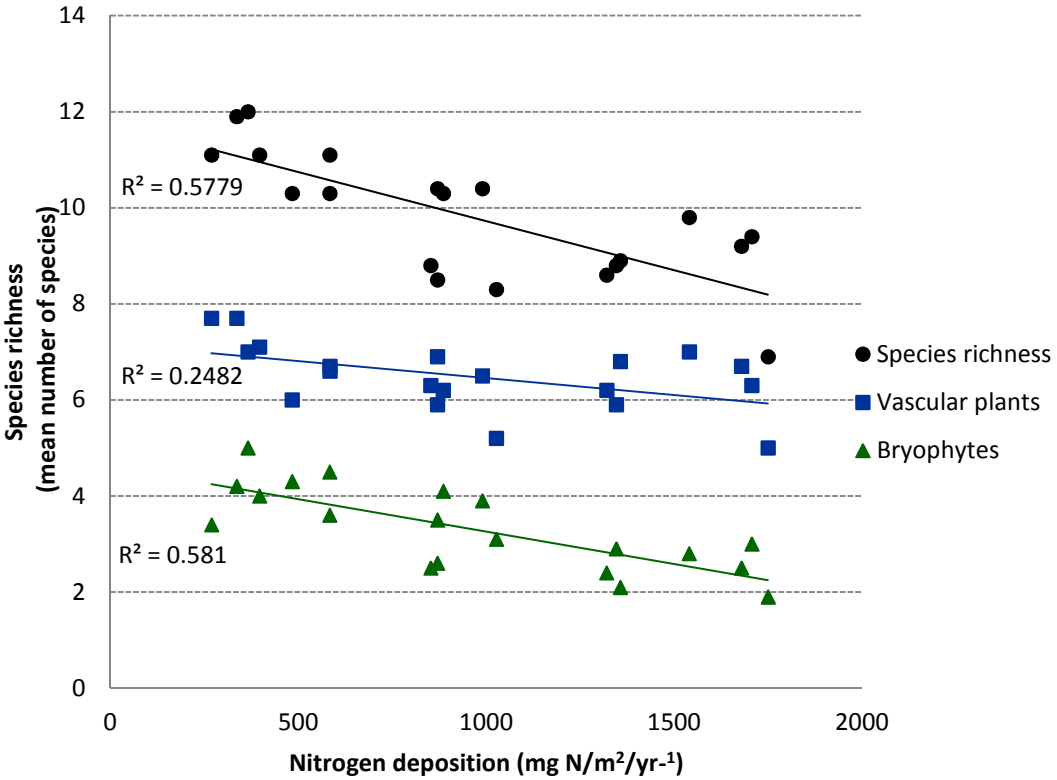


Figure 7. Ombrotrophic mire total species richness for 20 field sites plotted against average N deposition (black), vascular plant richness plotted against average N deposition (blue) and bryophyte richness blotted against average N deposition (green).

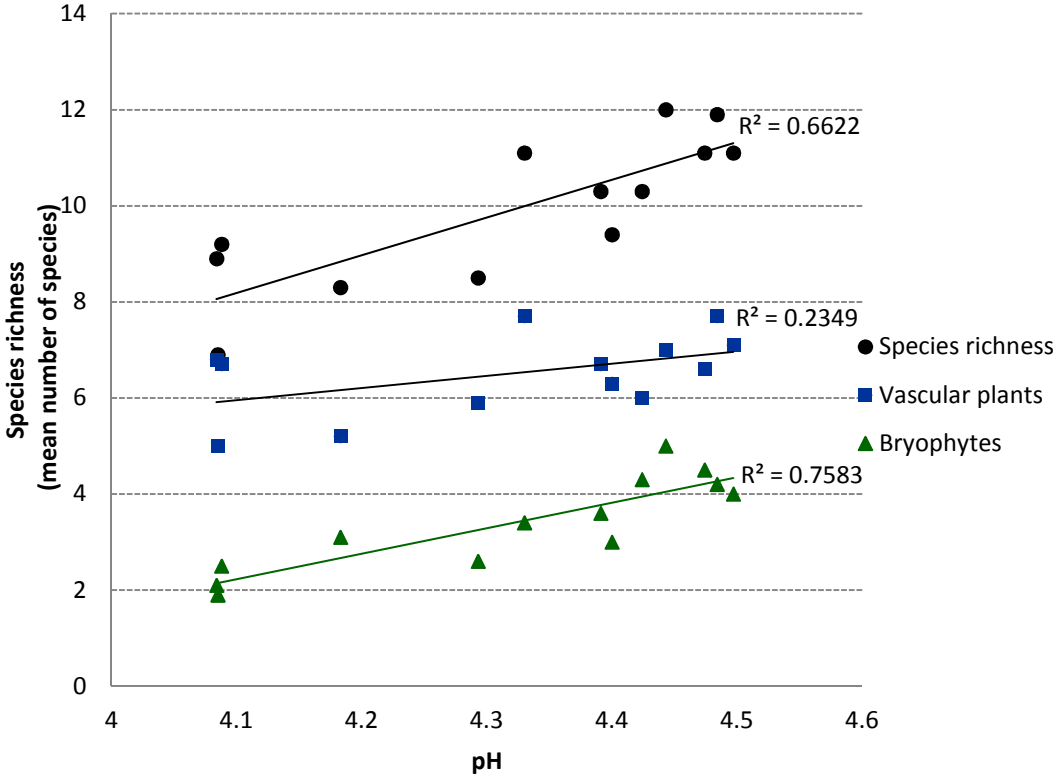


Figure 8. Ombrotrophic mire species richness plotted against average pH measures for 13 field sites (black), ombrotrophic mire vascular plant richness plotted against average pH measures for 13 field sites (blue) and ombrotrophic mire bryophyte richness blotted against average pH measures for 13 field sites (green).

5. DISCUSSION

5.1 HITRA

The correspondence analysis (CA) plot with both surveys show quite similar distribution of species composition indicating that the resurvey in 2010 successfully captured the vegetation sampled in the original data. When we examine the findings from Hitra we see clearly that changes have taken place the last 46 years. This fine-scale comparison of mire vegetation at Hitra found that total number of species has increased significantly whereas species number per plot has decreased significantly. Most of the species that decreased in frequency were lawn and hollow species (e.g. *Carex spp., Rhynchospora alba, Sphagnum majus* and *Sphagnum tenellum*). The high average Ellenberg indicator value in soil moisture for decreasing species also indicates that lawn and hollow species have decreased. Half of the species which had an increase in frequency grow on hummocks (e.g. *Calluna vulgaris, Racomitrium lanuginosum, Erica tetralix* and *Hypnum cupressiforme*), and they had a lower average Ellenberg indicator value for soil moisture than the decreasing species. The changes in species optimum were mainly in one direction for temperature and soil moisture environmental gradients. This implies that more species are now growing with species with higher Ellenberg indicator value for temperature and lower value for soil moisture, indicating that species composition have changed since more species are now found with species that grow in warmer and drier conditions than before. These changes suggest that the mires have become drier during the last 46 years, even though climate data indicate that temperature and precipitation have been more or less the same since 1978.

Half of the species which decreased in frequency have a relatively high average Ellenberg indicator value for pH and species that increased in frequency generally had a low average pH value. This implies that species growing on moderate acidic towards basic soil are now declining and species that grow on acidic soil is increasing. The changes in species optimum were mainly in one direction for the pH and this was also the environmental gradient that contained the highest number of species that changed their associates. More species are now probably growing with species with lower Ellenberg indicator pH values (acidic tolerant species), implying that species composition have changed. These changes suggest that the mires have become more acidic the last 46 years. The pH-measurement confirmed that pH has declined a little, but this might also be due to different sampling strategy. Gunnarsson et al. (2000) found that pH did not change much in nutrient poor areas with low pH values, but pH declined in intermediate areas with pH range of 5 to 6. Expansion

of ombrotrophic mire areas often results in vegetation acidifying the environment itself (Gunnarsson et al., 2000).

The findings from Hitra suggest that species richness has increased and species composition has been altered. The changes are increase of hummock species and decrease of lawn and hollow species suggesting that the mires have become drier and more acidic. These changes can be accounted for by natural succession and are most probably not linked to any external driver, as climate has remained relatively constant and nitrogen deposition is low (Gunnarsson et al., 2002, Gunnarsson et al., 2000). If nitrogen were the main cause then tall growing species e.g. *Eriophorum angustifolium, Molinia caerulea* and *Phragmites australis* are expected to increase, none tall growing species showed an increase (Berendse et al., 2001, Gunnarsson et al., 2002, Kapfer et al., 2011). However nitrogen deposition cannot be ruled out since it has increased slightly the last 20 years and might even increase more rapidly from 2006 due to the release of oxidized nitrogen from Tjeldbergodden, so nitrogen deposition might have enhanced these changes. I suggest that these changes can be understood in terms of Berendse et al.'s (2001) phases: the mires on Hitra are in phase one (at low deposition) were levels of nitrogen is still limiting *Sphagnum* growth, so that addition of nitrogen leads to increased peat moss growth.

5.2 Austre Moland

In the correspondence analysis (CA) *Sphagnum angustifolium, S. capillifolium* and *S. girgensohnii* associations plots have different distribution along the first axis over time, and they might have changed their species composition, and it could also be due to different sampling preference or just random difference. However the CA plot from both surveys has quite similar distribution in species composition, indicating that the resurvey in 2010 successfully captured the vegetation sampled in the original data. When we examine the findings from Austre Moland we see clearly that changes have taken place the last 43 years. This fine-scale comparison of mire vegetation in Austre Moland found that the total number of species and species number per plot had decreased significantly. Most of the species that decreased in frequency were low growing species e.g. C*arex pauciflora, Oxycoccus palustris* and *Rhynchospora alba*, and most of the species that increased in frequency were high growing species e.g. *Carex rostrata, Molinia caerulea* and *Myrica gale* (Berendse et al., 2001, Gunnarsson et al., 2002, Kapfer et al., 2011).

I suggest that these changes can be understood in terms of Berendse et al.'s (2001) phases: the mire is in a transition between phase two (at intermediate deposition) were N no longer limits Sphagnum growth, but the Sphagnum layer has not yet reached its maximum organic N content and phase three (at high deposition) where the Sphagnum layer has reached its maximum organic N content, so that additional N input will reach the soil solution (Berendse et al., 2001). First, The increase in frequency of *Drosera rotundifolia, Polytrichum strictum* and four *Sphagnum* species indicate that the mire has reached phase two. All of these species easily and efficient take up nutrients and will therefore absorb most of the increased N deposition up to the critical load, which for ombrotrophic mires in Norway is estimated to between 500 and 1000 mgN/m^2/year (Aarrestad and Stabbetorp, 2010, Berendse et al., 2001, Nordbakken et al., 2003, Rydin et al., 2006). This leads to increased Sphagnum growth and very little nitrogen will pass through the Sphagnum filter down to the roots of vascular plants (Berendse et al., 2001, Nordbakken et al., 2003, Rydin et al., 2006). However (Redbo-Torstensson, 1994) found that *Drosera rotundifolia* decreased and that the survivorship of the plants after 4 years of adding nitrogen was significantly reduced. *Polytrichum strictum* has been found to increase in density and cover with increased N deposition (Berendse et al., 2001, Mitchell et al., 2002). Second, the increased frequency of scrubs and larger species (*Erica tetralix, Carex rostrata, Molinia caerulea, Narthecium ossifragum* and *Myrica gale*) might have caused a decrease in low growing species in open vegetation types (*Carex pauciflora, Oxycoccus palustris* and *Rhynchospora alba*) which indicates that the mire is close to phase three (Berendse et al., 2001, Gunnarsson et al., 2002). Above the critical load Sphagnum is N saturated and growth will not increase, nitrogen will then be available for vascular plants through their roots plants (Berendse et al., 2001, Nordbakken et al., 2003, Rydin et al., 2006). The result of this is that the mosses will become P limited or co-limited by P and K (Aerts et al., 1992, Bragazza et al., 2004, Gunnarsson and Rydin, 2000), and large productive species will increase while bryophytes and other low growing species will decline (Berendse et al., 2001). Even though some species were not encountered in the resampling (*Agrostis canina* and *Carex pauciflora*) a real decrease in species occurrences is still a plausible explanation because most of the sedge species in the data decreased in occurrence. The alternative explanation for the observed change, namely errors in species determination, would result in that at least some of the some of the other sedges in the data to increase over time.

The changes in species optimum Ellenberg values tell the same story; changes in species optima were mainly in one direction for the pH and light environmental gradients. I found that the

estimated optimum values for Ellenberg pH and light decreased for several species, indicating that more species are now found with more acidic and shade tolerant species than before, probably because these species have expanded on the mire. This suggests that the mire has become more acidic and that the vegetation has become denser. Detecting changes in species optima for Ellenberg nutrient values in this dataset is more difficult because most of the species on ombrotrophic mires have low indicator values, typically 1 or 2. For instance *Molinia caerulea* which has repeatedly been found to increase due to increased nitrogen deposition has Ellenberg indicator nutrient value of 2 (Aarrestad and Stabbetorp, 2010, Bobbink et al., 2003).

The findings from Austre Moland indicate changes in species richness and composition and these changes are probably caused by increased nitrogen deposition, resulting in decreased species richness and altered species composition. The changes in the vegetation at Austre Moland coincide with findings from European nitrogen deposition and mire research e.g. decreased frequency in low growing species and increased frequency in high growing species (Aarrestad and Stabbetorp, 2010, Berendse et al., 2001, Bergamini and Pauli, 2001, Bobbink et al., 2003, Redbo-Torstensson, 1994).

5.3 The Gradient

Species richness generally decreases with latitude and altitude from equator, and this also applies for vascular plants in Norway (Cox and Moore, 2005, Grytnes et al., 1999). Weakly southern or south western *Sphagnum* species as *Sphagnum affine, S. cuspidatum* and *S. palustre* have steadily decreasing prevalence rates from the South west coast of Norway to Nordland (Kjell Ivar Flatberg, pers. comm.). However, a general trend in mosses with decreasing frequency both south and north along the coast of Trøndelag is probably not likely. This is certainly complex, and many variables could affect, among other things, human intervention and use of nature, natural succession, acid rain in different varieties (including N-deposition) and more (Kjell Ivar Flatberg, pers.comm).

In the fine-scale comparison of ombrotrophic mire vegetation along a latitudinal gradient along the west coast of Norway I found that the total number of species decreased significantly southwards. Nitrogen and sulphur deposition were highly correlated and showed the same pattern along the latitudinal gradient and they were strongly negative correlated with total species richness and bryophyte species richness. This indicates that both environmental variables can explain the decrease in species richness southwards. However the release of sulphur to the atmosphere has decreased dramatically (63%) the last 30 years and (Aas et al., 2008) the AIC showed that nitrogen

deposition was the best model explaining the decrease. The backward selection shows that nitrogen deposition is the environmental gradient that best explains the decrease in total species richness and bryophyte species richness, but when pH measurements are taken into account then pH is the variable that best explains this decrease. However these do not contradict each other since high nitrogen deposition is known to increase acidity in the soil (Sutton et al., 2011). The mire in Bjørnestølheia (4) has the lowest average species richness per site (6.9) and it is the mire that has the highest average nitrogen deposition (1750 mgN/m^2/yr) and the second lowest pH value (4.08) The mire next to Sletta (18) has the highest average species richness per site (12) and it has the third lowest average nitrogen deposition (366 mgN/m^2/yr) and the fourth highest pH value (4.44).

The findings from the gradient survey suggest decrease in total species richness, vascular species richness and bryophyte species richness on ombrotrophic mires southwards and is probably caused by increased nitrogen deposition southwards.

6. CONCLUSION

The findings from all three surveys suggest that nitrogen deposition is impacting the mire vegetation in the south where N deposition is highest and also above the critical load (500-1000 mgN/m^2/yr). Hitra showed changes in terms of increased species richness and alteration of species composition but these changes are probably caused by natural succession. Austre Moland showed decrease in species richness and alteration of species composition and these changes are most likely caused by increased nitrogen deposition. There was greater change in relative frequency of occurrence at Austre Moland (42%) than Hitra (33%). The gradient survey showed that nitrogen deposition decrease species richness on ombrotrophic mires.

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APPENDIX 1

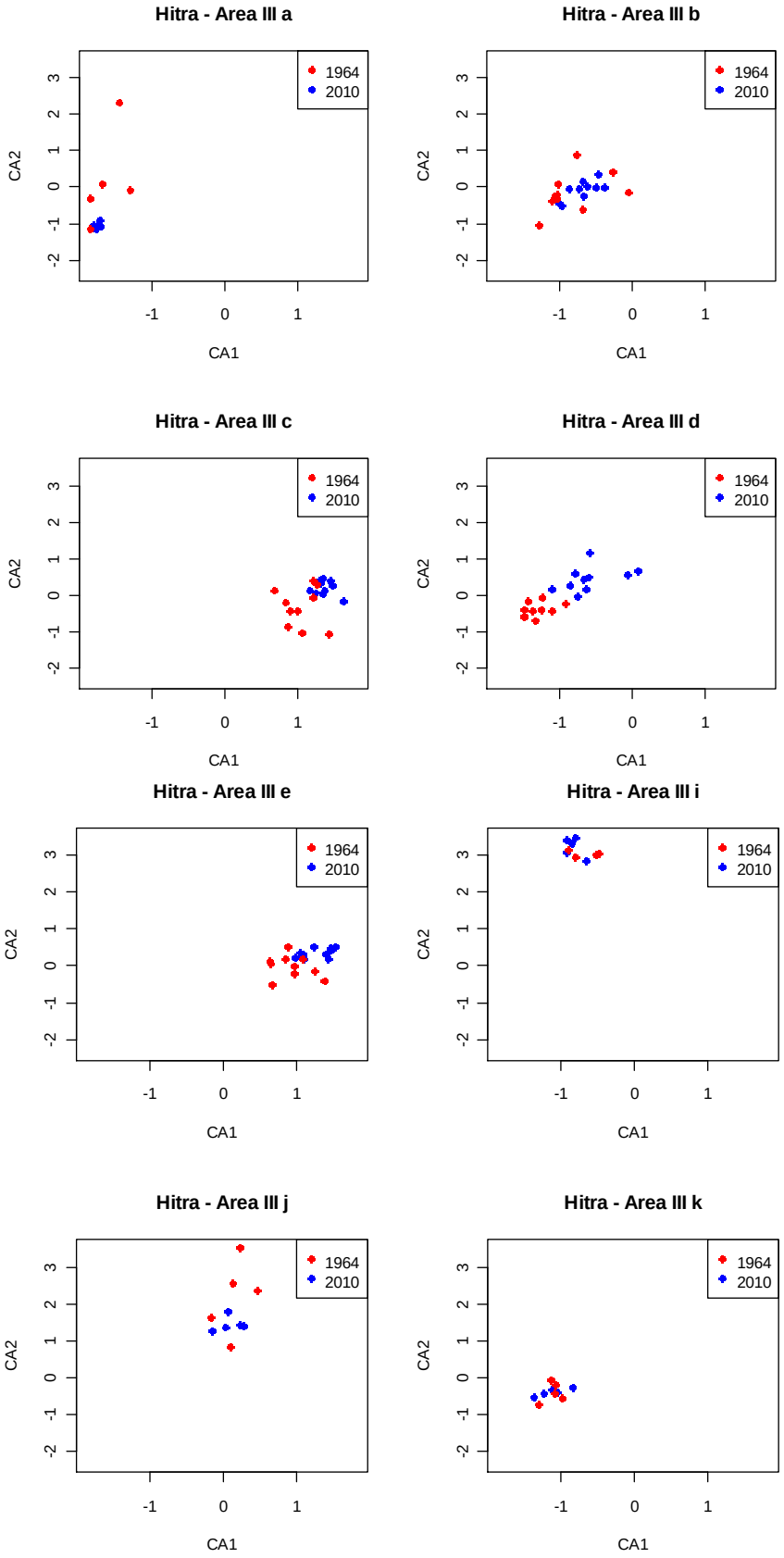

Figure A1.1.a) Correspondence analysis visualizing distribution of the different areas at Hitra based on the species composition of each plot. Red circles represent the original survey from 1965 and blue circles represent the resurvey from 2010.

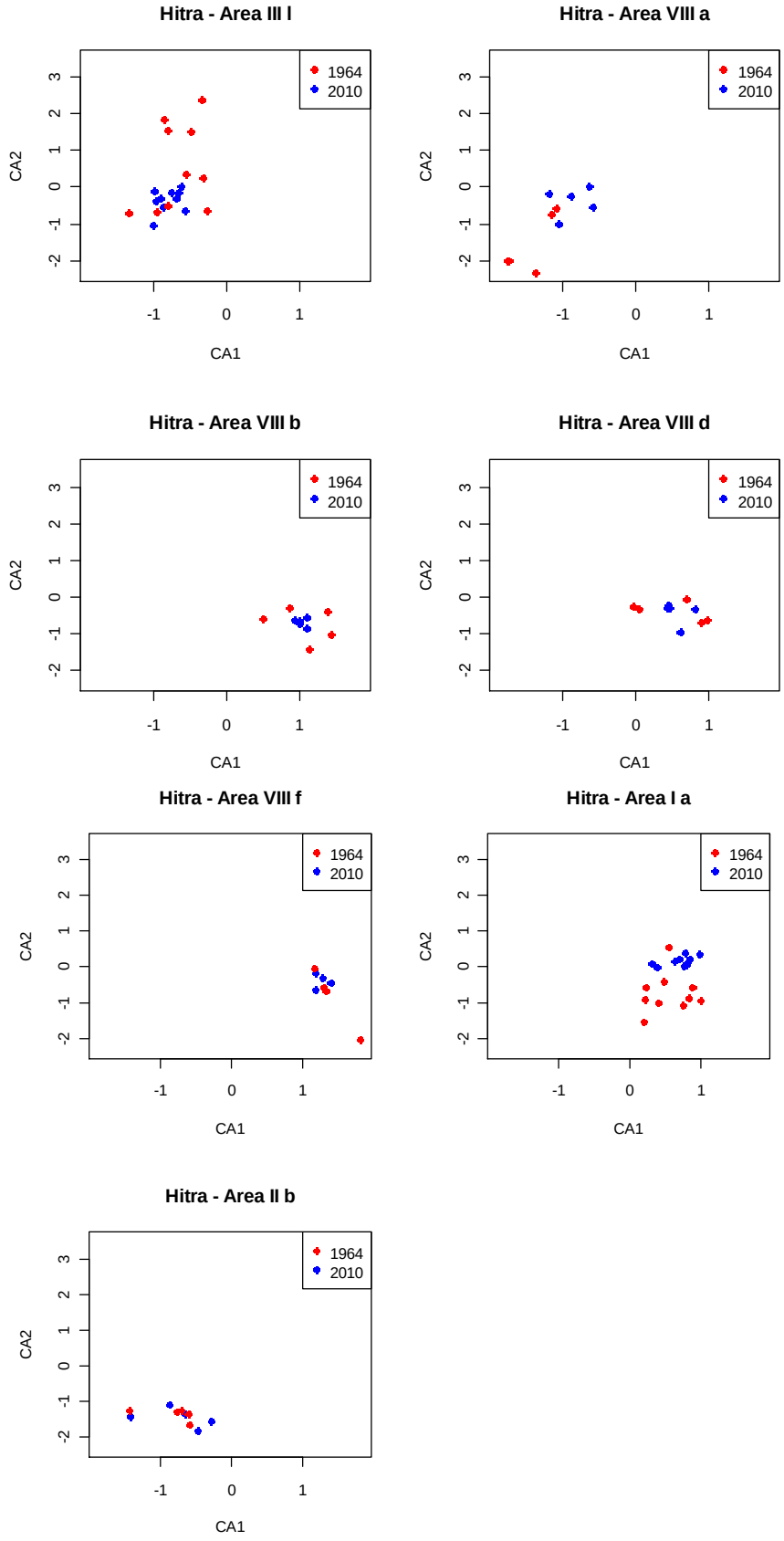

Figure A1.1.b) Correspondence analysis visualizing distribution of the different areas at Hitra based on the species composition of each plot. Red circles represent the original survey from 1965 and blue circles represent the resurvey from 2010.

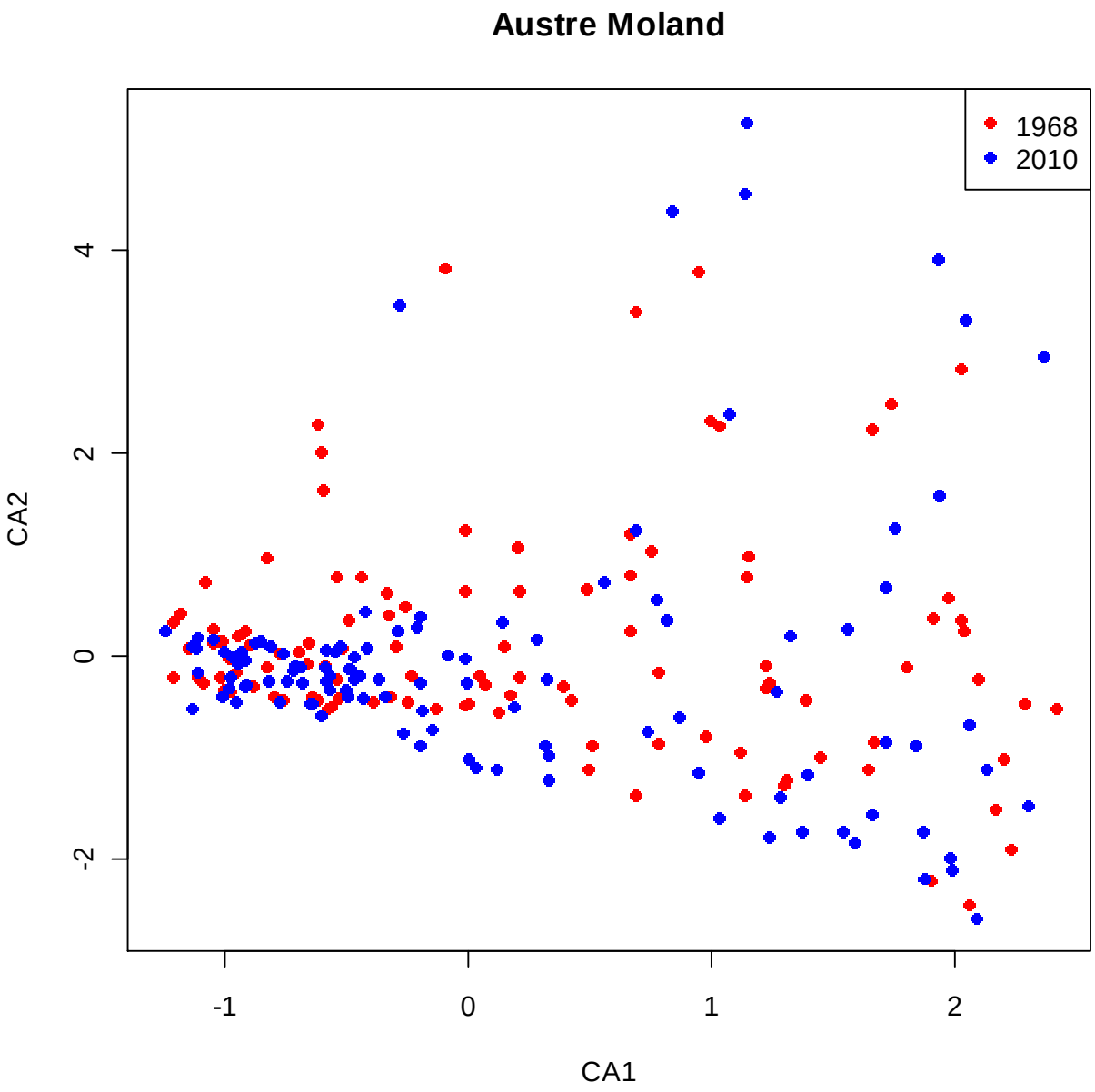

Figure A1.2. Correspondence analysis visualizing distribution of all the plots at Austre Moland based on the species composition of each plot. Black circles represent the resample survey from 2010 and coloured circles represent the different areas in the original survey from 1967.

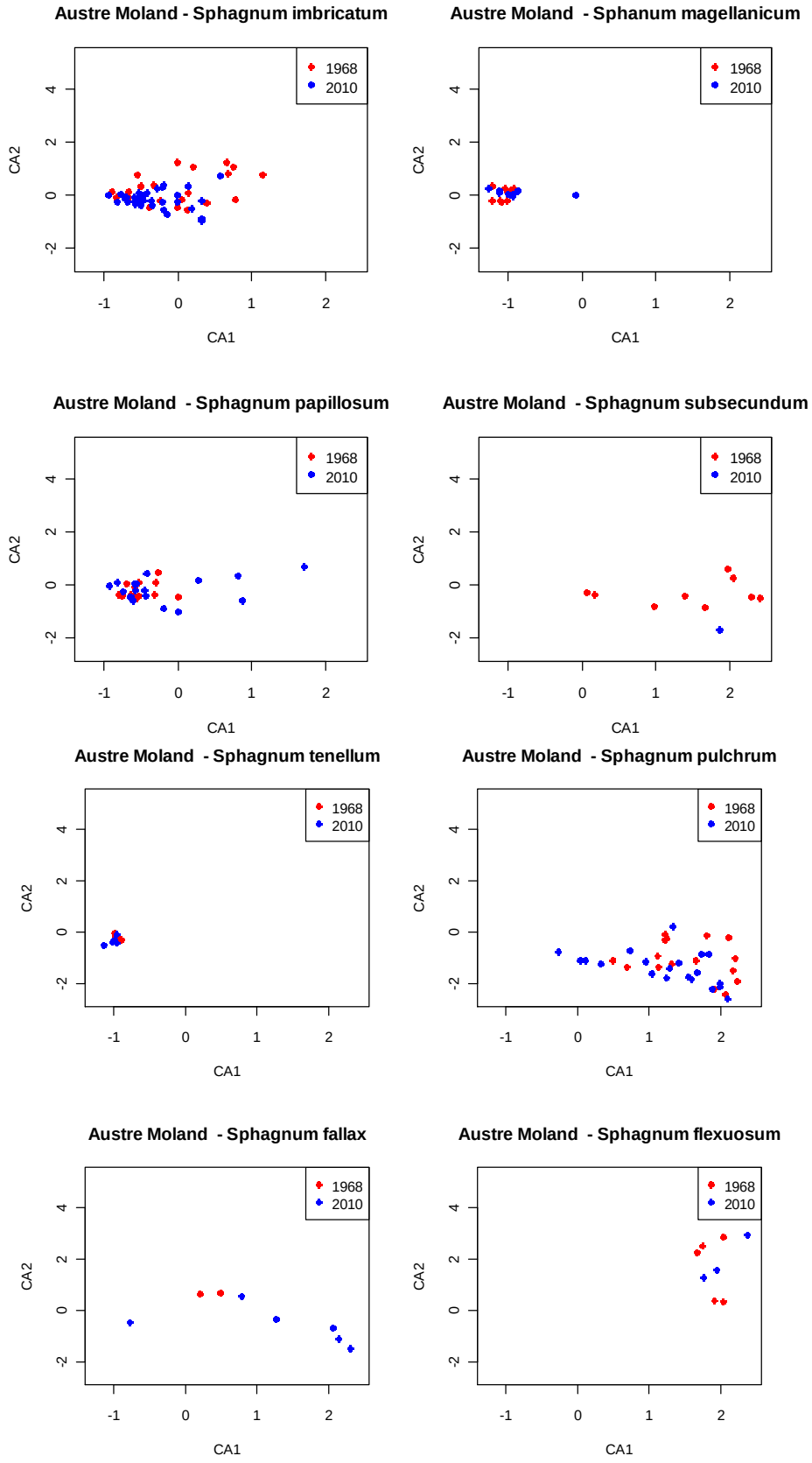

Figure A1.3.a) Correspondence analysis visualizing distribution of the different *Sphagnum* associations in Austre Moland based on the species composition of each plot. Red circles represent the original survey from 1968 and blue circles represent the resurvey from 2010.

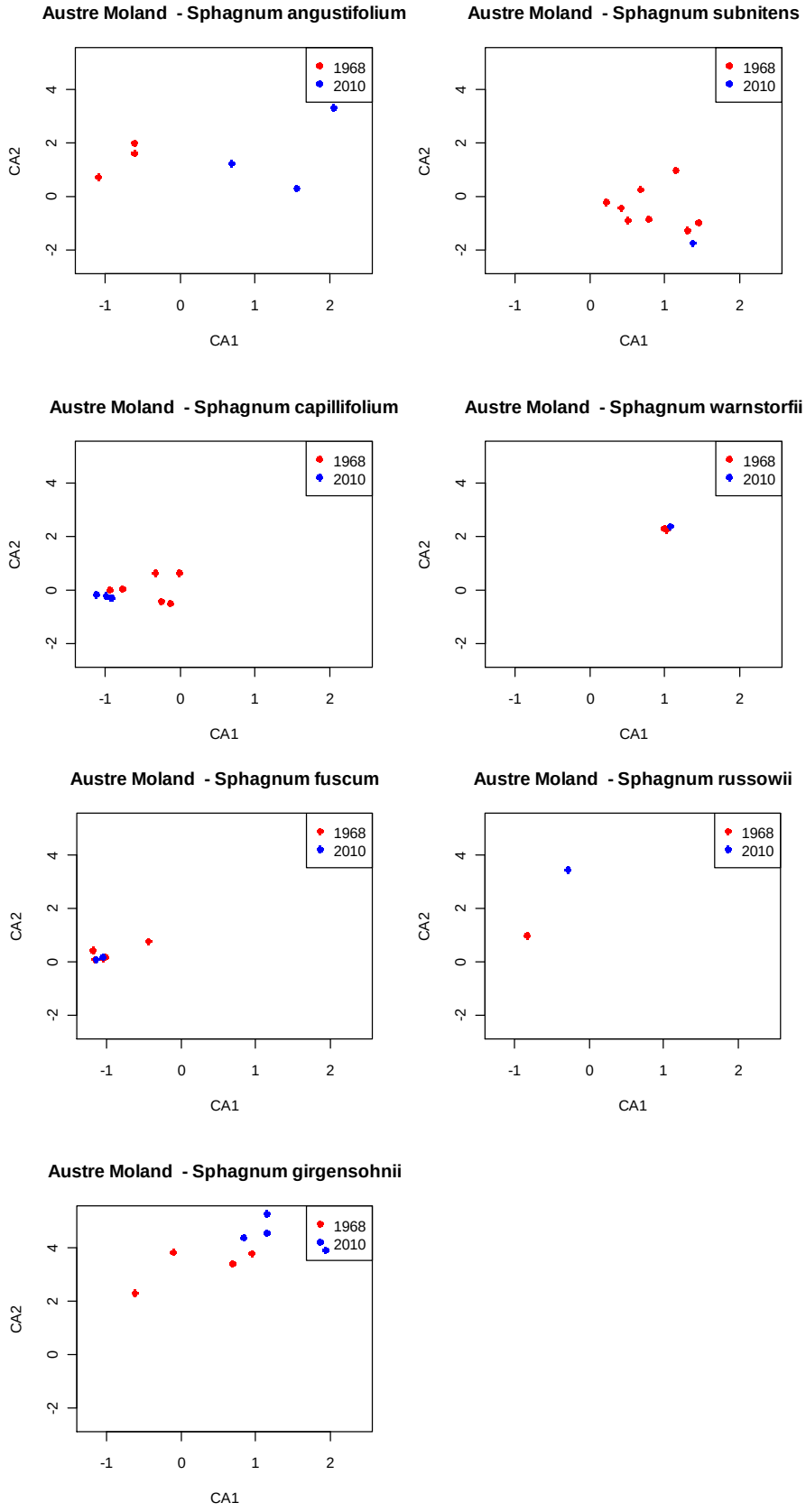

Figure A1.3.b) Correspondence analysis visualizing distribution of the different *Sphagnum* associations in Austre Moland based on the species composition of each plot. Red circles represent the original survey from 1968 and blue circles represent the resurvey from 2010.

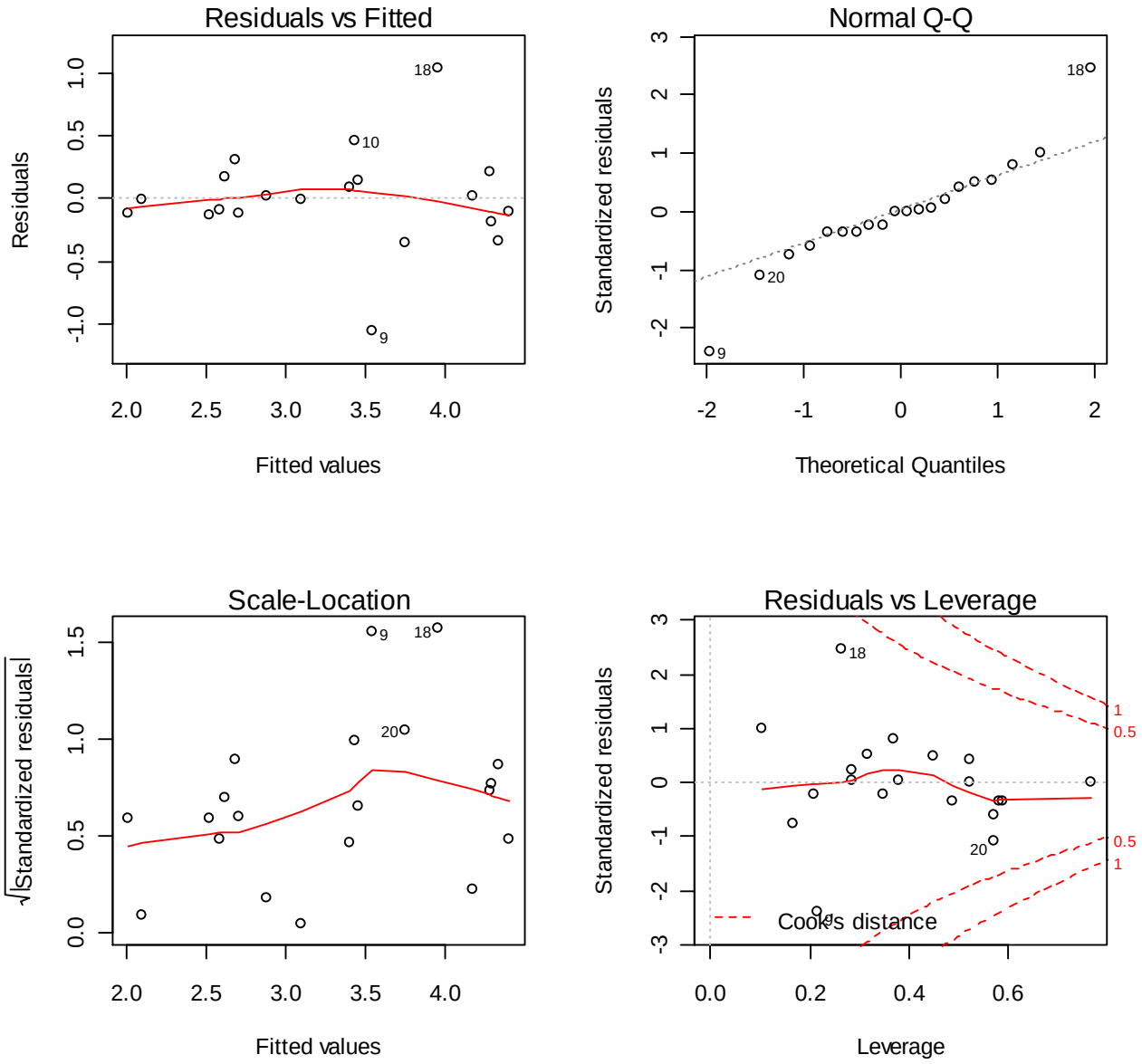

Figure A.1.4. Diagnostic plot from the linear multible regression in the gradient survey for model1<-lm(Species~Nitrogen*Precipitation*Tetraterm)

Table A1.1. Species occurrence on Hitra and Austre Moland during both surveys and in the gradient survey. It contains abbreviation name used in analysis, scientific and Norwegian name according to Lid and Lid (2007) for vascular plants and Artsdatabanken for bryophytes.

Abbreviation	Scientific name	Norwegian name	H1964	H2010	AM1967	AM2010	Gradient
Alnu.inca	*Alnus incana*	Gråor			2		
Andr.poli	*Andromeda polifolia*	Kvitlyng	95	78	55	34	187
Arct.uvau	*Arctostaphylos uva-ursi*	Mjølbær		5			
Arct.alpin	*Arctous alpinus*	Rypebær		2			1
Betu.nana	*Betula nana*	Dvergbjørk	18	25			41
Betu.pube	*Betula pubescens*	Bjørk			1		
Betu.juv.	*Betula pubescens (juv.)*	Bjørke spire			17	6	13
Call.vulg	*Callluna vulgaris*	Røsslyng	76	84	34	14	138
Empe.nigr	*Empetrum nigrum*	Krekling	37	32			11
Eric.tetr	*Erica tetralix*	Klokkelyng	38	55	51	55	13
Juni.comm	*Juniperus communis*	Einer	1		4		
Myri.gale	*Myrica gale*	Pors			78	72	24
Oxyc.palu	*Oxycoccus palustris*	Tranebær	18	2	91	42	64
Pice.abie	*Picea abis*	Gran			6		
Pice.juv.	*Picea abis (juv.)*	Gran spire			1		
Pinu.sylv	*Pinus sylvestris*	Furu			6	1	
Pinu.juv.	*Pinus sylvestris (juv.)*	Furu spire		1	42	22	4
Quer.petr	*Quecus petraea*	Vintereik			1		
Rubu.cham	*Rubus chamaemorus*	Molte	47	3			52
Sali.repe	*Salix repens*	Heivier			1		
Sorb.aucu	*Sorbus aucuparia (juv.)*	Rogn			1		
Vacc.myrt	*Vaccinium myrtillus*	Blåbær			1	5	5
Vacc.ulig	*Vaccinium uliginosum*	Blokkebær				1	6
Vacc.viti	*Vaccinium vitis-idea*	Tyttebær	9	7	1	3	11
Bart.alpi	*Bartsia alpina*	Svarttopp		3			
Cham.suec	*Chamaepericlymenum suecicum*	Skrubbær		4			
Coma.palu	*Comarum palustre*	Myrhatt	4		7	3	
Dach.macu	*Dactylorhiza maculata*	Flekkmarihand	8	4	2	7	1
Dros.inte	*Drosera intermedia*	Dikesoldogg		3	3		6
Dros.long	*Drosera longifolia*	Smalsoldogg	21	17	6		25
Dros.rotu	*Drosera rotundifolia*	Rundsoldagg	73	63	5	67	149
Equi.fluv	*Equisetum fluviatile*	Elvesnelle			6		
Equi.palu	*Equisetum palustre*	Myrsnelle		1			
Euph.spp.	*Euphrasia spp.*	Øyentrøst spp.	22	25			4
Gali.palu	*Galium palustre*	Myrmaure			3	3	
Hupe.sela	*Huperzia selago*	Lusegras			1		
List.cord	*Listeria cordata*	Småtviblad			2		
Lotu.corn	*Lotus corniculatus*	Tiriltunge		1			
Lyco.inun	*Lycopodiella inundata*	Myrkråkefot			1		
Lyco.anno	*Lycopodium annotium*	Stri kråkefot		5			
Lyco.clav	*Lycopodium clavatum*	Mjuk kråkefot			2		
Lysi.thyr	*Lysimachia thyrsiflora*	Gulldusk			4		
Maia.bifo	*Maianthemum bifolium*	Maiblom			1		

Abbreviation	Scientific name	Norwegian name	H1964	H2010	AM1967	AM2010	Gradient
Meny.trif	*Menyanthes trifoliata*	Bukkeblad	8	3	38	37	1
Nart.ossi	*Narthecium ossifragum*	Rome	66	59	35	39	93
Pedi.palu	*Pedicularis palustre*	Myrklegg		4			
Pedi.sylv	*Pedicularis sylvatica*	Kystmyrklegg		1			
Peuc.palu	*Peucedanum palustre*	Mjølkerot			9	6	
Ping.vulg	*Pinguicula vulgaris*	Tettegras	29	8			
Pote.erec	*Potentilla erecta*	Tepperot	31	36	34	17	8
Pter.aqui	*Pteridium aquilinum*	Einstape			3		
Pyro.mino	*Pyrola minor*	Perlevintergrøn			1		
Sela.sela	*Selaginella selaginoides*	Dvergjamne	14	13			2
Soli.virg	*Solidago virgaurea*	Gullris		1			
Succ.prat	*Succisa pratensis*	Blåknapp	12	13			1
Tofi.pusi	*Tofieldia pusilla*	Bjørnebrodd	11	1			
Trie.euro	*Trientalis europea*	Skogstjerne	13	5	38	27	1
Viol.palu	*Viola palustris*	Myrfiol	2	1	3	2	
Agro.cani	*Agrostis canina*	Hundekvein	3	1	18		
Agro.capi	*Agrostis capillaris*	Engkvein			4		
Aven.flex	*Avenella flexousa*	Smyle		5	2	4	
Care.cann	*Carex cannescens*	Gråstarr			6	2	
Care.demi	*Carex demissa*	Grønnstarr			2	1	
Care.dioi	*Carex dioica*	Sæbustarr	9	2	1	3	
Care.echi	*Carex echinata*	Sjernestarr	7	1	26	19	1
Care.host	*Carex hostiana*	Engstarr			3		
Care.lasi	*Carex lasiocarpa*	Trådstarr	26	13	5	3	
Care.limo	*Carex limosa*	Dystarr	13				
Care.nigr	*Carex nigra*	Slåttestarr			27	22	1
Care.pani	*Carex panicea*	Kornstarr	21	6	31		4
Care.pauc	*Carex pauciflora*	Sveltstarr	74	12	22	11	13
Care.paup	*Carex paupercula*	Frynsestarr	2		5	3	
Care.puli	*Carex pulicaris*	Loppestarr		2	4		
Care.rost	*Carex rostrata*	Flaskestarr	5	7	53	67	
Care.sero	*Carex serotina*	Beitestarr			5		
Care.vagi	*Carex vaginata*	Slirestarr		5		8	4
Dant.decu	*Danthonia decumbens*	Knegras			2		
Erio.angu	*Eriophorum angustifolium*	Duskull	41	33	42	15	23
Erio.vagi	*Eriophorum vaginatum*	Torvull	1	77	57	58	188
Fest.rubr	*Festuca rubra*	Raudsvingel			1		
Junc.alpin	*Juncus alpinoarticulatus c.f.*	Skogsiv				1	
Junc.fili	*Juncus filiformis*	Trådsiv			2	2	
Moli.caer	*Molinia caerulea*	Blåtopp	47	41	55	69	17
Phra.aust	*Phragmites australis*	Takrør	3	1			
Rhyn.alba	*Rhynchospora alba*	Kvitmyrak	1	2	16	4	37
Scho.ferr	*Schoenus ferrugineus*	Brunmyrak		3			
Tric.cesp	*Trichophorum cespitosum*	Bjørneskjegg	65	49	22	19	84
Aula.palu	*Aulacomnium palustre*	Myrfiltmose	17	14	25	19	2
Call.cusp	*Calliergonella cuspidata*	Sumpbroddmose				1	
Camp.stel	*Campylium stellatum*	Myrstjernemose	13	13	2		

Abbreviation	Scientific name	Norwegian name	H1964	H2010	AM1967	AM2010	Gradient
Dicr.leio	*Dicranum leioneuron cf.*	Akssigd		1			
Dicr.maju	*Dicranum majus*	Blanksigd		1			
Dicr.poly	*Dicranum polysetum*	Krussigd		1			
Dicr.scop	*Dicranum scoparium*	Ribbesigd	12	6			
Dicr.spp.	*Dicranum spp.*	[1] Sigdmoseslekta	7	7			
Dicr.undu	*Dicranum undulatum*	Sveltsigd	5	1			
Hylo.sple	*Hylocomium splendens*	Etasjemose	16	19			4
Hypn.cupr	*Hypnum cupressiforme*	Matteflette	13	2			4
Hypn.jutl	*Hypnum jutlandicum*	Heiflette	1	2			
Pleu.schr	*Pleurozium schreiberi*	Furumose	4	4	2		24
Pohl.spp.	*Pohlia spp.*	[2] Nikkemoseslekta	9	9	7	1	
Poly.comm	*Polytrichum commune*	Storbjørnemose				8	
Poly.stri	*Polytrichum strictum*	Filtbjørnemose	2	2	14	21	11
Ptil.cris	*Ptilium crista-castrensis*	Fjærmose	4				
Raco.lanu	*Racomitrum lanuginosum*	Heigråmose	6	66			5
Rhyt.lore	*Rhytidiadelphus loreus*	Kystkransmose	6	9			4
Sani.unic	*Sanionia uncinata*	Klobleikmose	1				
Sarm.exan	*Sarmentypnum exannulatum*	Vrangnøkkemose		3	11	5	
Sarm.sarm	*Sarmentypnum sarmentosum*	Blodnøkkemose	2	2			
Sarm.tric	*Sarmentypnum trichophyllum*	Tjernnøkkemose			1		
Scor.revo	*Scorpidium revolvens*	Rødmakkmose	3	4	4	1	
Stra.stra	*Straminergon stramineum*	[3] Grasmose	3	1	75	37	21
Warn.spcf	*Warnstorfia spp. cf.*	[4] Nøkkemoseslekta		7			
Warn.flui	*Warnstorfia fluitans*	Vassnøkkemose	5	12	1	3	
Spha.affi	*Sphagnum affine*	Gulltorvmose					3
Spha.aust	*Sphagnum austinii*	Kusttorvmose					14
Spha.angu	*Sphagnum angustifolium*	Klubbetorvmose	7	7	6	9	1
Spha.balt	*Sphagnum balticum*	Svelttorvmose			2		
Spha.capi	*Sphagnum capillifolium*	Furutorvmose	71	65	61	64	131
Spha.comp	*Sphagnum compactum*	Stivtorvmose	11	11			8
Spha.cusp	*Sphagnum cuspidatum*	Vasstorvmose	2	2	4	2	4
Spha.cucf	*Sphagnum cuspidatum c.f.*	Vasstorvmose c.f.				1	
Spha.fall	*Sphagnum fallax*	Broddtorvmose			12	16	5
Spha.facf	*Sphagnum fallx c.f.*	Broddtorvmose c.f.		1		3	
Spha.flex	*Sphagnum flexosum*	Bleiktorvmose			3	14	
Spha.fusc	*Sphagnum fuscum*	Rusttorvmose	1	1	7	2	28
Spha.girg	*Sphagnum girgensohnii*	Grantorvmose			7	5	
Spha.imbr	*Sphagnum imbricatum*	[5]	27	19	51	61	
Spha.mage	*Sphagnum magellanicum*	Kjøtt-torvmose	17	19	28	32	92
Spha.maju	*Sphagnum majus*	Lurvtorvmose	19	4		1	
Spha.palu	*Sphagnum palustre*	Sumptorvmose		5	5	14	16
Spha.papp	*Sphagnum papillosum*	Vortetorvmose	59	42	29	43	81
Spha.pulc	*Sphagnum pulchrum*	Fagertorvmose		1	43	37	7
Spha.quin	*Sphagnum quinquefarium*	Lyngtorvmose			1		
Spha.ripa	*Sphagnum riparium*	Skartorvmose			1		

Abbreviation	Scientific name	Norwegian name	H1964	H2010	AM1967	AM2010	Gradient
Spha.russ	*Sphagnum russowi*	Tvaretorvmose			8	6	
Spha.squa	*Sphagnum squarrosum*	Spriketorvmose			1		
Spha.stri	*Sphagnum strictum*	Heitorvmose	5	6			1
Spha.subn	*Sphagnum subnitens*	Blanktorvmose	2	15	22	3	1
Spha.subs	*Sphagnum sect. Subsecunda*	[6] Torvmose seksjon Subsecunda	26	11	14	7	1
Spha.tene	*Sphagnum tenellum*	Dvergtorvmose	73	41	14	9	98
Spha.tere	*Sphagnum teres*	Beitetorvmose			1	1	
Spha.warn	*Sphagnum warnstorfii*	Rosetorvmose	1	4	2	1	
Barb.hatc	*Barbilophozia hatcheri*	Grynskjeggmose		1			
Barb.kunz	*Barbilophozia kunzeana*	Myrskjeggmose	2				
Caly.fiss	*Calypogeia fissa*	Tannflak				1	
Caly.spha	*Calypogeia sphagnicola*	Sveltflak	23	18	5	1	
Ceph.spp.	*Cephalozia spp.*	[7] Glefsemoseslekta	56	41	16	12	
Chil.poly	*Chiloscyphus polyanthos*	Bekkeblonde			1		
Clad.flui	*Cladopodiella fluitans*	Myrsnutemose	34	8	19	12	
Gymn.infl	*Gymnocolea inflata*	Torvdymose		3	4		
Kurz.pauc	*Kurzia pauciflora*	Sveltfingermose	44	31	16	5	
Leio.bade	*Leiocolea badensis*	Dvergflik	2				
Loph.spp.	*Lophozia spp.*	[8] Flikmoseslekta	1	1			
Myli.anom	*Mylia anomala*	Myrmuslingmose	5	17	5	3	
Myli.tayl	*Mylia taylorii*	Rødmuslingmose	5	2			
Odon.spp.	*Odontoschisma spp.*	[9] Skovlmoseslekta	37	37	1	4	
Pell.epip	*Pellia epiphylla*	Flikvårmose				1	
Ptil.cili	*Ptilidium ciliare*	Bakkefrynse	31	21			
Ricc.spp.	*Riccardia spp.*	[10]	22	25	5	1	
Scap.spp.	*Scapania spp.*	[11] Tvebladmoseslekta	4		3	1	

[1] Individuals too difficult to identify to species and were only identified to genus *Dicranum*.

[2] Individuals too difficult to identify to species and were only identified to genus *Pohlia*.

[3] *Straminergon stramineum* consists of *Straminergon stramineum* and *Loeskypnum badium*.

[4] *Warnstorfia spp. cf.* Consist of individuals too difficult to identify to species and belongs to genus of either *Sarmentypnum* or *Warnstorfia*.

[5] *Sphagnum imbricatum* consist of *Sphagnum affine* and *Sphagnum austinii*.

[6] Individuals too difficult to identify to species and were only identified to *Sphagnum* section *Subsecunda*.

[7] Individuals too difficult to identify to species and were only identified to genus *Cephalozia*.

[8] Individuals too difficult to identify to species and were only identified to genus *Lophozia*.

[9] Some individuals were too difficult to identify to species and were therefore only identified to genus *Odontoschisma*.

[10] *Riccardia* spp. consists of species within the genus *Riccardia* and *Aneura pinguis*.

[11] *Scapania* spp. consists of the two species *Scapania irrigua* and *Scapania nemorea*.

Table A1.2. Correlation between species richness, vascular plant richness, bryophyte richness, latitude, nitrogen deposition, pH precipitation, temperature, Ellenberg indicator value for light, temperature, soil moisture, pH and nutrients.

	Species	Vascular	Bryophytes	Latitude	Nitrogen	pH	Sulphur	Precipitation	Temperature	Light	Temperature	Soil moisture	pH	Nutrients
Species	1	0.80	0.88	0.80	-0.76	0.84	-0.76	-0.01	-0.17	-0.36	-0.56	-0.48	0.43	0.34
Vascular	0.80	1	0.41	0.57	-0.50	0.48	-0.52	-0.07	-0.25	-0.28	-0.50	-0.50	0.41	0.30
Bryophytes	0.88	0.41	1	0.76	-0.76	0.90	-0.75	0.04	-0.06	-0.32	-0.44	-0.32	0.33	0.28
Latitude	0.80	0.57	0.76	1	-0.95	0.78	-0.93	0.10	-0.28	-0.39	-0.45	-0.50	0.42	0.36
Nitrogen	-0.76	-0.50	-0.76	-0.95	1	-0.75	0.99	0.06	0.14	0.31	0.37	0.38	-0.27	-0.26
pH						1								
Sulphur	-0.76	-0.52	-0.75	-0.93	0.99	-0.75	1	0.17	0.07	0.27	0.34	0.35	-0.25	-0.21
Precipitation	-0.01	-0.07	0.04	0.10	0.06	0.16	0.17	1	-0.67	-0.37	-0.34	-0.26	0.23	0.39
Temperature	-0.17	-0.25	-0.06	-0.28	0.14	-0.49	0.07	-0.67	1	0.63	0.71	0.59	-0.14	-0.36
Light	-0.36	-0.28	-0.32	-0.39	0.31		0.27	-0.37	0.63	1	0.75	0.64	-0.36	-0.67
Temperature	-0.56	-0.50	-0.44	-0.45	0.37		0.34	-0.34	0.71	0.75	1	0.57	-0.04	-0.25
Soil moisture	-0.48	-0.50	-0.32	-0.50	0.38		0.35	-0.26	0.59	0.64	0.57	1	-0.40	-0.51
pH	0.43	0.41	0.33	0.42	-0.27		-0.25	0.23	-0.14	-0.36	-0.04	-0.40	1	0.81
Nutrients	0.34	0.30	0.28	0.36	-0.26		-0.21	0.39	-0.36	-0.67	-0.25	-0.51	0.81	1

Table A1.3. Comparison of Akaike's Criterion for different linear multiple regression models.

Linear Multiple Regression Model	df	AIC
model1<-lm(Species~Nitrogen*Precipitation*Tetraterm)	9	59.16743
model2<-lm(Species~Svovel*Precipitation*Tetraterm)	9	59.30957
model1<-lm(Vascular~Nitrogen*Precipitation*Tetraterm)	9	46.58343
model2<-lm(Vascular~Svovel*Precipitation*Tetraterm)	9	46.79150
model1<-lm(Bryophytes~Nitrogen*Precipitation*Tetraterm)	9	36.38831
model2<-lm(Bryophytes~Svovel*Precipitation*Tetraterm)	9	37.24664
model1<-lm(Species~N*Moist*Temp*L)	17	71.02219
model2<-lm(Species~R*Moist*Temp*L)	17	68.29212
model1<-lm(Species~Nitrogen*Precipitation*Tetraterm)	9	59.16743
model2<-lm(Species~log(Nitrogen)*log(Precipitation)*Tetraterm)	9	58.16536