Last-century vegetational changes in northern Europe

Characterisation, causes, and consequences

Jutta Kapfer

Dissertation for the degree of philosophiae doctor (PhD)
at the University of Bergen
August 2011

“You cannot step twice into the same river”
- Heraklit -

Preface

This thesis is the result of my three years Ph.D. study at the Department of Biology, University of Bergen. The Ph.D. project was financed by the Norwegian Research Council as part of the programme Norsk Miljøforskning mot 2015 (Miljø 2015), and additional support was given by the Olaf Grolle Olsen legat. Fieldwork on Svalbard in 2009 and on Jan Mayen in 2010 was supported by The Norwegian Polar Institute.

The last three years of working for my dissertation were a unique, instructive, and exciting experience for me, which I would have never wanted to have missed. Yet in the face of all the ups and downs connected with this work, the thesis would not have been completed without the personal and practical help of several people. Thus, it is to them I wish to express my deep gratitude.

First of all, I want to thank my principal supervisor, John-Arvid Grytnes, for his constant support and readiness to help and for fruitful discussions, ideas, and countless valuable comments and feedback. Thanks for sharing permanent good humour, optimism, and enthusiasm both in the field and in the office from start to finish. I am grateful to my co-supervisor, John Birks, for valuable advice and encouragement. I appreciate his reliable support and motivating feedback I have been given, especially in key situations.

Many thanks to my field assistants Jessica Abbott, Walter Kapfer, Sondre Dahle, Brooke Wilkerson, Elisabeth Maquart, and Vivian Felde for their help, stamina, bravery, and reliability through long field seasons.

I am indebted to all my co-authors for keeping up the momentum in preparing the papers for submission. Thanks to them for their incredibly fast reading and helpful comments on the manuscripts.

Thanks particularly to Eric Meineri, Heidi Saure, and Fride Høistad Schei for company, discussions, and encouragement, and all other collegues in the Ecological and Environmental Change Research Group for inspiration and feedback.

I appreciate company and support from my collegues and friends Ulla Heikkilä, Norbert Kühl, and Gerald Jurasinski.

Thanks to Beate Helle for creative suggestions about poster layout, to Cathy Jenks for proof reading manuscripts, and to Eva Burrows for support with typesetting in LaTex.

I am very grateful to my parents, my sisters, and my brother in law, as well as my friends for their constant support, understanding, and encouragement for all the endeavours connected with my Ph.D. Thank you for being here for me at any time and reminding me that there is not only work in life.

Contents

Summary

In the face of recent changes in environmental conditions and climate, long-term studies provide important insights into patterns and processes of vegetational change. In northern Europe, however, long-term studies are rare for many ecosystems. This thesis uses a new approach that uses historical phytosociological data-sets to study changes in the vegetation of alpine, mire, and arctic habitats and regions across northern Europe over the past decades. Because plot relocation due to the use of non-permanent plots may bias the detection of change, the thesis investigates if observed changes are larger than what is expected by chance. Furthermore, to find out if observed changes in vegetation are consistent between different habitats and regions in northern Europe, a meta-analysis of 15 data sets from arctic, alpine, and mire sites is presented.

The results of the resurvey conducted in alpine Sikkilsdal, Central Norway, show that most species have shifted their distributional range upwards along the elevational gradient since the first sampling in the 1920s. These upward shifts were found to be independent of whether upper, lower, or optimum elevation were considered. As the largest shifts were found for species growing in snow-bed habitats, the results suggest climate warming and alterations in snow-cover duration to be important drivers of the observed range shifts.

In the Åkhult mire (South Sweden), changes over a period of 54 years were found predominantly for species of dwarf-shrubs and trees, whereas several typical mire species have decreased or disappeared from the study site. Drier mire surface and higher nutrient availability due to a warmer climate are identified as the most plausible drivers explaining the observed turnover in species composition.

On Jan Mayen Island, similar changes in vegetation were found during time periods of 19 and 80 years. Over both time-scales, graminoid and woody species were found to have increased, whereas several snow-bed related species have decreased. However, whereas the main trend is similar over both time-scales considered, discrepancies in the trends of some species suggest that long-term changes are only partly predictable from short-term studies.

The results of the meta-analysis show that the arrangement between species has changed more than is expected by chance, indicating that non-random changes have occurred in the studied arctic, alpine, and mire habitats during the past century. Vegetation stability was found to vary site-specifically. Observed patterns could not be explained by different factors, such as time-scale, plot number, species diversity, or productivity.

The thesis shows that non-random vegetational changes have occurred independent of which habitat or site is considered. As the observed changes in vegetation are in line with several other studies on vegetational dynamics focusing at different temporal and spatial scales and using permanent plots, this thesis demonstrates that historical phytosociological data-sets may successfully be used in the way presented here. These results unlock a valuable archive to identify recent vegetational changes in relation to environmental change. Moreover, observations of increased growth of woody plants and graminoids, upward shifts in species ranges, and decreases in species mostly associated with wetter habitats indicate trends in vegetation towards more competitive and nutrient-demanding species. With regard to predicted changes in climate, further changes may be assumed, the effects of which are likely to be most pronounced in areas where species are adapted to low temperatures and low nutrient availability, such as in high mountain areas, raised bogs, and in the Arctic.

Specification of contributions to the individual papers

Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway
Vivian A. Felde: *Data collection and preparation, analyses, interpretation, writing, editing, corresponding author*
Jutta Kapfer: *Data collection, interpretation, co-writing, editing*
John-Arvid Grytnes: *Data collection, ideas, analyses, interpretation, co-writing, editing*

Fine-scale changes in vegetation composition in a boreal mire over 50 years
Jutta Kapfer: *Data collection and preparation, ideas, analyses, interpretation, writing, editing, corresponding author*
John-Arvid Grytnes: *Data collection, ideas, analyses, editing*
Urban Gunnarsson: *Data collection, editing*
H. John B. Birks: *Advice, editing*

Changes in arctic vegetation composition on Jan Mayen Island - a comparison of two time scales
Jutta Kapfer: *Data collection and preparation, ideas, analyses, interpretation, writing, editing, corresponding author*
Risto Virtanen: *Data collection and preparation, co-writing*
John-Arvid Grytnes: *Analyses, ideas, editing*

Using species co-occurrences to quantify vegetation stability
Jutta Kapfer: *Data collection and preparation, ideas, analyses, interpretation, writing, editing, corresponding author*
H. John B. Birks: *Editing*
Vivian A. Felde: *Data collection and preparation, editing*
Kari Klanderud: *Data collection and preparation, editing*
Tone Martinessen: *Data collection and preparation, editing*
Fride Høistad Schei: *Data collection and preparation, editing*
Risto Virtanen: *Data collection and preparation, editing*
John-Arvid Grytnes: *Data collection, ideas, analyses, co-writing, editing*

List of individual papers

I Felde V. A., Kapfer J., and Grytnes J.-A. (submitted) Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. *Ecography*

II Kapfer J., Grytnes J.-A., Gunnarsson U., and Birks H. J. B. (2011) Fine-scale changes in vegetation composition in a boreal mire over 50 years. *Journal of Ecology*, **99**(5): 1179-1189

III Kapfer J., Virtanen R., and Grytnes J.-A. (submitted) Changes in arctic vegetation composition on Jan Mayen Island – a comparison of two time scales. *Journal of Vegetation Science*

IV Kapfer J., Birks H. J. B., Felde V. A., Klanderud, K., Martinessen T., Schei F. H., Virtanen R., and Grytnes J.-A. (manuscript) Using species co-occurrences to quantify vegetation stability. *Basic and Applied Ecology*

Introduction

BACKGROUND

Environmental conditions and climate are important determinants of distribution, diversity, and composition of species (Walther, 2003; IPCC, 2007). Changes in these important factors may cause substantial changes in vegetation regardless of geographic region, habitat, or vegetation type (e.g. Grabherr et al., 1994; Sturm et al., 2001; Klanderud and Birks, 2003; Parmesan and Yohe, 2003; Wilson and Nilsson, 2009; Odland et al., 2010). Over the past few decades, a close relation between large changes in terrestrial vegetation and the direct or indirect consequences of increased human activity has emerged. Not only changes in climate and land-use, but also habitat change and pollution have been identified as major threats to biodiversity of terrestrial vegetation (Millennium Assessment, www.maweb.org).

Vegetation of boreal, high alpine, and arctic habitats is considered particularly sensitive to changes in climate and to nutrient deposition, as plant species are closely related and restricted by low temperatures, short growing seasons, and low nutrient availability (Backéus, 1985; Grabherr et al., 1994; Tørseth and Semb, 1997; Körner, 2003; Smol et al., 2005). In Europe, effects of recent climate change have been observed, for instance, in distributional range shifts of species and tree-lines, as well as in changes in species abundances and richness (e.g. Grabherr et al., 1994; Walther, 2003; Walther et al., 2005; Jurasinski and Kreyling, 2007; Lenoir et al., 2008; Vittoz et al., 2008). To detect vegetational responses to recent changes in such environments, where vegetation has a low productivity and is dominated by slow growing species, long time-scales need to be considered. However, in northern Europe, long-term ecological studies are rare (but see e.g. Gunnarsson et al., 2000, 2002; Klanderud and Birks, 2003; Odland et al., 2010; Daniëls et al., 2011).

As environmental and climate change is predicted to progress, with increased precipitation and temperatures in northern Europe, further changes in vegetation and land-cover may be expected in the future (IPCC, 2007). It is therefore of crucial importance to understand and assess the effects of environmental change on vegetation in the past in order to design and implement appropriate conservation and management strategies for sustaining important ecosystem services such as biodiversity and ecosystem functioning (Hierl et al., 2008). Thus, to complement the present limited knowledge on recent vegetational changes, this thesis focuses on recent changes in vegetation of different habitats in northern Europe, namely alpine (I, IV), mire (II, IV), and arctic (III, IV) habitats.

IMPORTANCE OF LONG-TERM STUDIES

Monitoring studies are crucial tools to observe vegetational development in response to environmental change through time. However, with respect to the duration of monitoring projects, which only rarely exceed five years in duration, and considering the time lag between environmental cause and vegetational response, monitoring studies often do not cover time-scales that are long enough to ensure that vegetational changes are detectable after an environmental change (Delcourt and Delcourt, 1988; Bakker et al., 1996). Moreover, they cannot exclude the hypothesis that the observed vegetation changes are a result of short-term temporal or fine-scale spatial variability in vegetation due to natural variability (e.g. life cycle) or short-term fluctuations in response to fluctuations in abiotic conditions (e.g. water level) or extreme events (e.g. summer drought; Dodd et al., 1995; Bakker et al., 1996; Bennie et al., 2006). Thus, to detect trends in vegetation in relation to environmental change, long-term studies focusing on the time-scales that driving forces are operational at are needed. Such studies are, however, difficult to maintain.

One of the earliest, and apparently the world's longest running monitoring project is the Park Grass Experiment at Rothamsted (UK), where permanent plots and fertilizer treatments have been established and applied since 1856 enabling the study of vegetational changes over time scales more than 150 years. Unfortunately, monitoring studies covering such long time-scales are rare, but with the emerging challenges of human-related environmental change especially over the past few decades, different monitoring projects using permanent plots have lately been established enabling the study of both short- and long-term effects of climate change on biotic systems (e.g. ITEX: International Tundra Experiment, since 1989; GLORIA: Global Observation Research Initiative in Alpine Environments, since 1994). The monitoring of these permanent plots over the past 20 years and its continuation in the future will provide important insights into the relationships between vegetational dynamics and recent environmental change.

An alternative approach for investigating long-term vegetational change with regard to recent changes in environment over several decades is the resurveying of historical ecological data. Resurvey studies have increasingly been conducted to detect vegetational trends in response to recent changes in environment, such as climate or land-use (e.g. Grabherr et al., 1994; Gunnarsson et al., 2002; Klanderud and Birks, 2003; Walther et al., 2005; Bennie et al., 2006; Lenoir et al., 2008; Vittoz et al., 2008; Daniëls et al., 2011). Obviously, resurveying historical studies has the advantage of easily covering time-scales exceeding several decades as they circumvent the inevitable waiting time connected with the initiations of new long-term studies and experiments due to e.g. time-lagged vegetational responses (Bakker et al., 1996). Furthermore, resurveying after decadal time periods allows an investigation of trends even in habitats where vegetational responses due to long-lived and slow-growing species are rather slow, such as in high alpine and arctic vegetation and *Sphagnum*-dominated mires (e.g. Backéus, 1972; Hudson and Henry, 2009; Prach et al., 2010). As resurvey studies represent the actual state of vegetation as two snapshots at each time, these studies may be used to complement the results derived from long-term monitoring and short-term (experimental) studies (Kahmen et al., 2002).

In northern Europe, resurveys on changes in vegetation with regard to recent environmental change are still rare. However, several resurvey studies have been conducted, for instance, in boreal mires, where vegetational changes (increase of dwarf-shrubs and trees) over the past 10 to 50 years have been found in association with eutrophication and increased dryness (e.g. Backéus, 1972; Chapman and Rose, 1991; Hogg et al., 1995; Hedenäs and Kooijman, 1996; Gunnarsson et al., 2000, 2002). Resurveys in (high) mountain areas and in the Arctic consistently report climate-warming induced increases in deciduous shrubs and graminoids over the past decades, as well as species range shifts predominantly upwards and northwards (e.g. Sturm et al., 2001; Klanderud and Birks, 2003; Odland et al., 2010; Daniëls et al., 2011).

Most often, such resurveys are conducted by sampling vegetation from a permanent plot (e.g. Gunnarsson et al., 2000, 2002; Odland et al., 2010). In northern Europe, however, data-sets of many more historical studies are available (e.g. phytosociological studies), but which have so far only been utilized to a limited extent for analysing long-term vegetation changes (e.g. Klanderud and Birks, 2003; Daniëls et al., 2011). This is likely due to the lack of (1) permanent plots and plot-specific environmental measurements that hampers a direct comparison of vegetation and environment through time, and (2) appropriate methods to tackle this challenge. Thus, if an effective way can be found to utilize such phytosociological studies, a huge archive could be unlocked to detect vegetational changes over the past 50 to 100 years, thereby increasing the actual knowledge about the causes and consequences of environmental change on vegetation.

Aims of the thesis

The main aim of the thesis is to detect, describe, and interpret long-term changes in the distribution and composition of vegetation in common habitats in northern Europe using historical phytosociological data-sets. The thesis therefore considers the following questions:

1. Has the vegetation of alpine (I, IV), mire (II, IV), and arctic (III, IV) habitats changed more than is expected by chance?
2. Can observed vegetational changes be explained by changes in environmental factors directly or indirectly related to important ecosystem drivers (I - IV)?
3. Are the observed vegetational changes consistent between different habitats and regions (IV) and using different temporal (II - IV) and spatial scales (II)?

Material and Methods

UTILIZATION OF HISTORICAL PHYTOSOCIOLOGICAL DATA-SETS AND ITS IMPLICATIONS

Investigating patterns in vegetation using a phytosociological approach has a long tradition in Europe (e.g. Braun-Blanquet, 1928; Mueller-Dombois and Ellenberg, 1974; Dengler et al., 2008). To classify and describe vegetation of a particular region in detail and on a fine scale, it has become standard to use fine-scale squares ranging mostly between 0.25 m^2 to 1 m^2, from which the species composition is listed and species abundances are estimated (Knapp, 1971). Many of the resulting vegetation data-sets consist of at least hundred, sometimes several hundred plots. Re-sampling this type of study is ideal for analysing fine-scale succession at the community level over long time-scales (decades and centuries). However, historical phytosociological data-sets have so far only rarely been used for this purpose as difficulties compromising comparability often arise.

Probably the major challenge in re-sampling old phytosociological studies is in the repeatability of the sampling methods (Bennie et al., 2006). For instance, relocation of plots may become an important issue in resurveys when study sites and sampling units have not been permanently marked and the locations visited are only vaguely described in the original studies (Hedl, 2004). A new positioning of plots could generate false estimates of vegetational change and pseudo-turnover in vegetation, i.e. species absences might, for instance, misleadingly be interpreted as species having gone extinct (Fischer and Stöcklin, 1997; Ross et al., 2010). As local extinction applies especially to rare species and small populations and species with a short life-cycle (Fischer and Stöcklin, 1997), it is necessary to be able to re-find the same study sites as described in the original study and to re-sample vegetation types as close to their previous position as possible. If this is warranted and temporal changes are greater than spatial variation within vegetation types, long-term vegetation change may be assumed to be detected reliably and with some confidence (Ross et al., 2010).

Further problems in re-sampling studies in respect of comparability include the time spent on vegetation sampling. In order to obtain detailed descriptions of the vegetation in a defined area, in previous studies the sampling was often conducted over several vegetative periods (e.g. Nordhagen, 1943; Lunde, 1962; Rønning, 1965). In contrast, resurveys today are generally conducted within one field season. If non-permanent plots are used, this might affect both the number of plots re-sampled and thus reduce the chance of covering variation in vegetation comparable to the original data-sets. Moreover, estimation of species abundance using the same abundance scale as in the previous study (e.g. Hult-Sernander-Du Rietz five-point scale; Du Rietz 1921) is generally assumed to produce reliable data-sets, but using the same scale does not guarantee that both the surveyor and re-surveyor will record the vegetation in the same way. However, observer effects on the observation of vegetational changes such as these are only rarely tested (but see Vittoz and Guisan, 2007; Ross et al., 2010).

RE-SAMPLING NON-PERMANENT PLOTS

In order to describe the vegetation of a restricted area in great detail, plant sociologists recorded vegetation using small squares which were placed in homogenous vegetation of stands (Knapp, 1971). Depending on the variation in vegetation, the plots were more or less equally distributed over the study site. Since plots in the old studies were not permanently marked, in the re-samplings conducted for this thesis in alpine (I, IV), mire (II, IV), and arctic (III, IV) sites, the positioning of plots was done randomly. Following the sampling protocol of the original studies and aiming to cover (at least) the same variation in vegetation as in the previous sampling, plots were always placed in stands of homogenous vegetation of the vegetation types to be sampled at the study area. From these plots, species composition of the taxonomic group studied (vascular plants, bryophytes) was listed and species abundances were estimated using the same abundance scale as specified in the original study.

Whereas all different vegetation types could easily be re-found in the mire studied (II), some difficulties arose in the re-sampling in both the alpine (I) and arctic (III) areas. For instance, in Sikkilsdalen (I) due to vague descriptions in the original study (Nordhagen, 1943), at some locations not all the described stands could be re-found. Likewise, on Jan Mayen Island (III) at some locations the synedria around some specific species could not be re-found. Thus, depending on the research question behind the corresponding re-sampling, different approaches to solve the problem had to be used.

The re-sampling in Sikkilsdalen (I) was conducted with the aim of studying changes in composition (IV), but also in the elevational distribution of vascular plant species (I). For species of wide distributional ranges (e.g.

from below forest-line to alpine tundra) extreme low and high elevations are limited by factors such as climate and competition (MacArthur, 1972; Brown et al., 1996; Crawford, 2008). Thus, even if other stands are sampled at different locations, the extreme elevations of species will be similar within the same study site. Therefore, in the re-sampling, when at the different locations where specific stands described in the original study (Nordhagen, 1943) could not be re-found, vegetation was recorded by randomly sampling from all different vegetation types at that location.

In contrast, the re-sampling on Jan Mayen Island (III) was conducted to detect changes in vegetational composition in the so-called synedria (i.e. co-existing species) around certain focal species, whose sampling sites were relatively easy to locate. However, at some locations, the focal species could not be re-found. Since the obvious absence of the focal species does not shed light on whether the species has gone extinct or just could not be re-found, any sampling of other vegetational types found was abandoned. This reduced indeed the re-investigated data set in its number of plots not being available for later statistical analyses. However, this strategy guarantees that observations of vegetational change are real and not falsified due to relocation/spatial heterogeneity and overlooking of synedrial focal species (Dodd et al., 1995; Bennie et al., 2006).

Quantification and interpretation of vegetational change

On the basis of fine-scale plots, changes in vegetation may be calculated by temporal comparisons of, for instance, species elevational distribution (minimum, maximum, and optimum elevation; I), species richness, abundance, and frequency in occurrence (II, III) or co-occurrence patterns (II-IV). To answer one of the most important questions, namely whether vegetational changes are due to randomness (i.e. they have occurred due to natural dynamics under relatively constant environmental conditions) restricted permutation tests can be used (Fisher, 1951; Edgington, 1995; I-III). This procedure compares the observed vegetational changes with changes calculated after the plots from both inventories have been permuted (I-IV) with the restriction that only plots of the same group along a biotic or abiotic gradient (e.g. elevation I; environmental gradient II; vegetation type II, III) are allowed to be swapped. A change is considered significant (i.e. not random), if 95% of the permuted values are larger or smaller than the observed change. Besides calculating the significance of change, this procedure also accounts for the unequal number of plots between survey and resurvey as this inequality may occur due to differences in the sampling intensity and the use of non-permanent plots. This consideration is taken into account in the step when plots are permuted, where a randomly selected equal number of plots from each data set is always taken for further calculation of both the observed and permuted values of change.

Estimates of rates of species changes in distribution and occurrence may also indicate a turnover at the community level (species composition). However, to identify directly and to quantify changes in the assemblage of species, a different approach is necessary. From several studies it is known that species respond individualistically to alterations in their environment (e.g. Chapin and Shaver, 1985; Levin, 1992; Walther et al., 2002; Klanderud and Birks, 2003; LeRoux and McGeoch, 2008). If environmental conditions change, some species will increase or shift in their distributional range whereas other species will persist and stay unchanged, decrease, or go extinct. Individualistic responses such as these may be assumed to lead to changes in species composition and new arrangements between species. In this thesis, species co-occurrences with other species are considered so as to estimate if species have changed their associated species (III, IV). For estimation of a species' co-occurrence with other species, the number of plots is counted where the focus species co-occurs with all the other species. As this is done separately for the data-sets of the historical and the re-sampling surveys, a change in species co-occurrence can be calculated. Resulting positive change-values indicate that associated species are found to co-occur more often with the focus species in the resurvey than in the older survey, and vice versa for negative change-values. Hence, a change in species co-occurrence indicates a re-arrangement between species reflecting a turnover in vegetational composition. Species co-occurrences may further be used as indicators of vegetational stability if change values are averaged for one study area/habitat (IV), with low average values indicating a high stability.

Based on the same idea of individualistic species responses inducing changes in species composition, this thesis uses an indirect approach to relate changes in the arrangement between species with environment. When historical data-sets are used to study vegetational change, a direct identification of the driver of change is often hampered because historical studies often lack plot specific environmental measurements which could otherwise directly be related to the community data. In this thesis, 'species optimum analysis' is applied (II), which calculates the relative change of a species' realized optimum value for different environmental gradients using indicator values as representatives of environmental gradients (e.g. soil moisture, pH). For instance, if soil pH has changed, some species will tolerate the change and persist in the same place (either because they have a wide tolerance or because they are responding slowly), whereas other species will die or emigrate. It is then likely that the average pH-indicator value for the new associate species will be different from the average pH-indicator value of the previous species. To detect such changes in species composition, an indicator value for co-occurring species of a focus species today and in the previous sampling is calculated. A positive change in a species' optimum value will then indicate that the species was found more often in association with species of a different preference for the environmental gradient considered than in the previous sampling. Hence, changes in the indicator value may be used to identify important drivers of vegetational changes.

How much change may be expected?

Most often, vegetational changes observed from resurveys are accepted to be 'real' as soon as the observed changes are found to be statistically significant. However, it is rarely tested how much change actually may be expected due to the influences of important factors, such as different observers or relocation of plots as mentioned above. For instance, Ross et al. (2010) tested effects of relocation of plots on vegetation in the Scottish Highlands. By measuring compositional difference using dissimilarity indices (Bray-Curtis distance) they found that 50-year vegetational changes between historical plots and resurveyed plots were always greater than among replicate plots today. Another study tested observer effects on species observation using permanent vegetational plots (Vittoz and Guisan, 2007). They found that overlooking of species applied mostly to species with a low abundance.

Resurveys are usually conducted by observers who are not the original surveyor. The effects of this are often not possible to test and quantify. In this thesis, the resurveys in alpine Sikkilsdalen (I) and on Jan Mayen Island in the Arctic (III) have been conducted by two groups of botanists. Besides testing how much difference might be expected among replicate plots by comparing a randomly selected equal number of plots, I further used the data-sets of these two resurveys to quantify differences among replicate plots collected by the different re-surveyors. According to other studies that have tested similar effects (e.g. Vittoz and Guisan, 2007; Ross et al., 2010), it may be assumed that a real turnover in vegetation has occurred if differences found among both random and observer replicates are lower than the observed change (survey vs. resurvey).

Table 1 shows the results of the total number of species and changes in species co-occurrences (see III, IV for details in methods) found when analysing among re-sample plots (i.e. between different observers, and between plots that were randomly selected from plots of both observers together) and when analysing observed changes (survey vs. resurvey). As hypothesized from both the use of non-permanent plots and the lower number of

Table 1: *Results of testing differences in the detection of total number of species and change in species co-occurrence with other species on Jan Mayen Island (arctic) and Sikkilsdal (alpine) between different surveyors (Team a vs. Team b, and group a vs. group b of randomly selected re-sample plots) and survey vs. resurvey. Total = total data-set of survey and resurvey together. Numbers in bold = observed change between survey and resurvey, team 1 and team 2, and randomly selected plots from the resurvey data-set. Random re-sample plots were selected 50 times using approximately 50% of the total number of re-sample plots; results show average values.*

	Jan Mayen							Sikkilsdal						
	Total	Old	New	Team		Random		Total	Old	New	Team		Random	
				1	2	1	2				1	2	1	2
N_{plots}	508	254	254	114	140	125	125	1684	1263	421	224	197	200	200
N_{tot}species	53	49	50	49	48	49	49	319	294	233	215	198	213	208
$\triangle$ co-occurrence		**0.181**		**0.148**		**0.103**			**0.132**		**0.111**		**0.083**	

plots used for this test, different observers and observations from random plots found a lower total number of species, and that species turnover rate would increase (see also Appendix Fig. S3 in paper IV). However, other than expected from the negative relationship between plot number and observed change, changes in species co-occurrences were found to be smaller when replicate plots of both the two observer teams and the random selected plots were compared. Although smaller changes may be expected with increasing plot number, changes in species co-occurrences were found to be greater in the comparison of survey- with resurvey-plots. Hence, these examples indicate that the greater changes observed between survey and resurvey may be considered reliable and interpreted as real long-term changes in vegetation caused by factors other than randomness. This is in accordance with Vittoz et al.'s (2010) finding that if the driving forces are operating over long time-scales and in an unidirectional way, it may be assumed that changes in vegetation may be detected regardless of the observer. These findings further indicate that 'real' changes in species composition have occurred if species co-occurrences are found to change along environmental gradients (see 'species optimum analysis').

Thus, if factors influencing the observation of vegetational change (e.g. effects of different observers, relocation of plots) are minimised, a reliable detection of trends in vegetation due to external driving forces (e.g. changes in climate or land-use) is possible. It is therefore important to re-sample those historical studies which were selected carefully taking different criteria into account: The sampling area should be restricted and well-defined, so that vegetational types and stands can be re-found reliably. Moreover, the sampling methods used should be repeatable in an identical way and result in a sufficient number of samples to permit statistical analyses. The historical studies re-sampled for the purpose of this thesis (I-IV) meet all these criteria.

Results and discussion

VEGETATIONAL CHANGES IN ALPINE, MIRE, AND ARCTIC HABITATS

The results of re-sampling Nordhagen's (1943) phytosociological survey in the mountain area of Sikkilsdalen found that the majority of vascular plant species have shifted their range distribution upwards along the elevational gradient over the last approximately 90 years, independent of whether extreme elevation (minimum, maximum) or optimum elevation is considered. The general upward trend conforms with several other studies investigating plant elevational shifts in mountain areas in Europe at different temporal and spatial scales (e.g. Grabherr et al., 1994; Klanderud and Birks, 2003; Walther et al., 2005; Holzinger et al., 2008; Lenoir et al., 2008; Erschbamer et al., 2009; Odland et al., 2010). For most of the plants, the observed range shifts in Sikkilsdalen are found to be larger than they were expected by chance. Moreover, species that are associated with snow-beds were found to have shifted most in both their upper and optimum elevations. However, the magnitude of change found in Sikkilsdalen is smaller than it is reported from mountain areas in, for example, the European Alps over comparable or even shorter time periods (e.g. Walther et al., 2005; Parolo and Rossi, 2008). As range shifts in species upper-distribution limits are correlated with shifts in optimum elevation but not with shifts in the lower limits, this indicates that different processes are operating at the two ends of an elevational gradient resulting in individualistic species responses. Thus, besides the confirmation of other studies documenting individualistic species changes, this study highlights the importance of focusing on both the extreme and optimum elevation of species as it may give a more comprehensive picture about range shifts which may differ between species along an elevational gradient.

Mires have widely been considered to be relatively stable systems that only show slow changes in vegetation over time (e.g. Backéus, 1972; Svensson, 1988; Malmer et al., 1997; Rydin and Barber, 2001). However, especially over the past few decades relatively large changes have been reported from boreal mire habitats by studies focusing on broad scales and using permanent plots (e.g. Chapman and Rose, 1991; Gunnarsson et al., 2000, 2002). To identify fine-scale changes in the vegetation composition of a boreal mire, the *Sphagnum*-dominated Åkhult mire (South Sweden) was re-sampled 54 years after the first sampling by Nils Malmer in 1954 (Malmer, 1962; II). The results of this study show that nutrient demanding and competitive dwarf-shrubs and trees have increased in growth (frequency and abundance) over the past decades, whereas several typical mire species including species of high ecological value have decreased or disappeared. The resurvey of the Åkhult mire offered the unique chance to directly compare observed trends over 54 years at a fine-scale as observed using non-permanent plots and species optimum analysis with the trends found by Gunnarsson et al. (2002), who re-mapped the vegetation of the Åkhult mire using a permanent grid cell of a broader scale ca. 40 years after Malmer's sampling in 1954. Both studies found similar trends in species frequencies indicating that unidirectional changes in vegetation are detectable independent of differences in the spatial and temporal scales used and the use of permanent plots. Moreover, agreement between results from the two studies also confirmed the successful application of the indirect method (species optimum analysis) used to identify recent vegetational changes by comparing data-sets using non-permanent plots.

Similar observations as in the vegetation of Åkhult mire (II) were made in the vegetation on the arctic island Jan Mayen (III) for time periods of 19 and 80 years. Jan Mayen is virtually grazer free and direct human influence has always been low. Hence, the island is a unique location to study recent trends in vegetation which may be more directly linked to recent changes in climate. The results of the re-sampling of Lid's (1964) and Virtanen et al.'s (1997) studies confirm the main trends also observed for other regions in the Arctic or alpine areas in Scandinavia, namely that woody species and graminoids have increased, whereas species typical of snow-beds have decreased (e.g. Sturm et al., 2001; Bret-Harte et al., 2002; Klanderud and Birks, 2003; Tape et al., 2006; Wilson and Nilsson, 2009). The observed trends might indicate that snow-bed habitats are being invaded by more competitive species of surrounding drier habitats (e.g. Klanderud and Birks, 2003; Björk and Molau, 2007; Daniëls et al., 2011). However, the total number of species recorded in fine-scale plots has remained virtually stable, which might reflect the remoteness of the island lowering the arrival and establishment of new species. Moreover, for some species contrary trends in frequency and abundance were found, indicating that long-term vegetational changes are not predictable from short-term changes for every species.

As range shifts (I) and changes in frequency, abundance, and richness (II, III) have been found to differ depending on which species is considered, the results of these three resurveys confirm the general assumption of species responding individualistically to changes in their environment (e.g. Chapin and Shaver, 1985; Levin, 1992; Walther et al., 2002; Klanderud and Birks, 2003; LeRoux and McGeoch, 2008). Individualistic species responses are likely to lead to changes in the arrangement between species and species composition, but the extent to which different communities are stable has never been tested. In paper IV stability in the vegetation of different habitats across northern Europe is quantified for the first time using species co-occurrences (see also in III). The results show that the vegetation of arctic, alpine, and mire sites has changed significantly and has changed more than is expected by chance, independent of whether vascular plants or bryophytes (mosses and liverworts) are considered. The variation in stability could not be explained by time-scale, plot number, and other factors such as species diversity or productivity, which in other studies have been found to be important determinants (e.g. Lehman and Tilman, 2000; Tilman et al., 2006; Bezemer and van der Putten, 2007). Hence, other site-specific biotic (e.g. species interactions) and abiotic factors (e.g. land-use change) might be important for the stability of arctic, alpine, and mire vegetation in northern Europe.

Driving forces of observed vegetational changes

This thesis has found that the observed changes in species distribution (I) and composition (II, III) are most likely to be a direct or indirect result of climate change. In boreal and arctic-alpine areas, changes in species composition, productivity, and distributional ranges have most often been discussed to be a direct result of warmer temperatures and changes in both precipitation regime and snow-cover patterns resulting in an earlier onset and lengthening of the growing season for plants (e.g. Klanderud and Birks, 2003; Hallinger et al., 2010). These changes in patterns of climatic conditions may also explain the observed range shifts in Sikkilsdal (I) and changes in species composition on Jan Mayen (III), which were highlighted, for instance, by changes being mostly linked with snow-bed species. In the Åkhult mire (II), warmer temperatures over past decades may have directly influenced the depth of the water-table and, thus, changed water-availability for mire vegetation. In addition to a drying-out of the mire surface, this may have considerable impacts locally on species composition as it enables the successful establishment, increased growth, and regenerative success of dwarf-shrubs and trees (Weltzin et al., 2000; Gunnarsson et al., 2002; van der Linden et al., 2008; Murphy et al., 2009), the consequences of which are observed in the vegetation of the Åkhult mire.

Indirect consequences of climate change, such as alterations in nutrient availability, may also be important, in particular regarding changes in species interactions (Schuur et al., 2007). Vegetation of habitats which are naturally poor in nutrients and whose nutrient input is strongly determined by precipitation rates (e.g. high mountain areas, ombrotrophic bogs) and temperature (e.g. in the Arctic), are viewed to be especially sensitive to changes in nutrient regime (Backéus, 1985; Tørseth and Semb, 1997). In boreal *Sphagnum*-dominated mire habitats, for instance, increased nutrient availability due to changes in precipitation regime has increased the growth of nitrophilous species of high competitive ability, altering vegetation structure and composition in acidic and low productive peat bogs (e.g. Gunnarsson and Rydin, 2000; Berendse et al., 2001; Tomassen et al., 2003; Bragazza et al., 2004; Pearce and van der Wal, 2008). In northern Europe, the increased wet deposition of nitrogen in the last 50 years has contributed to an increased abundance of vascular plants (typically trees and shade-tolerant dwarf-shrubs) on bogs as well as having adverse effects on the productivity and vitality of dominant *Sphagnum* species (e.g. Gunnarsson and Rydin, 2000; Gunnarsson et al., 2000; Ohlson et al., 2001; Malmer et al., 2003; Gunnarsson and Flodin, 2007; Wiedermann et al., 2009). However, higher nutrient availability in the Åkhult mire may be due to higher decomposition rates induced by warming in addition to increased wet deposition. However, latter factor was not significant in this area since 1954. Thus, independent of which habitat is considered, it is likely that in response to changes in nutrient availability, species interactions have become more important, which may have changed species dominances and their competitive hierarchy in boreal (II, IV), alpine (I, IV), and arctic (III, IV) habitats towards a more competitive and nutrient-demanding vegetation as has also been documented in other studies (e.g. Chapin et al., 1995; Shaver and Jonasson, 1999; Gough et al., 2002; Wilson and Nilsson, 2009).

However, several other biotic and abiotic factors may also play an important role in influencing the observed changes in north European vegetation, but whose effects often are difficult to disentangle from each other. For instance, human-related changes in land-use and changes in grazing pressure may locally affect vegetation (Post and Pedersen, 2008; Olofsson et al., 2009; Virtanen et al., 2010). In the Scandinavian low and high Arctic, changes in reindeer grazing and trampling pressure may have large impacts on plant species richness, composition, plant growth, and nutrient cycling (Pajunen et al., 2008; Olofsson et al., 2009; Virtanen et al., 2010), the effects of which may confound the effects of climate warming (Dormann et al., 2004; Olofsson et al., 2009). This may lead to misinterpretations of observed changes. Moreover, internal processes such as natural succession should also not be ignored.

Conclusions and perspectives

This thesis uses historical phytosociological data-sets to desribe and interpret changes in the vegetation of different habitats and regions across northern Europe over the past decades. To identify changes in vegetation, different approaches have been applied, enabling temporal comparisons at the local-scale on the basis of non-permanent plots to establish the amount of species turnover. Species optimum analysis was used as a new indirect approach to identify changes in vegetation and to identify which drivers may be important for the changes in particular vegetational types. As vegetational changes observed in the individual studies accord with the findings of several other studies, this thesis shows that historical data-sets with non-permanent plots can be analysed successfully, an approach that to date has only been used to a limited extent for studying recent vegetational dynamics. Hence, the thesis not only contributes to a better knowledge and understanding of vegetational dynamics and processes of change in the past, which is essential with regard to future predictions, but also unlocks a valuable botanical archive for detecting, describing, and interpreting vegetational changes in the past century.

The four studies on alpine, mire, and arctic vegetation presented in this thesis show that vegetation (distribution, composition, abundance) has changed significantly and more than is expected by chance, independent of which time or spatial scale and site/area are considered. As reported from other observational and experimental studies using different approaches, individualistic species changes were found to change vegetation towards an increased growth of competitive and nutrient-demanding species, mostly deciduous shrubs, dwarf-shrubs, trees, and graminoids. With regard to the predicted climate changes due to increasing human activity, these changes can be assumed to be in progress and to become most effective in regions where climate is projected to change most, as for instance in the Arctic. In these cold regions, climate warming may be expected to initiate major (or accelerate ongoing) changes in land-cover, when, for instance, more and more nutrient reserves are released over wide areas due to warming-induced thawing of permafrost and increased soil microbiological activity. Furthermore, other driving factors of vegetational change indirectly linked to climate change might play an increasing role in the Arctic in the near future, with increased human pressures in land-use and tourism. Habitat loss is one of likely consequences of increased human impact. However, in mountain areas, both upward-shifting lowland species and potential extinction of higher alpine species might lead to a more homogenous vegetation on mountain summits. Further drying-out of mire habitats may be assumed to further the increase of dwarf-shrubs and trees, which in turn might feed-back on mire hydrology. Both these processes might lead to, for instance, further decreases and finally extinction of rare (high) alpine and mire species of high conservation value. However, these examples are only few of a long list of possible consequences (including the ones unknown to us at present) of predicted changes in the environment. This thesis has found that vegetation stability varies in a site-specific manner. Since the changes observed in regions of similar vegetation were not always similar, this new knowledge on variability in vegetational change stresses the importance of evaluating potential future vegetational changes with regard to site-specific conditions (e.g. soil conditions, exposition, grazing).

This thesis has raised several questions which should be accounted for in future research. For instance and first of all, in northern Europe, the number of studies on recent vegetational changes should be increased. More studies are needed to strengthen the results presented in this thesis and in other existing observational and experimental studies. For instance, the trends observed in the meta-analysis (IV) could be strengthened by the inclusion of several more data-sets from different regions across northern Europe. Furthermore, studies on plant elevational range shifts are rare particularly in both the Low and High Arctic. Moreover, by comparing different data-sets integrating different vegetation types, species co-occurrence analysis (see III, IV) found site-specific changes in vegetation stability. Thus, focusing on the different vegetational types covered by the different studies (e.g. forest, alpine shrub vegetation, alpine tundra) and analysing and interpreting species and vegetational type specifically will give more detailed insights into both the stability and the direction of change of different plant communities. This knowledge about trends in specific vegetational types is important with regard to present and future land-use planning and management. That vegetation changes occur independently of the plant group considered (e.g. bryophytes and vascular plants) has been shown in this thesis (II, IV). However, it is not known to which extent these groups depend on each other, i.e., how much, for instance, is vascular plant growth controlled by the cover of bryophytes. This might be an important factor influencing vascular plant dynamics, especially in regions where bryophytes are dominant, such as in mires and in the Arctic. Moreover, in this thesis, species optimum analysis has been found to be a useful method to identify vegetational changes in relation to environment. Applying this method to further data-sets, which so far have not been analysed, would help increase the present knowledge of recent vegetational dynamics, a knowledge of which is valuable for the understanding of environmental-change driven vegetation changes and its predictions. More research should also be focusing on possible effects of direct human impacts such as land-use changes (e.g. due to a longer growing season), which are expected to become increasingly relevant in the near future, in particular at higher latitudes.

Acknowledgements

I am grateful to John-Arvid Grytnes and John Birks for comments and linguistic corrections to the manuscript.

References

Backéus, I. (1972). Bog vegetation re-mapped after sixty years. *OIKOS*, 23:384–393.

Backéus, I. (1985). Aboveground production and growth dynamics of vascular bog plants in Central Sweden. *Acta Phytogeographica Suecica*, 74:1–98.

Bakker, J. P., Olff, H., Willems, J. H., and Zobel, M. (1996). Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science*, 7(2):147–155.

Bennie, J., Hill, M. O., Baxter, R., and Huntley, B. (2006). Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, 94(2):355–368.

Berendse, F., van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M. R., Lee, J. A., Mitchell, E., Saarinen, T., Vasander, H., and Wallen, B. (2001). Raised atmospheric CO2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Global Change Biology*, 7(5):591–598.

Bezemer, T. M. and van der Putten, W. H. (2007). Diversity and stability in plant communities. *Nature*, 446:E6–E7.

Björk, R. G. and Molau, U. (2007). Ecology of alpine snowbeds and the impact of global change. *Arctic Antarctic and Alpine Research*, 39(1):34–43.

Bragazza, L., Tahvanainen, T., Kutnar, L., Rydin, H., Limpens, J., Hájek, M., Grosvernier, P., Hájek, T., Hajkova, P., Hansen, I., Iacumin, P., and Gerdol, R. (2004). Nutritional constraints in ombrotrophic Sphagnum plants under increasing atmospheric nitrogen deposition in Europe. *New Phytologist*, 163:609–616.

Braun-Blanquet, J. (1928). *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Springer, Wien.

Bret-Harte, M. S., Shaver, G. R., and Chapin, F. S. (2002). Primary and secondary stem growth in arctic shrubs: Implications for community response to environmental change. *Journal of Ecology*, 90(2):251–267.

Brown, J. H., Stevens, G. C., and Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27:597–623.

Chapin, F. S. and Shaver, G. R. (1985). Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, 66(2):564–576.

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A. (1995). Responses of arctic Tundra to experimental and observed changes in climate. *Ecology*, 76(3):694–711.

Chapman, S. B. and Rose, R. J. (1991). Changes in the vegetation at Coom Rigg Moss National Nature Reserve within the period 1958-86. *Journal of Applied Ecology*, 28:140–153.

Crawford, R. M. M. (2008). *Plants at the margin: Ecological limits and climate change*. Cambridge University Press, Cambridge.

Daniëls, F. J. A., de Molenaar, J. G., Chytry, M., and Tichy, L. (2011). Vegetation change in Southeast Greenland? Tasiilaq revisited after 40 years. *Applied Vegetation Science*, 14(2):230–241.

Delcourt, H. R. and Delcourt, P. A. (1988). Quaternary landscape ecology: Relevant scales in space and time. *Landscape Ecology*, 2(1):23–44.

Dengler, J., Chytry, M., and Ewald, J. (2008). Phytosociology. In Fath, S. E. and Jørgensen, B. D., editors, *Encyclopedia of Ecology*, pages 2767–2779. Elsevier, Oxford.

Dodd, M., Silvertown, J., McConway, K., Potts, J., and Crawley, M. (1995). Community stability: A 60-year record of trends and outbreaks in the occurrence of species in the Park Grass Experiment. *Journal of Ecology*, 83(2):277–285.

Dormann, C. F., van der Wal, R., and Woodin, S. J. (2004). Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic. *Global Change Biology*, 10(9):1587–1598.

Edgington, E. S. (1995). *Randomization tests*, volume 3. Marcel Dekker, New York.

Erschbamer, B., Kiebacher, T., Mallaun, M., and Unterluggauer, P. (2009). Short-term signals of climate change along an altitudinal gradient in the South Alps. *Plant Ecology*, 202:79–89.

Fischer, M. and Stöcklin, J. (1997). Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. *Conservation Biology*, 11(3):727–737.

Fisher, R. A. (1951). *The design of Experiments*, volume 6. Hafner, London.

Gough, L., Wookey, P. A., and Shaver, G. R. (2002). Dry heath arctic tundra responses to long-term nutrient and light manipulation. *Arctic Antarctic and Alpine Research*, 34(2):211–218.

Grabherr, G., Gottfried, M., and Pauli, H. (1994). Climate effects on mountain plants. *Nature*, 369(6480):448.

Gunnarsson, U. and Flodin, L.-A. (2007). Vegetation shifts towards wetter site conditions on oceanic ombrotrophic bogs in southwestern Sweden. *Journal of Vegetation Science*, 18:595–604.

Gunnarsson, U., Malmer, N., and Rydin, H. (2002). Dynamics or constancy in Sphagnum dominated mire ecosystems? A 40-year study. *Ecography*, 25:685–704.

Gunnarsson, U. and Rydin, H. (2000). Nitrogen fertilization reduces Sphagnum production in bog communities. *New Phytologist*, 147:527–537.

Gunnarsson, U., Rydin, H., and Sjörs, H. (2000). Diversity and pH changes after 50 years on the boreal mire Skattlössbergs Stormosse, Central Sweden. *Journal of Vegetation Science*, 11:277–286.

Hallinger, M., Manthey, M., and Wilmking, M. (2010). Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist*, 186(4):890–899.

Hedenäs, L. and Kooijman, A. M. (1996). Förändringar i rikkärssvegetationen SV om Mellansjön i Västergötaland. *Sven Bot Tidskr*, 90:113–121.

Hedl, R. (2004). Vegetation of beech forests in the Rychlebske Mountains, Czech Republic, re-inspected after 60 years with assessment of environmental changes. *Plant Ecology*, 170(2):243–265.

Hierl, L. A., Franklin, J., Deutschman, D. H., Regan, H. M., and Johnson, B. S. (2008). Assessing and prioritizing ecological communities for monitoring in a regional habitat conservation plan. *Environmental Management*, 42(1):165–179.

Hogg, P., Squires, P., and Fitter, A. H. (1995). Acidification, nitrogen deposition and rapid vegetational change in a small valley mire in Yorkshire. *Biological Conservation*, 71:143–153.

Holzinger, B., Hülber, K., Camenisch, M., and Grabherr, G. (2008). Changes in plant species richness over the last century in the eastern Swiss Alps: Elevational gradient, bedrock effects and migration rates. *Plant Ecology*, 195:179–196.

Hudson, J. M. G. and Henry, G. H. R. (2009). Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology*, 90(10):2657–2663.

IPCC (2007). Climate change 2007- The physical science basis. Contribution of Working Group 1 to the fourth assessment report of the IPCC. Technical report.

Jurasinski, G. and Kreyling, J. (2007). Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science*, 18(5):711–718.

Kahmen, S., Poschlod, P., and Schreiber, K. F. (2002). Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, 104(3):319–328.

Klanderud, K. and Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene*, 13(1):1–6.

Knapp, R. (1971). *Einführung in die Pflanzensoziologie*. Ulmer, Stuttgart.

Körner, C. (2003). *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems.* Springer, Berlin, New York.

Lehman, C. L. and Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *American Naturalist*, 156(5):534–552.

Lenoir, J., Gègout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320:1768–1771.

LeRoux, P. C. and McGeoch, M. A. (2008). Rapid range expansion and community reorganization in response to warming. *Global Change Biology*, 14(12):2950–2962.

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6):1943–1967.

Lid, J. (1964). *The Flora of Jan Mayen*, volume 130. Norsk Polarinstitutt, Oslo.

Lunde, T. (1962). *An investigation into the* pH*-amplitude of some mountain plants in the county of* T*roms*, volume 20. Universitetsforlaget, Tromsø, Oslo.

MacArthur, R. H. (1972). *Geographical Ecology: Patterns in the distribution of species*. Harper and Row.

Malmer, N. (1962). Studies on mire vegetation in the archean area of southwestern Goetaland (South Sweden). *Opera Botanica*, 7:1.

Malmer, N., Albinsson, C., Svensson, B. M., and Wallén, B. (2003). Interferences between Sphagnum and vascular plants: effects on plant community structure and peat formation. *Oikos*, 100:469–482.

Malmer, N., Svensson, G., and Wallén, B. (1997). Mass balance and nitrogen accumulation in hummocks on a South Swedish bog during the late Holocene. *Ecography*, 20:535–549.

Mueller-Dombois, D. and Ellenberg, H. (1974). *Aims and methods of Vegetation Ecology*. John Wiley and Sons, New York.

Murphy, M., Laiho, R., and Moore, T. R. (2009). Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems*, 12(8):1268–1282.

Nordhagen, R. (1943). *Sikilsdalen og Norges fjellbeiter. En plantesosiologisk monografi*, volume 22. Bergens museum skrifter, Bergen.

Odland, A., Hoitomt, T., and Olsen, S. L. (2010). Increasing vascular plant richness on 13 high mountain summits in Southern Norway since the early 1970s. *Arctic Antarctic and Alpine Research*, 42(4):458–470.

Ohlson, M., Okland, R. H., Nordbakken, J. F., and Dahlberg, B. (2001). Fatal interactions between Scots pine and Sphagnum mosses in bog ecosystems. *Oikos*, 94(3):425–432.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., and Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, 15(11):2681–2693.

Pajunen, A., Virtanen, R., and Roininen, H. (2008). The effects of reindeer grazing on the composition and species richness in forest-tundra ecotone. *Polar Biology*, 31:1233–1244.

Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918):37–42.

Parolo, G. and Rossi, G. (2008). Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology*, 9(2):100–107.

Pearce, I. S. K. and van der Wal, R. (2008). Interpreting nitrogen pollution thresholds for sensitive habitats: the importance of concentration versus dose. *Environmental Pollution*, 152:253–256.

Post, E. and Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, 105(34):12353–12358.

Prach, K., Kosnar, J., Klimesova, J., and Hais, M. (2010). High Arctic vegetation after 70 years: a repeated analysis from Svalbard. *Polar Biology*, 33(5):635–639.

Rønning, O. I. (1965). *Studies in Dryadion of Svalbard*, volume 134. Norsk Polarinstitutt, Oslo.

Ross, L. C., Woodin, S. J., Hester, A., Thompson, D. B. A., and Birks, H. J. B. (2010). How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? *Plant Ecology Diversity*, 1:1–8.

Rydin, H. and Barber, K. E. (2001). Long-term and fine-scale co-existence of closely related species. *Folia Geobotanica*, 36:53–62.

Schuur, E. A. G., Crummer, K. G., Vogel, J. G., and Mack, M. C. (2007). Plant species composition and productivity following permafrost thaw and thermokarst in alaskan tundra. *Ecosystems*, 10(2):280–292.

Shaver, G. R. and Jonasson, S. (1999). Response of arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. *Polar Research*, 18(2):245–252.

Smol, J. P., Wolfe, A. P., Birks, H. J. B., Douglas, M. S. V., Jones, V. J., Korhola, A., Pienitz, R., Ruhland, K., Sorvari, S., Antoniades, D., Brooks, S. J., Fallu, M. A., Hughes, M., Keatley, B. E., Laing, T. E., Michelutti, N., Nazarova, L., Nyman, M., Paterson, A. M., Perren, B., Quinlan, R., Rautio, M., Saulnier-Talbot, E., Siitoneni, S., Solovieva, N., and Weckstrom, J. (2005). Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences of the United States of America*, 102(12):4397–4402.

Sturm, M., Racine, C., and Tape, K. (2001). Climate change - increasing shrub abundance in the Arctic. *Nature*, 411(6837):546–547.

Svensson, G. (1988). Fossil plant communities and regeneration patterns on a raised bog in south Sweden. *Journal of Ecology*, 76:41–59.

Tape, K., Sturm, M., and Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4):686–702.

Tilman, D., Reich, P. B., and Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441(7093):629–632.

Tomassen, H. B. M., Smolders, A. J. P., Lamers, L. P. M., and Roelofs, J. G. M. (2003). Stimulated growth of Betula pubescens and Molinia caerulea on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition. *Journal of Ecology*, 91(3):357–370.

Tørseth, K. and Semb, A. (1997). Atmospheric deposition of nitrogen, sulfur and chloride in two watersheds located in southern Norway. *Ambio*, 26(5):258–265.

van der Linden, M., Vickery, E., Charman, D. J., and van Geel, B. (2008). Effects of human impact and climate change during the last 350 years recorded in a Swedish raised bog deposit. *Palaeogeography Palaeoclimatology Palaeoecology*, 262(1-2):1–31.

Virtanen, R., Lundberg, P. A., Moen, J., and Oksanen, L. (1997). Topographic and altitudinal patterns in plant communities on European arctic islands. *Polar Biology*, 17(2):95–113.

Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J.-A., and Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography*, 19:810–821.

Vittoz, P., Bayfield, N., Brooker, R., Elston, D. A., Duff, E. I., Theurillat, J. P., and Guisan, A. (2010). Reproducibility of species lists, visual cover estimates and frequency methods for recording high-mountain vegetation. *Journal of Vegetation Science*, 21(6):1035–1047.

Vittoz, P., Bodin, J., Ungricht, S., Burga, C., and Walther, G. R. (2008). One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *Journal of Vegetation Science*, 19(5):671–680.

Vittoz, P. and Guisan, A. (2007). How reliable is the monitoring of permanent vegetation plots? A test with multiple observers. *Journal of Vegetation Science*, 18(3):413–422.

Walther, G. R. (2003). Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics*, 6(3):169–185.

Walther, G. R., Beissner, S., and Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16(5):541–548.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416:389–395.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., and Chapin, C. T. (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, 81(12):3464–3478.

Wiedermann, M. M., Gunnarsson, U., Ericson, L., and Nordin, A. (2009). Ecophysiological adjustment of two Sphagnum species in response to anthropogenic nitrogen deposition. *New Phytologist*, 181(1):208–217.

Wilson, S. D. and Nilsson, C. (2009). Arctic alpine vegetation change over 20 years. *Global Change Biology*, 15(7):1676–1684.

Declaration

I declare that this thesis is my own work. It is submitted for the degree of Doctor of Philosophy at the University of Bergen, Norway. Contributions given by others and all sources of information are acknowledged where relevant. This thesis has not been submitted before for any degree or examination for a degree.

Jutta Kapfer
Bergen, August 2011