LAST-CENTURY VEGETATIONAL CHANGES IN NORTHERN EUROPE

Characterisation, causes, and consequences

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

Preface

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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 dominant species of the genus *Sphagnum* and other 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**: 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
△ 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 accord with the findings of several other studies showing nutrient demanding and competitive dwarf-shrubs and trees to have increased in growth (frequency and abundance) over the past decades, whereas several dominant *Sphagnum* species and 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 may also be due to higher decomposition rates induced by warming, which in the Åkhult mire is likely to have occurred in addition to increased wet deposition. 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 feedback 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.

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Paper I

Upward shift in elevational plant species ranges in Sikkilsdalen, Central Norway

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Abstract

Phytosociological studies are an important tool to detect temporal vegetation changes in response to global climate change. In this study, we present the results of a resurvey of a plot-based phytosociological study from Sikkilsdalen, central Norway, originally executed between 1922 and 1932. By using a detailed phytosociological study we are able to investigate several aspects of elevational shifts in species ranges. Here we tested for upward and downward shifts in observed upper and lower distribution limits of species, as well as changes in species optima along an elevational gradient, and related the observed range shifts to species traits that could explain the observed trends. More species shifted upwards than downwards, independently of whether we were investigating shifts in species' upper or lower distribution ranges or in species optima. However, shifts in species upper range margins changed independently of their lower range margins. Linking different species traits to the magnitude of shifts we found that species with a higher preference for prolonged snow cover shifted upwards more in their upper elevational limits and in their optima than species that prefer a shorter snow cover, whereas no species traits were correlated with the magnitude of changes in lower limits. The observed change in species ranges concord both with studies on other mountains in the region and with studies from other alpine areas. Furthermore, our study indicates that different factors are influencing species ranges at the upper and lower range limits. Increased precipitation rates and increased temperatures are considered the most important factors for the observed changes, probably mainly through altering the pattern in snow cover dynamics in the area.

Introduction

Changes in species distribution ranges concordant with expectations from a warming climate have been reported by many studies (e.g. Parmesan 2003, 2006, Rosenzweig et al. 2008, Walther 2010). Along elevational gradients, several observations and studies report substantial changes in plant species composition and distribution (Grabherr et al. 1994, Gottfried et al. 1998, Klanderud and Birks 2003, Walther et al. 2005, Pauli et al. 2007, Parolo and Rossi 2008, Kullman 2010). General patterns from arctic and alpine habitats show an upward trend for species (Grabherr et al. 1994, Klanderud and Birks 2003, Lenoir et al. 2008, Odland et al. 2010), with dwarf shrub and lowland plant species increasing in abundance (Wilson and Nilsson 2009), and an elevational advance of the tree line (Kullman 2002, Harsch et al. 2009). The common explanations for these observations have been that it is a consequence of both increased growth, and increased reproductive and dispersal success due to warmer climate, or due to earlier snow melts and hence longer growing seasons (Grabherr et al. 1994, Gottfried et al. 1998, Arft et al. 1999, Körner 2003, Klanderud and Birks 2003, Walther et al. 2005, Pauli et al. 2007). Downward shifts of species ranges have usually been ignored (but see Frei et al. 2010, Walther 2010), because it is thought that this is most likely a result of species interactions and land-use modifications and not because of physical environmental changes (Lenoir et al. 2010a). Recently, Crimmins et al. (2011) detected large-scale downward shifts in species to track water availability, instead of upward shifts as expected to track increases in temperature.

Most studies show that species respond individualistically to environmental changes (Walther et al. 2002, Klanderud and Birks 2003, Parmesan 2006, Holzinger et al. 2008, Lenoir et al. 2008, LeRoux and McGeoch 2008, Erschbamer et al. 2009). Hence, even though an upward shift is the most commonly observed pattern along altitudinal gradients, investigating differences between species showing changes of different direction and magnitude may give us a better understanding of the exact processes behind the dynamic ranges. Dispersal ability, ecological tolerance, and life-form are prominent examples of traits identified to explain differences in range shifts in alpine areas (e.g. Klanderud and Birks 2003, Lenoir et al. 2008, Parolo and Rossi 2008, Vittoz et al. 2009). If increased nitrogen deposition enhanced the upward range shifts, nitrogen-demanding species would probably have shifted their range more than other species (Körner 2003), and if changes in the duration of snow cover have influenced the ranges this will be detected by a comparison of range shifts of species that avoid a long snow cover with species that only are found in areas with an extensive snow cover. Changes in land-use have often been discussed in connection with observations of upwards shifts in species ranges (Körner 2003, Olsson et al. 2004, Becker et al. 2007) but species traits related to these factors are difficult to find and are therefore rarely directly related to range shifts.

The common approach to investigate temporal range shifts has been to resample historic floristic surveys and directly compare species maximum observed elevations (Grabherr et al. 1994, Klanderud and Birks 2003) or species composition on mountain tops (Walther et al. 2005, Pauli et al. 2007, Holzinger et al. 2008, Odland et al. 2010). Since many of the studies have focused on total species number on mountain summits or on changes in uppermost observations of species (e.g. Grabherr et al. 1994, Klanderud and Birks 2003, Holzinger et al. 2008), information about other aspects of range shifts apart from the upper range limits are generally lacking. However, different types of upward range shifts can be observed (Breshears 2009, Lenoir et al. 2010a, Walther 2010). These include shifts in the whole range, i.e. upper and lower distribution limits shift simultaneously, or expansion and/or contraction of only one side of their boundaries (Klanderud and Birks 2003, Pauli et al. 2007, Breshears 2009, Erschbamer et al. 2009, Crimmins et al. 2009). By only focusing on the upper range limit, important information about how species respond to climatic changes are lost, and also information about potential threats to biodiversity. It is, after all, upward movements of the lower limit that will cause local extinction of a species in a mountain region. Comparing changes in the central tendency for a species with changes in the range limits may give valuable additional information on how species respond to environmental changes.

Some recent studies have focused on other aspects of species ranges like variation in species central positions (e.g. mean, optimum) along elevational gradients (Lenoir et al. 2008, Kelly and Goulden 2008, Bergamini et al. 2009, Chen et al. 2009, Popy et al. 2010). To enable the detection of a species optimum elevation, presence/absence or abundance data from the main part of the elevational range of a species' occurrence are needed (Wisz et al. 2008, Lenoir et al. 2008). The data-set used in this study includes this type of vegetation data allowing for the study of patterns in both extreme (maximum and minimum) and optimum elevation.

In this study, we present the results of a resurvey in a local valley in Jotunheimen mountain area, central southern Norway. In 1922-32, Rolf Nordhagen sampled a large number of vegetation plots with the aim of describing the vegetation of Sikkilsdalen phytosociologically (Nordhagen 1943). We carried out a similar sampling in 2008 to test for elevational range shifts, looking at changes in upper and lower species distributions, in addition to changes in species optima. Following the findings of Klanderud and Birks (2003) of great changes in species occurrences in nearby mountain areas, we expected significant changes in species elevational distribution limits. In addition to describing the changes, we explore their potential links with biological traits of the species.

MATERIAL AND METHODS

Study site

The study area, Sikkilsdalen, is a part of the Caledonian mountain chain, located in eastern Jotunheimen, central southern Norway, at 61°28′ N and 09°00′ E (Fig. 1). It is a 10 km long U-shaped valley stretching from east to west with elevations ranging from 992 m a.s.l. to 1778 m a.s.l. The bedrock consists of gneiss and quartzite rock (Nordhagen 1943), and is covered by morainic soil generally rich in calcium and phosphate as a result of weathering of the igneous mountain rocks (Nordhagen 1943).

The climate in Sikkilsdalen is continental with oceanic influence. Average temperature is -10.6°C in January and 8.8°C in July, and average precipitation is 66.8 mm and 95 mm in the respective months. The area is normally covered by snow from October to May. Climatic trends between the two study periods show an increase both in temperature and precipitation. Mean annual temperature in the decade prior to the historic inventory (1910-1920) was -1.0°C and prior to 2008 (1998-2008) it was -0.2°C (Fig. 2a). Mean summer temperature has not changed considerably, but mean temperatures have increased in both spring (-1.9 °C to -1.6 °C) and autumn (-0.1°C to 1.2 °C) in the previous decades (see Appendix, Fig. A1a, c, e). Precipitation shows a steady increase throughout the period 1901-2008 (Fig. 2b), most notably in winter (in form of snow) and spring (Appendix, Fig. A1b, h). During the decade before the historic inventory, mean annual precipitation was 714 mm, and 1169 mm in the corresponding period before 2008.

A summer farm is located in the eastern part of Sikkilsdalen at approximately 1015 m a.s.l. Sikkilsdalen has a long cultural history which dates back to at least the 16^{th} century (Vigerust 1949). Since 1881, the area has been used for grazing for the Norwegian Horse, the Dole, and there were permanent human settlements until 1956 at the summer farm. Since 1956 land-use has reduced from year-round to seasonal farming (grazing), and the summer farm is now used for tourism. The changes in land-use have resulted in decreased grazing intensity which is expected to be more important in the lowland and alpine area closest to the summer farm. In the 1920-40s, grazing pressure in Sikkilsdalen was imposed by cows, sheep, goats, and horses, where the cows and goats grazed relatively close to the summer farm, and sheep and horses grazed over larger areas (Vigerust 1949). During the last few decades, horse grazing is approximately the same as before, but cows and goats have disappeared, and sheep grazing has decreased. Reindeer grazing has increased and reindeer were commonly observed during field work in the alpine area in 2008.

The hills in the study area are mainly dominated by birch forest (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) with openings of grassland. Two lakes, separated by a large mire complex, constitute the main valley floor. The mid-alpine belt consists of ericaceous shrubs such as *Empetrum nigrum* L. and *Vaccinium* spp., low shrubs (e.g. *Betula nana* L. and *Salix* spp.), and small-stature forbs and grasses such as *Antennaria* spp., *Omalotheca supina* (L.) DC., *Festuca ovina* L., etc. The vegetation close to the summer farm is dominated by grasses (e.g. *Agrostis capillaris* L., *Festuca rubra* L., *Poa pratensis* L.) and species thriving in disturbed areas (e.g. *Epilobium angustifolium* L., *Alchemilla* spp.). All mountain tops in Sikkilsdalen reach the mid-alpine zone. However, high-alpine species such as *Juncus trifidus* L., *Luzula confusa* Lindeb., and *Harrimanella hypnoides* (L.) Coville can also be found on the mountain tops on poor soil (Nordhagen 1943).

Vegetation re-sampling

Between 1922 and 1932, Nordhagen conducted a study of the vegetation in Sikkilsdalen to estimate the economical value of the vegetation for grazing (Nordhagen 1943). Nordhagen described all different vegetation types in Sikkilsdalen, from calcium-poor snow beds to tall-herb communities in birch forests, mires, cliffs, pastures, and aquatic vegetation types. In total, Nordhagen (1943) described vegetation from 1476 plots of mostly 1 m^2, but 260 plots of 4 m^2 are also included in the analyses (two plots of 16 m^2 were excluded). All these plots were placed in homogenous vegetation of all vegetation types found in an area and vascular plants, bryophytes, and lichens were recorded in the plots. Most of the plots were given an exact elevation (637 plots), or were said to be placed at the valley floor (341 plots). For a substantial number of plots Nordhagen noted an elevational interval for the plots. This was usually done because several plots were then sampled within this interval. The size of these intervals varied between 20 m (68 plots), 25 m (30 plots), 30 m (10 plots), 50 m (220 plots), 100 m (155 plots) and 150 m (15 plots).

In 2008, we re-investigated the vegetation (vascular plants) of Sikkilsdalen during four weeks in August/September. Since the site descriptions in the original study were vague, an exact relocation of the sampling sites was hampered. Vegetation was therefore recorded by sampling as close as possible to the same areas as investigated by Nordhagen using the information about localities and vegetation types

Figure 1: *Topographical map of Sikkilsdalen, and its approximate location in central Norway. (Map of Sikkilsdalen: Norwegian Mapping Authority, Geovekst and Norwegian municipalities, Overview of Norway: Norwegian Mapping Authority, cc-by-sa-3.0).*

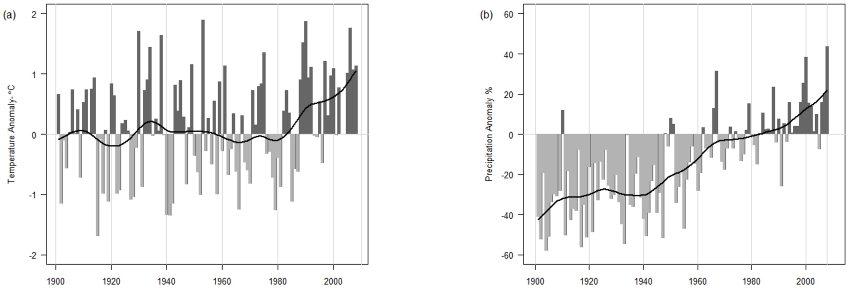

Figure 2: *Climate trend charts for Sikkilsdalen from 1901 to 2008, (a) mean annual temperature, and (b) total annual precipitation. The data were collected from a grid from a point close to the summer farm in the eastern part of the study area at approximate 1015 m a.s.l. Trend lines represent a smooth spline with 10 degrees of freedom. Data source: Tveito OE at Climatology Department, Norwegian Meteorological Institute.*

(e.g. tall herb communities, alpine grassland, low-stature shrub vegetation) available. In these vegetation types, plots were placed randomly aiming to capture a comparable variation of vegetation types to the one in Nordhagen (1943) but avoiding the most human-influenced vegetation (e.g. around the summer farm). In 2008, we sampled vegetation from a total of 424 plots of 1 m^2. For each plot, elevation was measured using a GPS (Garmin eTrex Legend HCx).

We used similar nomenclature to Nordhagen (1943), but updated the species names following Lid (2005). Taxa difficult to separate, such as *Hieracium* spp., *Alchemilla* spp. and *Taraxacum* spp., have been merged to avoid any bias regarding different species definitions and misidentifications.

Statistical analyses

Data preparation

Even though efforts were made to have as equal sampling to the original sampling as possible with respect to distribution of elevation and vegetation types, preliminary analyses of the data showed several differences between the two surveys that might have an effect on the analyses. Therefore, to make the two data-sets comparable, data pruning was done before analysing changes in species range limits and species optima.

The first step in the pruning was to remove samples from the historic survey with missing elevation data or those within intervals larger than 50 m (189 samples removed from the historic survey). Samples from the lowest part of the valley from the historic survey were assumed to be between 995 and 1000 m, as indicated from approximate site description and maps. All observations from 2008 lower than 995 m (lowest record 985 m) were set to 995 m because they were sampled at the same locations in the lowest region defined as 995 m for Nordhagen's samples. Because of the low sampling intensity at the highest elevations we excluded all samples above 1550 m a.s.l. (32 samples removed from the historic survey and one sample from the 2008 survey).

The next step in the pruning was to exclude samples from vegetation types that were only found in one of the surveys. This was done using correspondence analysis on the samples of both data-sets together (CA; Jongman et al. 1995, Legendre and Legendre 1998) and removing samples that were found to be outside the range of the other inventory along the two first axes. This resulted in removing 137 samples from the historic survey and two samples from the 2008 survey. A total of 358 samples was removed from the historic survey, and three samples from the 2008 survey, resulting in 1118 samples in the historic survey and 421 samples in the 2008 survey available for further analysis. In the final data preparation we included only species observed more than 10 times in both time periods, reducing the total number from 207 to 106 species that could be analysed.

All statistical analyses were conducted using R, version 2.10.2 (R Development Core Team 2009), and the vegan package for ordination analysis (Oksanen et al. 2009).

Changes in species elevational limits

Based on the pruned data-set, a test was developed to evaluate if species distribution limits were observed at higher or lower elevations in 2008 than in the historic survey. Before quantifying the changes, we made the elevational distributions of the samples comparable between the two surveys. The historic survey had more samples at lower elevations, while the original 2008 survey contained a higher frequency of samples from the mid-elevational belt. This bias was corrected for by dividing the samples into 50 m elevational bands and randomly selecting samples from each elevational band so that the ratio of the number of samples from the old survey and the 2008 survey is constant (approximately three times larger in the historic survey). From the resulting 796 samples of the old and 271 samples of the 2008 survey, the maximum and minimum elevation was identified for each species separately for the two inventories. Because each plot was assigned an elevational interval from the historic survey, different values were used when testing whether species had moved upwards or downwards. When testing for upward movement, the uppermost elevation given for each plot from the 1923 survey was used, whereas the lowermost elevation was used when testing for downwards movements. This may result in an underestimation of changes and as a result the tests will be a conservative test of the differences between the two time periods. Restricted permutation tests were developed to test if 1) the highest observed elevation of a species in 2008 was higher or lower than in the historic survey and 2) the lowest observed elevation limit of a species in 2008 was higher or lower than in the historic survey. The use of elevation intervals for each sample from the historic survey restricted the testing by allowing us to only test for upward or downward changes in the extremes in a single test.

Restrictions in the permutation tests were included to allow only samples from the same elevation to be swapped in the permutations. To do this the gradient was divided into the same 50 m elevational bands as above and the inventory identity was randomised only within these bands. Note that the random selection of samples to equalise the elevational distribution of samples between the two inventories described above was done for each permutation. Because the difference in extreme elevation observed is dependent on elevational distribution of samples, we present the mean elevational difference after equalising the distributions, and use this value in subsequent analyses (e.g. relating the changes to species traits). An approximate *p*-value was calculated based on how many times the randomised elevational difference was larger than (or equal to) the observed difference in a more extreme direction than was tested for, divided by number of permutations (including the observed) (Edgington 1995, Legendre and Legendre 1998), i.e. a one-tail test was used, and a *p*-value of 0.025 or lower was declared to be statistically significant.

Some changes could not be evaluated because sample boundaries did not allow a proper comparison. For example, when testing for upward or downward shifts of maximum observed elevation, we excluded species that were already observed less than 25 m below the highest elevation sampled. This was because the maximum is considered unknown as it could potentially be higher than the highest sample. This procedure excludes species that were found at the highest elevation in the historic survey, but we included species that were found lower in 2008, indicating that the maximum was lower in 2008. Correspondingly, when testing for upward or downward movement of minimum observed elevation we excluded species that were observed at less than 25 m above the lowermost sampled elevation in both the historic survey and 2008. This reduces the number of species testable to 91 species for changes in upper limits and 25 species for changes in lower limits from the initial 106 species for the different tests.

Species optima

Changes in species optima between the two inventories were quantified using logistic regression on the two surveys separately. This is based on a generalised linear model assuming a binomial distribution and using a logit link function (ter Braak and Looman 1986, Jongman et al. 1995, Oksanen et al. 2001, Lenoir et al. 2008). This method is commonly used to investigate species relationships along environmental gradients (ter Braak and Looman 1986, Jongman et al. 1995, Oksanen et al. 2001, Lenoir et al. 2008), where the Gaussian species response curves are fitted to the data. In these analyses, we solved the issue with Nordhagen's use of elevation intervals for each sample by using the mean of the elevation interval. Species optima analysis is less sensitive to sample frequency along the elevational gradients, and the differences in elevational distribution of samples were not corrected for in this analysis (i.e. all samples were kept after the initial pruning). The sensitivity of these analyses to differences in sampling frequency along altitude was also evaluated by using a data-set where the distribution was equalised, but this had only a minor impact on the results. We therefore use the data- set with the initial pruning only in these analyses.

We tested both a linear and a unimodal model against each other and against a null model using a chi-square test. For species with a unimodal response to elevation in both time periods we tested for differences in the optima by estimating the 95% confidence interval of the optima. Based on the coefficients for optimum, tolerance, and maximum probability of species occurrence following ter Braak and Looman (1986), the 95% confidence intervals of each species' optimum were calculated for the two time periods separately following Oksanen et al. (2001, see also Lenoir et al. 2008). Elevational optimum was considered statistically significantly different when the confidence intervals did not overlap, indicating that a change in optimum along the elevation gradient between the two inventories has occurred (Oksanen et al. 2001, Lenoir et al. 2008).

Species traits

Species traits were related to observed trends in species ranges by using simple linear regression models. The selected species traits include functional type (forbs, graminoids, shrubs, trees; USDA database), woodiness (herbaceous, woody; USDA database), life-form (based on Raunkiers system, Ellenberg et al. 1991 complemented with Hill et al. 2004) and various dispersal mechanism such as wind (boleochory, meteorochory), animal (endochory, epichory, dysochory, myrmekochory), human (anthropochory), water (hydrochory) and self-dispersal (autochory) (from Landolt et al. 2010). To evaluate if species show different responses dependent on whether the species are found at high or low elevations, we regressed the species estimated optimum and observed maximum position in 2008 vs. the observed difference between the two time periods. In addition, we used Ellenberg et al. (1991) species indicator values for light, soil moisture, soil reaction, temperature, and nutrients and Hill et al. (2004) values for species not covered by Ellenberg et al. (1991). We also included the snow-index values developed for Norwegian mountain plants, ranking the species' tendency to occur in snowbeds versus ridges (Odland and Munkejord 2008), and grazing pressure indicator values as developed by Vigerust (1949). The latter was estimated by observing how often a species was damaged by grazing in plots spread around in different vegetation stands of Sikkilsdalen. We used the mean value from the different vegetation types to test if the variation in observed distribution shifts could be related to variation in how much a species was grazed in the area.

Table 1: *Number of species (Nosp.) changing their elevational limits upwards or downwards. Mean elevational shift for species evaluated for each test include positive and negative values.*

Tested for:	Nosp. evaluated	Nosp. changing in tested direction	Nosp. with significant change	Mean elevational shift for species evaluated for each test
Upward shifts in upper limits	91	64	20	46 m
Upward shifts in lower limits	25	21	9	123 m
Downward shifts in upper limits	91	26	3	51 m
Downward shifts in lower limits	25	4	0	129 m

RESULTS

Changes in species elevational distribution limits

For changes in species upper elevational limits, 91 species were evaluated. Of these, 20 species are found at statistically significant higher elevations in 2008 than in the historic survey (Table 1). Only three species are recorded at significantly lower elevations. For upward or downward movement of species lower elevational limits, 25 species could be evaluated. Of these, nine species are observed at significantly higher elevation. When testing for a decrease in lower elevation limit, no statistically significant downward shift was found for any of the species evaluated.

The correlation between the upper and lower limit for the 19 species that could be evaluated for changes in both extremes showed that species have shifted independently in their upper and lower elevational limits (Pearson r = 0.016, Spearman rank rS = -0.06, p > 0.05 in both cases). Three of the 19 species (*Euphrasia wettsteinii*, *Juncus trifidus*, *Veronica alpina*) have shifted both upper and lower elevational limits significantly upwards (Appendix, Table A1). Two species (*Beckwithia glacialis*, *Luzula confusa*) have shifted the lower elevational limit significantly upwards and at the same time changed the higher elevational limit significantly downwards, i.e. their total elevational ranges have decreased (Appendix, Table A1).

Changes in species optima

Species responses along the elevation gradient differ both within and between the two surveys. More species show a unimodal response along the elevation gradient in the historic survey than in 2008, where more species are found to have a linear relationship (Table 2). This is probably due to more samples and hence increased power to accept a more complex model in the analyses of the historic survey than the 2008 data set (1126 vs. 421 samples). To avoid this sampling effect we use only those species for which a unimodal relationship is found in both time periods when comparing species elevational optima. We found 45 species with a unimodal response in both the historic survey and 2008 (Table 2). Eighteen out of 45 species had non-overlapping confidence intervals (Fig. 3). Of these, 14 species shifted their optima statistically significantly upwards, while four species shifted their optima statistically significantly downwards. On average, species optima increased significantly upwards by 41.3 m in the time period between the two inventories (paired t-test on optimum in historic and 2008 surveys: t = 3.65, n = 45, p = 0.001).

The observed changes in species upper limits and species optimum between the time periods are highly consistent (Pearson r = 0.57, n = 41, p < 0.001). In contrast, the shifts in optima and minimum observed elevation are negative but not statistically significantly (r = -0.21, n = 9, p = 0.556).

Species traits

Species traits analyses show that species with a higher preference for prolonged snow cover had larger upward shifts than species that avoid long snow cover both for species optima (F = 15.32, n = 22, p < 0.001) and species maximum elevations (F = 15.21, n = 37, p

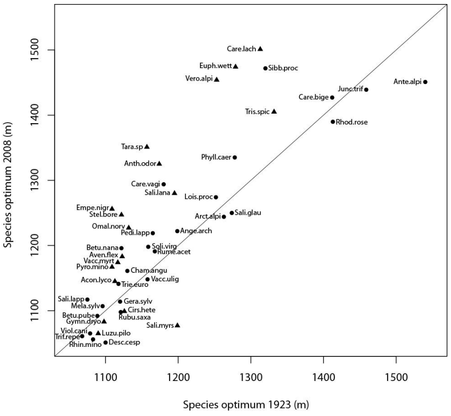

Figure 3: *Species optimum elevation in 1923 versus 2008. The line indicates no change and deviations from the line indicate a change in species opimum upwards (above the line) or downwards (below the line). Species with triangle symbols show statistically significant changes in optimum elevation. The species abbreviations are listed in Appendix, Table A2.*

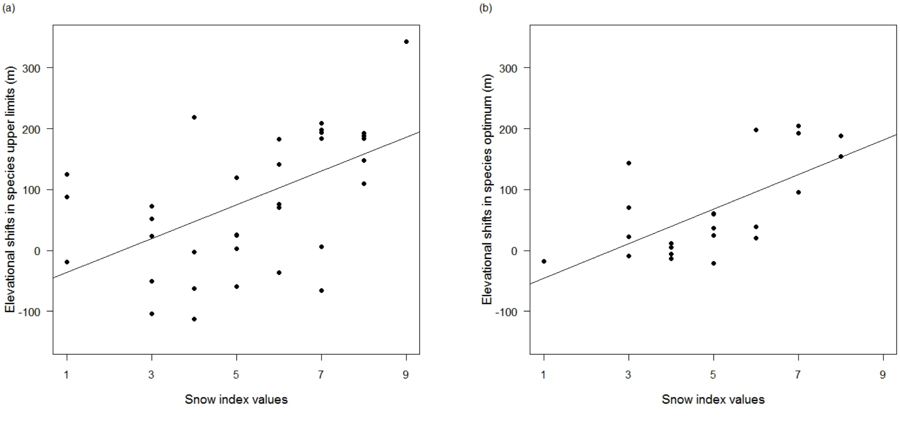

Figure 4: *Snow-index values against (a) shifts in species upper elevational limits (no. species = 37) and (b) shifts in species optimum elevation (no. species = 22).*

Table 2: *Number of species (n tested = 106) showing no (null), linear, or unimodal response along the elevational gradient in the historic survey and in 2008.*

Response model	Historic survey	2008
Null	5	8
Linear	26	43
Unimodal	75	55

< 0.001) (Fig. 4). Furthermore, species at higher elevation showed larger shifts in both species estimated optima ($F = 20.61$, n = 45, $p < 0.001$) and species maximum elevations ($F = 67.27$, n = 91, $p < 0.001$; Fig. 5). A corresponding pattern is also found when relating range shifts with species indicator values for temperature, i.e. a significant trend was found indicating that species with a preference for low temperatures had larger shifts in their upper limits than species preferring higher temperatures ($F = 6.80$, n = 43, $p = 0.012$; Fig. 6). There is also a significant relationship between upward shifts in species optima and species with boleochorial dispersal mechanism (i.e. seeds released by an explosive mechanism and wind dispersed over a short distance) ($F = 7.26$, $p = 0.011$). There are no consistent trends for species of different structure such as forb, graminoid, shrub, and tree, nor for life-form or any other dispersal mechanisms with any of the estimates of range shifts. There is no consistent trend between species upward shifts and species favoured by grazing animals either, and the magnitude of changes in species optima is not significantly related to any of the Ellenberg indicator values other than temperature.

Discussion

Using Nordhagen's detailed floristic survey from the 1920s as a baseline, this study found a general upward trend in species distributions independent of whether observed maximum, observed minimum, or estimated optimum elevation for species is considered. This observed trend is consistent with other studies investigating elevational trends in plant species distributions in European mountains at different scales in time and space (e.g. Grabherr et al. 1994, Gottfried et al. 1998, Klanderud and Birks 2003, Holzinger et al. 2008, Erschbamer et al. 2009). The magnitude of species range shifts in this study is found to be smaller in comparison with those reported from central Europe where trends are estimated of 27.8 m/decade (Walther et al. 2005) and 23.9 m/decade (Parolo and Rossi 2006) in the upper gradient and 29.4 m/decade along the entire elevational gradient (Lenoir et al. 2008). In our study we found an upward shift after 80 years of 41 m for optimum, 46 m for observed upper limit, and 123 m for observed lower limit. For statistically significant species only, the mean elevation shift is larger, i.e. 82 m for optimum, 192 m for upward shifts in species upper elevation, and 202 m for upward shift in lower elevations. Upward shifts in upper limits compared to lower limits can be limited as species at the uppermost elevations are closer to the mountain summits and are constrained by a lack of land, while species at the lowermost elevations have a better potential to shift upwards.

Although a clear upward trend is found for most species in this study there is a large variation between how much the species elevational distribution has shifted, with some species shifting downwards. The different directions and magnitudes of shifts between species indicate that species have responded individualistically to potential drivers for vegetation change between the two study periods. Individualistic responses of species are consistent with several previous studies of range shifts over similar time scales (e.g. Walther et al. 2002, Parmesan 2006, LeRoux and McGeoch 2008). Species specific responses do not appear to be linked to functional traits, as no significant trends between traits and observed range shifts have been detected. The only exception is the significant relationship between upward shift in species optima and species with boleochory dispersal (i.e. short distance dispersal by wind). The relationship between species optima change and boleochory was based on only five species with this particular trait. Considering the many tests performed when relating species functional traits to range shifts, finding one significant relationship is no more than would be expected by chance. We will therefore not put too much emphasis on this finding.

In addition to the different responses of different species, there is little consistency in how species respond when looking at different aspects of the species' distributions. While the general trend is qualitatively similar for the observed upper and lower species limits as well as for species optima,

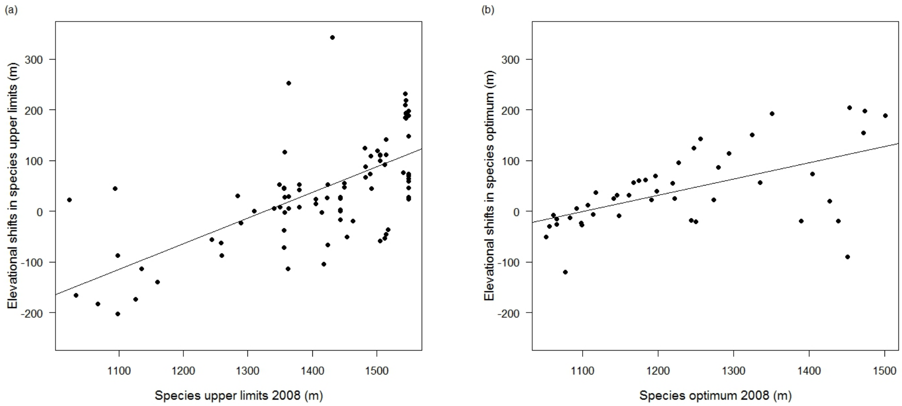

Figure 5: *Species upper limits and estimated optima along the elevational gradient in 2008 vs. (a) the magnitude of shifts in upper limits and (b) shifts in species optimum elevation between the time periods.*

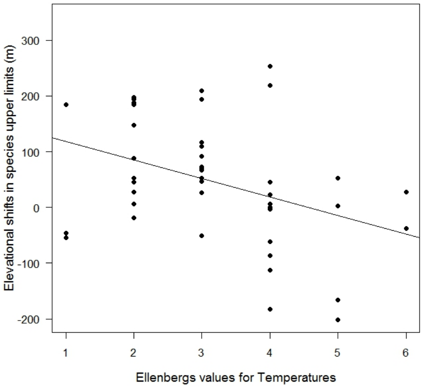

Figure 6: *Changes in species upper elevational limits vs. Ellenberg values for temperature.*

there are no consistent trends in the magnitude of changes in upper and lower limits. This suggests that the two extremes respond independently within the same species, which in turn indicates that different processes are involved in the shifting of upper and lower elevational limits. Classically, the upper, or cold-end limit, has been explained by tolerance to harsh climate, whereas the lower, or warm-end limit, has often been explained by tolerance to competition (MacArthur 1972, Brown et al. 1996, Crawford 2008). An alternative explanation for the different response of the two extremes might be that shifts in the upper limit as a response to better climate are dependent on dispersal ability, whereas being able to keep the same lower limit with a warmer climate is dependent on persistence traits, like longevity. An explanation for a decrease in lower elevational limit is also offered by Lenoir et al. (2010a). They assume that as climate changes, dispersal will delay the invasion of good competitors into the new environment and weak competitors can temporarily move downwards until the optimal competitors in the new climate arrive.

Two of the 19 species pairs (*Luzula confusa* and *Beckwithia glacialis*) showed statistically significant trends in opposite directions for the upper and lower limits resulting in a range contraction. Both these species are high-alpine species with low temperature tolerance, narrow distribution ranges, low density in the area, and are assumed to be restricted to high elevations by high maximum summer temperature limits (Dahl 1998) and are among the species in Scandinavia that have been predicted to suffer most from global warming (Sætersdal and Birks 1997). Species niche modelling predicts that these species would only suffer in the lower part and the range contraction observed in the upper limit of these species is not expected, and is not concordant with the observations made by Klanderud and Birks (2003) where *Beckwithia glacialis* had retracted via its lower elevation limits, but increased in abundance at higher elevations. One possible reason for the lowering of the upper range of the species could be that snow cover in this high elevational area is actually prolonged. Precipitation has increased giving a thicker snow cover during winter. This increased snow cover could be neutralised by warmer temperatures that, at lower elevations, would result in an earlier snow melt. However, in the high-alpine areas, where the snow melts later, and because the summer temperatures has not decreased (Appendix, Fig. A1c) the snow may still be plentiful in summer in the highest areas, and an increase in snow cover may have caused habitat loss at the upper elevations for these high-alpine species. The increased snow cover may be specific to these western areas of Jotunheimen which receives more precipitation than the eastern part, explaining the difference observed between our study and the study by Klanderud and Birks (2003).

Most of the studies on range shifts along altitude or latitude identify climate change as the most important variable for upward shifts in species distributions (e.g. Walther 2003, Lenoir et al. 2008, Parolo and Rossi 2008). Support for this explanation is also found in this study as a statistically significant relationship was found between species shifts in upper elevational limit and Ellenberg indicator values for temperature. However, investigating temperature changes and precipitation rates over the investigated period in this study, the changes in precipitation rates are more pronounced (Fig. 2). This implies that changes in water dynamics and balance may be an important driver for the observed changes, where species associated with moist habitats may have shifted upwards towards drier sites because of enhanced water availability through precipitation. Increased frequencies of species associated with wetter habitats have also been observed by Odland et al. (2010) at different mountain summits close to our study region, and are considered as an indicator of climate change towards a more oceanic climate. Changes in precipitation regime have also been used to explain downward shifts (Lenoir et al. 2010a, Crimmins et al. 2011). However, in our study region, water demands are probably rarely a limiting factor because the temperature is generally low and the area receives a relatively large amount of precipitation throughout the whole year. Thus, even though there is an increase in precipitation rate throughout the time periods, the observed shifts in species ranges in the study area are probably more directly associated with changes in snow cover duration and pattern than with water availability as such. Although temperature increased during the last 30 years, and species with low demands for temperatures in upper ranges tend to display larger shifts in their upper ranges, the increase in temperature seems to be a more indirect driver of these observed changes. In northern regions, winter and spring events have been shown to have a large impact on plant performance (Aerts et al. 2006, Kullman 2010), and in our study area there has been little or no change in summer and winter temperatures between 1920 and today (Fig. 2). The increase in spring and autumn temperatures are more pronounced (Appendix, Fig. A1a, e), and this warming may change snow cover patterns over time by higher melting rates in spring and later snow cover in autumn/winter resulting in longer growing seasons at some elevations. In addition, the precipitation increased more during winter and spring time (Appendix, Fig. A1b, h), and this can counteract the effect of warmer springs on the length of growing season. That changes in duration of snow cover might be involved in explaining the observed pattern is supported in our study by the observation that several species dependent on long snow cover (e.g. *Carex lachenalii*, *Juncus biglumis*, *Anthoxanthum odoratum*) are found to have major upwards shifts in optima, whereas species typically found in areas with low snow cover during winter (e.g. *Juncus trifidus*, *Arctous alpinus*) have not changed their optima. This is confirmed by the highly significant correlations found between the snow-index values and both species' upper range margins and optimum elevation. Klanderud and Birks (2003), who did a study of species elevational shifts on mountains close to our study area, used the extended snow-free period to explain increased frequencies of dwarf shrubs (e.g. *Empetrum nigrum*, *Vaccinium myrtillus*) and several snowbed related species (e.g. *Omalotheca supina*, *Sibbaldia procumbens*, *Veronica alpina*).

Besides direct effects of climate warming, many studies have discussed increased deposition of atmospheric nitrogen as an important driver for changes in plant elevational distribution in European mountain areas (e.g. Klanderud and Birks 2003, Körner 2003, Britton et al. 2009). With increased nitrogen deposition due to increased precipitation rates with elevation (Vitousek et al. 1997, Galloway et al. 2008), nutrient-demanding species with higher competitive ability may successfully establish at higher elevations, and start interacting with and potentially cause elevational shifts for species of higher elevation with lower demands for nutrients. If this is the case, we would expect upper elevational limits for nitrogen-demanding species to increase and lower elevational limits for species with low tolerance for competition or nitrogen to increase. However, no indication of this is found in our study as we do not find any correlation between species upward shifts and Ellenberg indicator values for nutrients. Klanderud and Birks (2003) reported more pronounced vegetation changes in the eastern areas of Jotunheimen, whereas precipitation rates, and hence nitrogen deposition, are generally higher in the west. This indicates that the observed changes cannot be satisfactorily explained by increased nitrogen deposition.

Changes in grazing pressures may enhance or mask species responses to climate change (Hofgaard 1997, Olsson et al. 2000, Körner 2003, Olsson et al. 2004, Becker et al. 2007). Traditional land-use has formed the landscape in Sikkilsdalen for many years, and the end of these activities has resulted in re-growth of forest and succession on abandoned grassland areas in the lower regions of the area (Sterten 1997). In our area it is especially the animals that usually graze relatively close to the summer farms that have decreased markedly in the period between the two surveys (cows and goats have disappeared). Reduced grazing in the lower regions may be the reason for some of the lower optima found for some species (e.g. *Luzula pilosa*, *Cirsium heterophyllum*, *Gymnocarpium dryopteris*). If the reduced grazing intensity has a general influence on the observed upward movement of species in this study, we would expect that species favoured by grazers would have increased in growth and reproduction, and thereby shifted upwards. However, we found no correlation between species distributional shifts and the values for grazing intensity of plant species in Sikkilsdalen (Vigerust 1949). A possible explanation for the lack of importance of decreased grazing intensity is that the domesticated reindeer populations in the alpine region have increased (Olsson et al. 2004), which may compensate for reduced grazing intensity by other domestic animals. Thus, apart from some potential impact on species range shifts in the lower part by the relief of grazing we find no indication that changes in grazing regimes have caused range shifts.

Conclusions

This study used a detailed phytsociological survey consisting of a large number of vegetation plots as a baseline to quantify changes in species elevational distributions. By focusing on several aspects of species elevational distributions (i.e. species upper, lower and optimum distribution) a general upward trend in species ranges was found. However, upper and lower distribution limits were found to shift individualistically. Thus, this study demonstrates the importance of considering different aspects of species elevational distributions within the same study, which so far has only rarely been done in other studies (but see Moritz et al. 2008, Bergamini et al. 2009, Crimmins et al. 2009, Lenoir et al. 2010b).

Many phytosociological studies of similar quality to the one used in this study exist in the literature, especially from the European Alps and the Scandes, but resurveying this type of study is still rare, as sampling methods often hamper a direct comparison of vegetation and environment through time. Our study shows that such studies can effectively be used as baselines for studying long-term changes in species distributions along environmental gradients, even when non-permanent plots are used.

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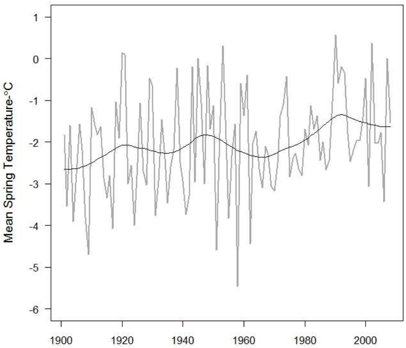
Appendix

(a)



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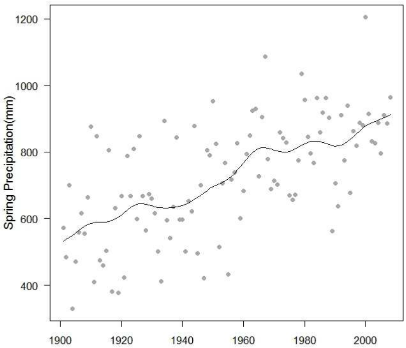

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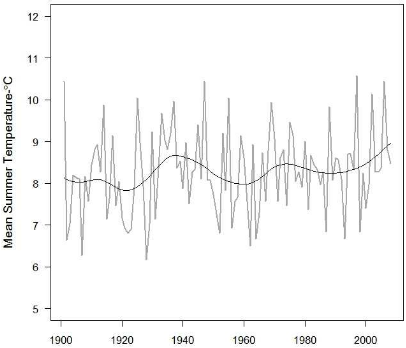

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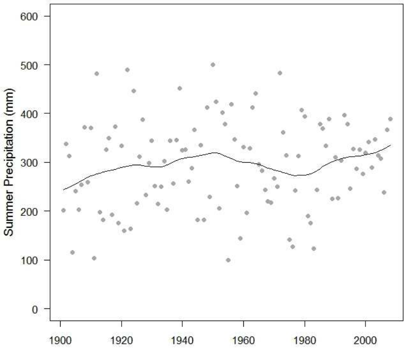

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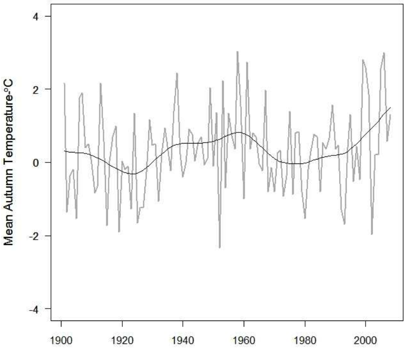

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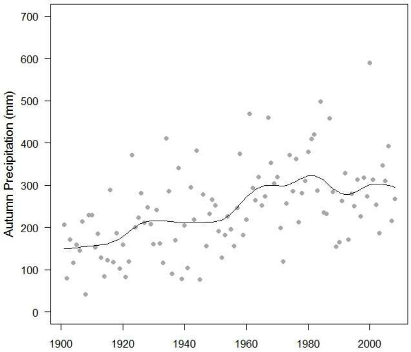

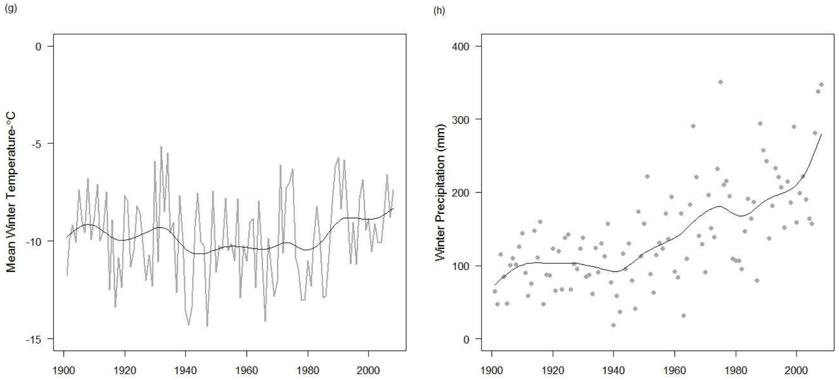

Figure A1: Climate trend charts for temperature and precipitation in spring (March-April; (a), (b)), summer (June-August; (c), (d)), autumn (September-November; (e), (f)) and winter (December-February; (g), (h)). Mean spring temperatures (a) show a small increase in temperature between the study periods of 1920 and 2008 of approximate 0.5 ºC, while absolute spring precipitation rates (b) show a steady increase of approximate 300 mm. Mean summer temperatures (c) and absolute summer precipitation rates (d) have fluctuated much between 8-9ºC and 200-300 mm, respectively, but show rather small changes between the periods investigated. Mean autumn temperatures (e) seem to have increased the most between the two study periods by approximately 1ºC, while absolute autumn precipitation rates (f) have increased only a little (approximate 60 mm). Finally, mean winter temperatures (g) have fluctuated much around -10ºC, with a small increase since 1980, whereas absolute winter precipitation rates (h) have increased steadily from 75 mm to 290 mm throughout the period of 1901-2008.

Table A1: Changes in species elevational distribution limits. Statistically significant changes are printed in bold. n.e = not evaluated.

			Upward shifts in upper limits					**Upward shifts in lower limits**					**Downward shifts in upper limits**					**Downward shifts in lower limits**					
Species	**Species occurrences 2008**	**Species occurrences old record**	**Highest observation 2008 (m)**	**Highest observation old record (m)**	**Observed elevational difference (m)**	**Mean randomized difference (m)**	***p*-value**	**Lowest observation 2008 (m)**	**Lowest observation old record (m)**	**Observed elevational difference (m)**	**Mean randomized difference (m)**	***p*-value**	**Highest observation 2008 (m)**	**Highest observation old record (m)**	**Observed elevational difference (m)**	**Mean randomized difference (m)**	***p*-value**	**Lowest observation 2008 (m)**	**Lowest observation old record (m)**	**Observed elevational difference (m)**	**Mean randomized difference (m)**	***p*-value**	**Species tested for both upper and lower limits**
Achillea millefolium	25	52	1094	1050	44	44	0.243	995	1000	-5	-5	n.e	1094	1015	79	79	1.000	995	1000	-5	-5	n.e	
Aconitum lycoctonum	24	89	1310	1300	10	0	0.313	995	1000	-5	-5	n.e	1310	1300	10	-1	0.876	995	995	0	-3	n.e	
Agrostis capillaris	64	90	1363	1300	63	29	0.362	995	1000	-5	-5	n.e	1363	1300	63	24	0.822	995	995	0	0	n.e	
Agrostis mertensii	63	43	**1549**	**1350**	**199**	**198**	**0.000**	1034	1000	34	34	0.045	1549	1300	249	248	1.000	1034	995	39	71	0.960	x
Alchemilla alpina	24	32	1363	1340	23	6	0.370	1004	1000	4	3	n.e	1363	1340	23	3	0.788	1004	995	9	11	n.e	
Alchemilla vulgaris	62	158	1544	1300	244	232	0.089	995	1000	-5	-5	n.e	1544	1300	244	238	0.991	995	995	0	-1	n.e	
Andromeda polifolia	24	94	**1023**	**1000**	**23**	**23**	**0.000**	995	1000	-5	-5	n.e	1023	995	28	20	1.000	995	995	0	0	n.e	
Angelica archangelica	11	34	1357	1300	57	28	0.248	995	1000	-5	-16	n.e	1357	1300	57	24	0.908	995	995	0	-25	n.e	
Antennaria alpina	34	48	1541	1550	-9	-36	n.e	1144	1050	94	94	0.461	1541	1550	-9	-29	n.e	1144	1000	144	63	0.393	
Antennaria dioica	71	153	1549	1475	74	64	0.046	1005	1000	5	5	n.e	1549	1450	99	92	1.000	1005	995	10	17	n.e	
Anthoxanthum odoratum	149	268	**1549**	**1475**	**74**	**73**	**0.003**	995	1000	-5	-5	n.e	1549	1450	99	98	1.000	995	995	0	-1	n.e	
Arctostaphylos uva-ursi	17	109	1482	1300	182	125	0.115	1004	1010	-6	-6	n.e	1482	1300	182	70	0.898	1004	995	9	115	n.e	
Arctous alpinus	17	35	1463	1400	63	-19	0.576	1160	1010	150	150	0.380	1463	1350	113	-11	0.574	1160	1000	160	155	0.637	x
Astragalus alpinus	12	37	1483	1300	183	88	0.412	1038	1010	28	27	0.186	1483	1300	183	-8	0.499	1038	1000	38	43	0.971	x
Avenella flexuosa	142	337	1501	1360	141	119	0.078	995	1000	-5	-5	n.e	1501	1360	141	126	0.995	995	995	0	0	n.e	
Bartsia alpina	51	59	1450	1350	100	47	0.082	995	1000	-5	-6	n.e	1450	1350	100	64	0.957	995	995	0	-1	n.e	
Beckwithia glacialis	11	49	1514	1550	-36	-46	0.999	**1336**	**1225**	**111**	**136**	**0.010**	**1514**	**1550**	**-36**	**-54**	**0.000**	1336	1225	111	150	0.951	x
Betula nana	111	373	1454	1475	-21	-51	0.767	995	1000	-5	-5	n.e	1454	1450	4	-21	0.595	995	995	0	0	n.e	

Betula pubescens	51	180	1415	1300	115	-3	0.427	995	1000	-5	-5	n.e	1415	1300	115	0	0.706	995	995	0	0	n.e	
Bistorta vivipara	175	405	1549	1540	9	8	n.e	995	1000	-5	-5	n.e	1549	1540	9	8	n.e	995	995	0	0	n.e	
Calamagrostis phragmitoides	14	41	1341	1300	41	6	0.462	995	1000	-5	-5	n.e	1341	1300	41	-1	0.798	995	995	0	-4	n.e	
Campanula rotundifolia	78	291	1549	1550	-1	-3	n.e	995	1000	-5	-5	n.e	1549	1550	-1	-2	n.e	995	995	0	0	n.e	
Carex bigelowii	127	259	1545	1540	5	2	n.e	995	1000	-5	-5	n.e	1545	1540	5	4	n.e	995	995	0	0	n.e	
Carex canescens	23	157	1356	1250	106	46	0.133	995	1000	-5	-5	n.e	1356	1225	131	55	0.998	995	995	0	0	n.e	
Carex dioica	19	112	1067	1250	-183	-183	1.000	995	1000	-5	-5	n.e	**1067**	**1200**	**-133**	**-133**	**0.002**	995	995	0	0	n.e	
Carex lachenalii	44	50	**1545**	**1350**	**195**	**193**	**0.001**	1213	1250	-37	-40	0.981	1545	1350	195	195	1.000	1213	1250	-37	-37	0.261	x
Carex nigra	22	115	1244	1300	-56	-56	0.446	995	1000	-5	-5	n.e	1244	1300	-56	-56	0.734	995	995	0	0	n.e	
Carex paupercula	16	101	1349	1200	149	53	0.355	995	1000	-5	-5	n.e	1349	1200	149	15	0.699	995	995	0	0	n.e	
Carex rostrata	41	214	1350	1225	125	8	0.748	995	1000	-5	-5	n.e	1350	1225	125	11	0.361	995	995	0	0	n.e	
Carex rupestris	16	57	1549	1540	9	4	n.e	**1359**	**1020**	**339**	**376**	**0.007**	1549	1540	9	6	n.e	1359	1000	359	362	0.997	
Carex saxatilis	12	21	1491	1300	191	109	0.275	995	1000	-5	-121	n.e	1491	1300	191	55	0.859	995	995	0	-142	n.e	
Carex vaginata	138	270	1549	1475	74	69	0.068	995	1000	-5	-5	n.e	1549	1450	99	96	0.988	995	995	0	0	n.e	
Cerastium alpinum	33	121	1541	1550	-9	-17	n.e	1004	1000	4	2	n.e	1541	1550	-9	-14	n.e	1004	1000	4	141	n.e	
Cerastium cerastoides	29	60	**1544**	**1350**	**194**	**184**	**0.008**	1154	1000	154	154	0.193	1544	1350	194	188	1.000	1154	995	159	156	0.684	x
Cerastium fontanum	18	31	1357	1200	157	117	0.197	995	1000	-5	-7	n.e	1357	1200	157	125	0.943	995	1000	-5	-5	n.e	
Chamerion angustifolium	35	122	1380	1350	30	8	0.282	995	1000	-5	-8	n.e	1380	1325	55	25	0.885	995	995	0	0	n.e	
Cirsium heterophyllum	12	43	1260	1300	-40	-87	0.694	1014	1000	14	11	n.e	1260	1300	-40	-112	0.329	1014	995	19	27	n.e	
Comarum palustre	32	151	1356	1250	106	44	0.092	995	1000	-5	-5	n.e	1356	1225	131	45	0.997	995	995	0	0	n.e	
Deschampsia cespitosa	67	122	1505	1350	155	100	0.416	995	1000	-5	-5	n.e	1505	1350	155	120	0.841	995	995	0	0	n.e	
Empetrum nigrum	130	313	1490	1400	90	73	0.136	995	1000	-5	-5	n.e	1490	1350	140	92	0.999	995	995	0	0	n.e	
Equisetum arvense	16	106	1505	1350	155	111	0.189	995	1000	-5	-5	n.e	1505	1350	155	131	0.967	995	995	0	0	n.e	
Equisetum fluviatile	12	16	**1363**	**1000**	**363**	**253**	**0.006**	996	1000	-4	-4	n.e	1363	995	368	250	1.000	996	995	1	1	n.e	
Eriophorum angustifolium	45	329	1492	1350	142	45	0.466	995	1000	-5	-5	n.e	1492	1350	142	21	0.752	995	995	0	0	n.e	
Euphrasia wettsteinii	73	157	**1549**	**1475**	**74**	**71**	**0.003**	**1144**	**1000**	**144**	**144**	**0.000**	1549	1450	99	97	1.000	1144	995	149	149	0.996	x
Festuca ovina	152	507	1549	1550	-1	-4	n.e	995	1000	-5	-5	n.e	1549	1550	-1	-2	n.e	995	995	0	0	n.e	
Festuca rubra	34	81	1357	1300	57	-3	0.623	995	1000	-5	-5	n.e	1357	1300	57	-24	0.390	995	995	0	-1	n.e	
Geranium sylvaticum	88	186	1545	1325	220	219	0.025	995	1000	-5	-5	n.e	1545	1325	220	220	1.000	995	995	0	-1	n.e	
Geum rivale	18	66	1289	1300	-11	-24	0.617	996	1000	-4	-4	n.e	1289	1300	-11	-44	0.508	996	995	1	-1	n.e	

Gymnocarpium dryopteris	14	75	1135	1250	-115	-113	0.910	1020	1000	20	20	n.e	1135	1250	-115	-113	0.208	1020	995	25	29	n.e	
Hieracium sp.	138	196	1549	1550	-1	-5	n.e	1011	1000	11	8	n.e	1549	1550	-1	-3	n.e	1011	995	16	22	n.e	
Juncus biglumis	14	25	1514	1400	114	112	0.039	1147	1200	-53	-53	0.995	1514	1400	114	114	1.000	1147	1200	-53	-56	0.230	x
Juncus trifidus	93	147	**1549**	**1500**	**49**	**46**	**0.007**	**1203**	**1000**	**203**	**203**	**0.007**	1549	1500	49	48	1.000	1203	995	208	204	1.000	x
Juniperus communis	34	139	1405	1360	45	24	0.160	1010	1000	10	10	n.e	1405	1360	45	19	0.910	1010	995	15	21	n.e	
Leontodon autumnalis	43	73	**1545**	**1350**	**195**	**183**	**0.008**	995	1000	-5	-5	n.e	1545	1350	195	188	1.000	995	995	0	0	n.e	
Loiseleuria procumbens	13	20	1424	1300	124	52	0.318	1203	1000	203	163	0.596	1424	1250	174	98	0.941	1203	995	208	134	0.423	x
Luzula confusa	15	58	1517	1550	-33	-36	1.000	**1336**	**1200**	**136**	**169**	**0.002**	**1517**	**1550**	**-33**	**-35**	**0.000**	1336	1200	136	166	0.991	x
Luzula multiflora	73	100	**1514**	**1350**	**164**	**141**	**0.020**	995	1000	-5	-5	n.e	1514	1300	214	199	1.000	995	995	0	0	n.e	
Luzula pilosa	27	110	1160	1300	-140	-140	0.911	996	1000	-4	-4	n.e	1160	1300	-140	-140	0.498	996	995	1	1	n.e	
Luzula spicata	57	164	1545	1550	-5	-7	n.e	**1269**	**1000**	**269**	**279**	**0.000**	1545	1550	-5	-5	n.e	1269	1000	269	288	1.000	
Melampyrum sylvaticum	24	122	1259	1300	-41	-62	0.605	996	1000	-4	-4	n.e	1259	1300	-41	-74	0.490	996	995	1	1	n.e	
Myosotis decumbens	16	85	1444	1300	144	27	0.285	995	1000	-5	-7	n.e	1444	1300	144	36	0.856	995	995	0	-3	n.e	
Nardus stricta	13	51	1424	1340	84	-66	0.701	995	1000	-5	-8	n.e	1424	1340	84	-75	0.458	995	995	0	-2	n.e	
Omalotheca norvegica	32	100	1544	1325	219	209	0.046	1017	1000	17	16	n.e	1544	1325	219	214	0.984	1017	995	22	32	n.e	
Omalotheca supina	64	82	**1549**	**1360**	**189**	**188**	**0.000**	1017	1000	17	5	n.e	1549	1360	189	188	1.000	1017	1000	17	106	n.e	
Oxycoccus sp.	14	77	1356	1250	106	-72	0.508	995	1000	-5	-5	n.e	1356	1200	156	-48	0.719	995	995	0	0	n.e	
Oxyria digyna	38	29	**1549**	**1400**	**149**	**148**	**0.006**	1213	1000	213	155	0.448	1549	1400	149	148	1.000	1213	1000	213	144	0.658	x
Pedicularis lapponica	29	128	1405	1350	55	14	0.210	1006	1000	6	6	n.e	1405	1350	55	11	0.839	1006	995	11	30	n.e	
Pedicularis oederi	25	51	1545	1550	-5	-18	n.e	1029	1150	-121	-143	0.994	1545	1550	-5	-12	n.e	1029	1150	-121	-112	0.102	
Pedicularis sceptrum-carolinum	11	19	1034	1200	-166	-166	0.736	995	1000	-5	-5	n.e	1034	1200	-166	-161	0.523	995	995	0	0	n.e	
Phleum alpinum	59	139	**1545**	**1350**	**195**	**194**	**0.013**	995	1000	-5	-5	n.e	1545	1350	195	195	0.999	995	995	0	0	n.e	
Phyllodoce caerulea	55	27	**1450**	**1350**	**100**	**55**	**0.004**	1005	1125	-120	-149	0.968	1450	1325	125	102	0.999	1005	1125	-120	-85	0.171	x
Poa alpina	13	119	1512	1400	112	92	0.220	**1289**	**1000**	**289**	**302**	**0.000**	1512	1400	112	88	0.894	1289	995	294	320	1.000	x
Poa pratensis	23	129	1444	1350	94	-17	0.729	995	1000	-5	-5	n.e	1444	1340	104	8	0.594	995	995	0	0	n.e	
Potentilla crantzii	62	146	1549	1520	29	28	0.072	995	1000	-5	-6	n.e	1549	1520	29	28	1.000	995	995	0	-3	n.e	
Pulsatilla vernalis	32	93	1549	1475	74	59	0.087	1004	1000	4	2	n.e	1549	1450	99	89	0.990	1004	995	9	43	n.e	
Pyrola minor	51	133	1444	1360	84	0	0.307	995	1000	-5	-5	n.e	1444	1360	84	3	0.766	995	995	0	0	n.e	
Ranunculus acris	98	208	**1545**	**1350**	**195**	**194**	**0.006**	995	1000	-5	-5	n.e	1545	1340	205	205	1.000	995	995	0	0	n.e	
Rhinanthus minor	14	43	1098	1300	-202	-202	0.928	995	1000	-5	-11	n.e	1098	1300	-202	-202	0.127	995	995	0	-3	n.e	

Rhodiola rosea	63	132	1549	1550	-1	-4	n.e	995	1000	-5	-5	n.e	1549	1550	-1	-2	n.e	995	995	0	-1	n.e	
Rubus saxatilis	12	49	1362	1300	62	-114	0.800	1014	1000	14	11	n.e	1362	1300	62	-136	0.222	1014	995	19	25	n.e	
Rumex acetosa	104	203	**1545**	**1350**	**195**	**194**	**0.015**	995	1000	-5	-5	n.e	1545	1340	205	205	1.000	995	995	0	0	n.e	
Salix glauca	76	254	1505	1540	-35	-59	0.570	995	1000	-5	-5	n.e	1505	1540	-35	-51	0.650	995	995	0	0	n.e	
Salix herbacea	164	178	1549	1550	-1	-2	n.e	1178	1000	178	178	0.106	1549	1550	-1	-2	n.e	1178	995	183	181	0.875	
Salix lanata	22	54	1405	1350	55	15	0.175	1158	1000	158	157	0.129	1405	1350	55	12	0.871	1158	995	163	162	0.905	x
Salix lapponum	65	268	1423	1350	73	26	0.166	995	1000	-5	-5	n.e	1423	1300	123	83	0.980	995	995	0	0	n.e	
Salix myrsinites	23	23	1284	1250	34	30	0.220	995	1000	-5	-143	n.e	1284	1200	84	74	1.000	995	995	0	-149	n.e	
Saussurea alpina	119	247	1549	1550	-1	-2	n.e	995	1000	-5	-5	n.e	1549	1550	-1	-2	n.e	995	995	0	0	n.e	
Saxifraga stellaris	13	43	1505	1350	155	110	0.420	**1213**	**1000**	**213**	**213**	**0.011**	1505	1350	155	127	0.852	1213	995	218	218	0.951	x
Selaginella selaginoides	37	91	1483	1360	123	67	0.107	995	1000	-5	-5	n.e	1483	1360	123	61	0.957	995	995	0	0	n.e	
Sibbaldia procumbens	65	96	**1545**	**1360**	**185**	**184**	**0.001**	1013	1010	3	3	n.e	1545	1360	185	185	1.000	1013	1000	13	84	n.e	
Silene acaulis	37	46	1549	1550	-1	-4	n.e	1337	1150	187	170	0.049	1549	1550	-1	-2	n.e	1337	1150	187	162	0.975	
Solidago virgaurea	160	325	1541	1450	91	76	0.139	995	1000	-5	-5	n.e	1541	1450	91	82	0.955	995	995	0	0	n.e	
Stellaria borealis	12	19	1380	1300	80	42	0.245	1001	1000	1	1	n.e	1380	1250	130	86	0.997	1001	1000	1	119	n.e	
Taraxacum sp.	73	150	**1545**	**1360**	**185**	**184**	**0.001**	995	1000	-5	-5	n.e	1545	1360	185	185	1.000	995	995	0	-3	n.e	
Thalictrum alpinum	83	156	1549	1520	29	24	0.166	995	1000	-5	-5	n.e	1549	1520	29	26	0.957	995	995	0	0	n.e	
Trientalis europaea	87	240	1444	1360	84	3	0.484	998	1000	-2	-2	n.e	1444	1360	84	8	0.741	998	995	3	3	n.e	
Trifolium repens	24	65	1126	1300	-174	-174	0.534	995	1000	-5	-6	n.e	1126	1300	-174	-174	0.662	995	995	0	-2	n.e	
Trisetum spicatum	23	44	1512	1540	-28	-54	0.434	1270	1225	45	48	0.274	1512	1540	-28	-47	0.725	1270	1225	45	56	0.983	x
Vaccinium myrtillus	91	208	1444	1360	84	25	0.137	995	1000	-5	-5	n.e	1444	1360	84	34	0.928	995	995	0	0	n.e	
Vaccinium uliginosum	70	296	1418	1475	-57	-104	0.929	995	1000	-5	-5	n.e	1418	1450	-32	-67	0.162	995	995	0	0	n.e	
Vaccinium vitis-idaea	195	453	1549	1540	9	6	n.e	995	1000	-5	-5	n.e	1549	1540	9	8	n.e	995	995	0	0	n.e	
Vahlodea atropurpurea	12	19	**1431**	**1020**	**411**	**343**	**0.015**	1235	1000	235	235	0.065	1431	1000	431	372	0.999	1235	995	240	240	0.913	x
Valeriana sambucifolia	11	70	1356	1300	56	-38	0.502	1001	1000	1	1	n.e	1356	1300	56	-76	0.487	1001	995	6	8	n.e	
Veronica alpina	41	100	**1545**	**1350**	**195**	**194**	**0.002**	**1086**	**1000**	**86**	**83**	**0.000**	1545	1340	205	205	1.000	1086	995	91	90	0.993	x
Viola canina	14	27	1098	1200	-102	-88	0.708	1004	1010	-6	-6	n.e	1098	1200	-102	-62	0.467	1004	1000	4	7	n.e	
Viola epipsila	30	82	1380	1300	80	53	0.245	996	1000	-4	-4	n.e	1380	1300	80	38	0.803	996	995	1	1	n.e	

Table A2: Changes in species optima. Species abb. = Species abbreviations. Numbers in bold = significant species; NA = no values calculated neg. = negative linear response; pos. = positive linear response; null = no response. Occ08/421 = species occurrences in 2008 in 421 plots; Occ43/1118 = species occurrences in Nordhagen's (1943) survey in 1118 plots; opt = estimated optimum; tol = estimated tolerance; CI.low = lower Confidence Interval; CI.high = higher Confidence Interval; opt.diff = estimated change in optima; tol.diff = estimated change in tolerance.

Species	**Species abb.**	**occ08/421**	**occ43/1118**	**opt08**	**tol08**	**CI.low08**	**CI.high08**	**opt43**	**tol43**	**CI.low43**	**CI.high43**	**opt.diff**	**tol.diff**
Achillea millefolium	Achi.mill	25	52	NA	NA	neg.		1017	8	1016	1018	NA	NA
Aconitum lycoctonum	Acon.lyco	**24**	**89**	**1145**	**81**	**1127**	**1160**	**1113**	**52**	**1108**	**1118**	**32**	**30**
Agrostis capillaris	Agro.capi	64	90	NA	NA	neg.		1075	51	1067	1083	NA	NA
Agrostis mertensii	Agro.mert	63	43	NA	NA	pos.		NA	NA	null		NA	NA
Alchemilla alpina	Alch.alpi	24	32	1178	130	1132	1215	NA	NA	null		NA	NA
Alchemilla vulgaris	Alch.vulg	62	158	NA	NA	neg.		1097	70	1086	1105	NA	NA
Andromeda polifolia	Andr.poli	24	94	NA	NA	neg.		NA	NA	neg.		NA	NA
Angelica archangelica	Ange.arch	11	34	1222	96	1194	1253	1197	87	1182	1218	24	9
Antennaria alpina	Ante.alpi	34	48	1451	112	1403	1726	1541	175	1462	1744	-90	-63
Antennaria dioica	Ante.dioc	71	153	NA	NA	pos.		NA	NA	pos.		NA	NA
Anthoxanthum odoratum	Anth.odor	**149**	**268**	**1325**	**196**	**1261**	**1701**	**1175**	**123**	**1158**	**1198**	**150**	**73**
Arctous alpinus	Arct.alpi	17	35	1244	82	1217	1269	1262	108	1237	1297	-18	-26
Arctostaphylos uva-ursi	Arct.uvau	17	109	NA	NA	pos.		1144	115	1125	1164	NA	NA
Astragalus alpinus	Astr.alpi	12	37	NA	NA	null		1108	107	1076	1127	NA	NA
Avenella flexuosa	Aven.flex	**142**	**337**	**1183**	**105**	**1163**	**1201**	**1122**	**101**	**1106**	**1134**	**61**	**5**
Bartsia alpina	Bart.alpi	51	59	NA	NA	null		1202	127	1179	1241	NA	NA
Beckwithia glacialis	Beck.glac	11	49	NA	NA	pos.		NA	NA	pos.		NA	NA
Betula nana	Betu.nana	111	373	1196	174	1117	1252	1126	192	1033	1165	70	-18
Betula pubescens	Betu.pube	51	180	1092	77	1065	1108	1087	44	1083	1092	5	33
Bistorta vivipara	Bist.vivi	175	405	NA	NA	pos.		1303	266	1228	2179	NA	NA
Calamagrostis phragmitoides	Cala.phra	14	41	NA	NA	neg.		1127	68	1119	1137	NA	NA
Campanula rotundifolia	Camp.rotu	78	291	NA	NA	pos.		NA	NA	pos.		NA	NA
Carex bigelowii	Care.bige	127	259	1427	142	1369	1593	1407	184	1346	1537	21	-42
Carex canescens	Care.cane	23	157	NA	NA	neg.		1026	137	689	1075	NA	NA
Carex dioica	Care.dioi	19	112	NA	NA	neg.		1128	75	1119	1137	NA	NA
Carex lachenalii	Care.lach	**44**	**50**	**1501**	**132**	**1428**	**2708**	**1313**	**29**	**1309**	**1318**	**188**	**103**
Carex nigra	Care.nigr	22	115	NA	NA	neg.		1046	117	894	1081	NA	NA
Carex paupercula	Care.paup	16	101	NA	NA	neg.		NA	NA	neg.		NA	NA
Carex rostrata	Care.rost	41	214	NA	NA	neg.		975	138	-15	1047	NA	NA
Carex rupestris	Care.rupe	16	57	NA	NA	pos.		NA	NA	pos.		NA	NA
Carex saxatilis	Care.saxa	12	21	NA	NA	null		1191	59	1180	1203	NA	NA
Carex vaginata	Care.vagi	138	270	1294	185	1241	1492	1180	206	1125	1245	115	-21
Cerastium alpinum	Cera.alpi	33	121	NA	NA	pos.		NA	NA	pos.		NA	NA
Cerastium cerastoides	Cera.cera	29	60	NA	NA	pos.		1337	156	1294	1416	NA	NA
Cerastium fontanum	Cera.font	18	31	NA	NA	neg.		1077	44	1070	1084	NA	NA

Chamerion angustifolium	Cham.angu	35	122	1161	126	1113	1191	1130	80	1120	1140	31	46
Cirsium heterophyllum	**Cirs.hete**	**12**	**43**	**1099**	**45**	**1091**	**1109**	**1126**	**65**	**1118**	**1135**	**-26**	**-20**
Comarum palustre	Coma.palu	32	151	NA	NA	neg.		1070	108	1006	1093	NA	NA
Deschampsia cespitosa	Desc.cesp	67	122	1051	135	784	1103	1102	82	1087	1113	-51	54
Empetrum nigrum	**Empe.nigr**	**130**	**313**	**1256**	**135**	**1227**	**1301**	**1113**	**145**	**1063**	**1137**	**144**	**-10**
Equisetum arvense	Equi.arve	16	106	NA	NA	null		1195	102	1179	1217	NA	NA
Equisetum fluviatile	Equi.fluv	12	16	NA	NA	neg.		NA	NA	neg.		NA	NA
Eriophorum angustifolium	Erio.angu	45	329	NA	NA	neg.		NA	NA	neg.		NA	NA
Euphrasia wettsteinii	**Euph.wett**	**73**	**157**	**1474**	**137**	**1406**	**1861**	**1276**	**142**	**1247**	**1324**	**198**	**-5**
Festuca ovina	Fest.ovin	152	507	NA	NA	pos.		NA	NA	pos.		NA	NA
Festuca rubra	Fest.rubr	34	81	NA	NA	neg.		NA	NA	neg.		NA	NA
Geranium sylvaticum	Gera.sylv	88	186	1114	130	1030	1146	1120	65	1114	1126	-6	65
Geum rivale	Geum.riva	18	66	NA	NA	neg.		1114	57	1108	1121	NA	NA
Gymnocarpium dryopteris	**Gymn.dryo**	**14**	**75**	**1083**	**28**	**1078**	**1089**	**1096**	**54**	**1090**	**1103**	**-13**	**-27**
Hieracium sp.	Hier.sp	138	196	1401	176	1328	1704	NA	NA	pos.		NA	NA
Juncus biglumis	Junc.bigl	14	25	NA	NA	pos.		1371	86	1353	1398	NA	NA
Juncus trifidus	Junc.trif	93	147	1439	102	1402	1547	1459	199	1379	1664	-21	-97
Juniperus communis	Juni.comm	34	139	NA	NA	null		1117	103	1098	1132	NA	NA
Leontodon autumnalis	Leon.autu	43	73	NA	NA	pos.		NA	NA	neg.		NA	NA
Loiseleuria procumbens	Lois.proc	13	20	1274	89	1239	1307	1251	113	1224	1292	23	-24
Luzula confusa	Luzu.conf	15	58	1484	67	1458	1562	NA	NA	pos.		NA	NA
Luzula multiflora	Luzu.mult	73	100	NA	NA	null		NA	NA	neg.		NA	NA
Luzula pilosa	**Luzu.pilo**	**27**	**110**	**1065**	**40**	**1055**	**1077**	**1091**	**39**	**1087**	**1095**	**-26**	**1**
Luzula spicata	Luzu.spic	57	164	1479	80	1447	1577	NA	NA	pos.		NA	NA
Melampyrum sylvaticum	Mela.sylv	24	122	1107	52	1098	1116	1095	53	1089	1100	12	0
Myosotis decumbens	Myos.decu	16	85	NA	NA	neg.		1114	52	1109	1119	NA	NA
Nardus stricta	Nard.stri	13	51	NA	NA	neg.		NA	NA	neg.		NA	NA
Omalotheca norvegica	**Omal.norv**	**32**	**100**	**1227**	**145**	**1182**	**1289**	**1132**	**82**	**1122**	**1144**	**94**	**63**
Omalotheca supina	Omal.supi	64	82	NA	NA	pos.		1310	110	1287	1342	NA	NA
Oxycoccus sp.	Oxyc.sp	14	77	NA	NA	neg.		NA	NA	neg.		NA	NA
Oxyria digyna	Oxyr.digy	38	29	NA	NA	pos.		1347	120	1317	1393	NA	NA
Pedicularis lapponica	Pedi.lapp	29	128	1219	112	1190	1253	1164	135	1141	1194	55	-23
Pedicularis oederi	Pedi.oede	25	51	NA	NA	pos.		1390	140	1352	1453	NA	NA
Pedicularis sceptrum-carolinum	Pedi.scep	11	19	1015	14	1010	1020	NA	NA	neg.		NA	NA
Phleum alpinum	Phle.alpi	59	139	NA	NA	null		1136	176	1064	1176	NA	NA
Phyllodoce caerulea	Phyl.caer	55	27	1335	117	1298	1394	1278	75	1261	1299	57	41
Poa alpina	Poa.alpi	13	119	NA	NA	pos.		NA	NA	null		NA	NA
Poa pratensis	Poa.prat	23	129	NA	NA	neg.		NA	NA	neg.		NA	NA
Potentilla crantzii	Pote.cran	62	146	NA	NA	pos.		NA	NA	null		NA	NA
Pulsatilla vernalis	Puls.vern	32	93	NA	NA	pos.		NA	NA	pos.		NA	NA
Pyrola minor	**Pyro.mino**	**51**	**133**	**1167**	**106**	**1142**	**1189**	**1110**	**110**	**1082**	**1127**	**58**	**-4**
Ranunculus acris	Ranu.acri	98	208	NA	NA	neg.		1116	108	1095	1131	NA	NA
Rhinanthus minor	Rhin.mino	14	43	1056	45	1037	1073	1086	100	1040	1106	-30	-55
Rhodiola rosea	Rhod.rose	63	132	1390	160	1325	1627	1409	194	1342	1575	-20	-34
Rubus saxatilis	Rubu.saxa	12	49	1098	80	1064	1117	1121	57	1115	1128	-24	23
Rumex acetosa	Rume.acet	104	203	1191	126	1161	1218	1168	124	1149	1191	23	1
Salix glauca	Sali.glau	76	254	1250	118	1222	1287	1271	157	1239	1325	-21	-39
Salix herbacea	Sali.herb	164	178	1574	140	1454	2939	NA	NA	pos.		NA	NA
Salix lanata	**Sali.lana**	**22**	**54**	**1280**	**80**	**1249**	**1306**	**1194**	**92**	**1178**	**1215**	**86**	**-13**
Salix lapponum	Sali.lapp	65	268	1117	169	791	1166	1080	107	1037	1099	37	62
Salix myrsinites	**Sali.myrs**	**23**	**23**	**1077**	**98**	**989**	**1106**	**1197**	**55**	**1186**	**1209**	**-121**	**43**
Saussurea alpina	Saus.alpi	119	247	NA	NA	pos.		NA	NA	pos.		NA	NA
Saxifraga stellaris	Saxi.stel	13	43	1330	91	1290	1377	NA	NA	null		NA	NA
Selaginella selaginoides	Sela.sela	37	91	NA	NA	null		1128	178	1022	1170	NA	NA

Sibbaldia procumbens	Sibb.proc	65	96	1472	156	1391	1992	1318	160	1277	1394	155	-4
Silene acaulis	Sile.acau	37	46	1474	66	1451	1531	NA	NA	pos.		NA	NA
Solidago virgaurea	Soli.virg	160	325	1198	115	1177	1220	1159	124	1141	1179	39	-9
Stellaria borealis	Stel.bore	**12**	**19**	**1247**	**104**	**1213**	**1287**	**1122**	**85**	**1108**	**1137**	**125**	**19**
Taraxacum sp.	Tara.sp	**73**	**150**	**1351**	**192**	**1278**	**1892**	**1158**	**178**	**1108**	**1204**	**193**	**14**
Thalictrum alpinum	Thal.alpi	83	156	NA	NA	pos.		1225	142	1199	1268	NA	NA
Trientalis europaea	Trie.euro	87	240	1141	92	1121	1156	1116	98	1099	1128	26	-6
Trifolium repens	Trif.repe	24	65	1061	40	1051	1074	1069	40	1063	1076	-8	-1
Trisetum spicatum	Tris.spic	**23**	**44**	**1405**	**80**	**1379**	**1462**	**1332**	**61**	**1320**	**1348**	**74**	**19**
Vaccinium myrtillus	Vacc.myrt	**91**	**208**	**1174**	**101**	**1154**	**1193**	**1114**	**107**	**1092**	**1129**	**61**	**-6**
Vaccinium uliginosum	Vacc.ulig	70	296	1148	135	1087	1179	1157	154	1128	1186	-9	-19
Vaccinium vitis-idaea	Vacc.viti	195	453	1273	177	1228	1391	NA	NA	pos.		NA	NA
Vahlodea atropurpurea	Vahl.atro	12	19	1347	67	1322	1377	NA	NA	neg.		NA	NA
Valeriana sambucifolia	Vale.samb	11	70	NA	NA	neg.		1135	65	1128	1144	NA	NA
Veronica alpina	Vero.alpi	**41**	**100**	**1454**	**169**	**1366**	**2258**	**1250**	**155**	**1217**	**1313**	**204**	**14**
Viola canina	Viol.cani	14	27	1065	28	1059	1075	1080	41	1075	1087	-15	-12
Viola epipsila	Viol.epip	30	82	NA	NA	neg.		1138	73	1130	1148	NA	NA

Paper II

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Fine-scale changes in vegetation composition in a boreal mire over 50 years

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Summary

1. In the face of a rapidly changing environment, long-term studies provide important insights into patterns of vegetation and processes of change, but long-term studies are rare for many ecosystems.

2. We studied recent vegetation changes at a fine scale in a *Sphagnum*-dominated bog in south Sweden by resurveying part of the bog 54 years after the original phytosociological survey. We used an indirect approach to identify changes in vegetation composition in relation to environment because of a lack of permanent sampling units. By applying a weighted averaging technique, we calculated relative changes in species optimum values for different environmental gradients as represented by indicator values for light, temperature, pH, moisture and nutrients.

3. Species composition of the mire vegetation has changed significantly over the past five decades, as indicated by significant changes in species frequencies and species optima for the gradients examined. Species with lower indicator values for moisture and light and higher indicator values for nutrients have become more frequent on the mire. In particular, species of trees and dwarf shrubs increased in frequency, whereas typical mire species decreased (e.g. *Trichophorum cespitosum* (L.) Hartm.) or disappeared from the study site (e.g. *Scheuchzeria palustris* L.).

4. *Synthesis*. Composition of the mire vegetation is found to be dynamic at different temporal and spatial scales. Increased air temperature and nutrient availability in south Sweden over the past few decades may have augmented productivity (e.g. tree growth), resulting in drier and shadier conditions for several species. This study successfully demonstrated the applicability of an indirect approach for detecting long-term vegetation change at a fine scale. This approach is an effective way of using historic and modern phytosociological data sets to detect vegetation and environmental change through time.

Key-words: environmental change, indicator values, non-permanent plots, ombrotrophic bog, plant population and community dynamics, productivity, species optimum, *Sphagnum*, vegetation dynamics, weighted averaging

Introduction

The structure and composition of vegetation are constantly changing, and the driving factors may be both internal (e.g. succession) and external (e.g. environmental change). Different aspects of human activity have become increasingly important as drivers of ecosystem changes during recent decades, either directly through habitat modification or indirectly through, for example, atmospheric pollution (Vitousek *et al.* 1997; Lee 1998; Walther *et al.* 2002). Species distribution patterns and floristic composition in boreal *Sphagnum*-dominated mires are predominantly determined by gradients in acidity, fertility and depth to the water-table (Malmer 1986; Wheeler & Proctor 2000; Økland, Økland & Rydgren 2001; Sjörs & Gunnarsson 2002; Bragazza, Rydin & Gerdol 2005). Changes in any of these important gradients will usually cause changes in the vegetation of boreal mires in addition to ongoing changes due to autogenic processes. In comparison with other terrestrial ecosystems, mires have widely been considered as rather stable ecosystems that show slow changes in vegetation over time (Backéus 1972; Svensson 1988; Malmer, Svensson & Wallén 1997; Rydin & Barber 2001). However, relatively large responses of mire vegetation to human-induced changes in the environment have been documented in several recent studies (e.g. Lee, Baxter & Emes 1990; Chapman & Rose 1991; Hogg, Squires & Fitter 1995; Gunnarsson, Håkan & Hugo 2000;

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Gunnarsson, Malmer & Rydin 2002; Gunnarsson & Flodin 2007; van der Linden *et al.* 2008; Mälson, Backéus & Rydin 2008).

Climate change is one factor that may have a large effect on vegetation composition in mires. In addition to the effects on broad-scale species distributions, temperature and precipitation may affect the depth of the water-table, thereby having an effect locally on mire vegetation (Weltzin *et al.* 2000; van der Linden *et al.* 2008; Murphy, Laiho & Moore 2009). Precipitation patterns and evaporation and their interaction with nitrogen input from the atmosphere are also important (Tahvanainen, Sallantaus & Heikkilä 2003; Bragazza, Rydin & Gerdol 2005; Gerdol *et al.* 2007; Gunnarsson & Flodin 2007). Ombrotrophic bogs are naturally nutrient-poor habitats (Backéus 1985) and the nutrient balance strongly depends on atmospheric deposition (Bragazza *et al.* 2004). Increased nutrient availability due to atmospheric nitrogen pollution will therefore be expected to have a pronounced effect on acidic and low-productivity peat bogs. It may both enhance plant productivity and cause severe alterations in vegetation structure and composition by shifting dominance ratios in favour of nitrophilic species of high competitive ability (e.g. Gunnarsson & Rydin 2000; Berendse *et al.* 2001; Tomassen *et al.* 2003; Bragazza *et al.* 2004; Pearce & van der Wal 2008). The higher nitrogen deposition in the last 50 years has contributed to an increased abundance of vascular plants (typically trees and shade-tolerant dwarf shrubs) in bogs in central and south Sweden as well as adverse effects on the productivity and vitality of several of the dominant *Sphagnum* species (e.g. Gunnarsson, Håkan & Hugo 2000; Gunnarsson & Rydin 2000; Ohlson *et al.* 2001; Gunnarsson, Malmer & Rydin 2002; Malmer *et al.* 2003; Gunnarsson & Flodin 2007; Wiedermann *et al.* 2009).

Whenever a species responds to an environmental change, it does so individualistically (Chapin & Shaver 1985; Levin 1992; Walther *et al.* 2002; Le Roux & McGeoch 2008). By tracking a change in environment individualistically, species will change their associates (co-occurring species) over time, because species differ both in their response time and in their tolerance to an environmental change. A stable environment is thought to result in relatively stable vegetation with a steady-state composition (Zobel 1988), whereas vegetation that is affected by large environmental changes will experience large changes in vegetation composition. The temporal and spatial scale of a study will affect the degree of vegetation change observed and which environmental driver is found to be important for changes in vegetation composition and diversity.

Re-investigating historical studies provides a unique opportunity to study vegetation change over several decades. Most of the resurveys in boreal mire vegetation of northern Europe have re-sampled permanent plots to identify decadal (10–50 years) vegetation change by focusing on changes in species distributions, frequencies and composition (e.g. Backéus 1972; Chapman & Rose 1991; Hogg, Squires & Fitter 1995; Hedenäs & Kooijman 1996; Gunnarsson, Håkan & Hugo 2000; Gunnarsson, Malmer & Rydin 2002). These studies show that changes in mire vegetation are often found in association with eutrophication (increase of nitrogen-demanding species) and drying (tree-cover increase). Numerous high-quality historic studies are available that are based on fine-scale phytosociological vegetation records, but a re-investigation of these types of studies is rare and often thought to be impossible as many of these studies lack plot-specific environmental measurements and permanently marked sampling units. The use of these data sets for the identification of long-term vegetation change and exploring potential driving forces behind this change is a challenge, but if we can use them for this purpose, much data would become available for studying long-term vegetation dynamics.

In this paper, we present the results of a re-sampling of the vegetation of Åkhult mire in southern Sweden. The original phytosociological study described in detail the vegetation on this mire in 1954 (Malmer 1962). Malmer's study consists of two types of vegetation analysis. One is the mapping of species distributions based on broad-scale grid cells, which are possible to relocate; the other describes the vegetation types on a fine scale. In 1997, a re-mapping of the vegetation based on the semi-permanent broad-scale grid cells was performed by Gunnarsson, Malmer & Rydin (2002), who compared species distribution patterns and species frequencies after about 40 years. In the present study, we document fine-scale changes in the vegetation types in the same mire over more than 50 years using Malmer's phytosociological vegetation records for comparison. We focus on relative changes in species optima along important environmental gradients to identify changes in mire vegetation composition and to discuss the driving forces causing these changes. We also investigate if changes in species frequencies in the fine-scale study are comparable with the changes found for the broad-scale grid.

Materials and methods

INVESTIGATION AREA

Åkhult mire is in Småland, southern Sweden (57°10′ N, 14°30′ E), and covers a total area of 1.1 km^2 at an altitude of 230 m a.s.l. The bedrock is Växjö granite. Climate data covering the last century are available from the meteorological stations closest to the Åkhult mire, namely Lannaskede and Nävelsjö, about 38 km NE of the mire (Swedish Meteorological and Hydrologic Institute; http://www.smhi.se). The mean annual air temperature is about 6 °C (1903–2008) and annual precipitation is 650 mm (1901–2008; see Appendix S1.1 in Supporting Information). Both climatic measures were lower in the 10-year period before the first inventory (1944–54: 5.86 °C, 668 mm) than in the corresponding period before our resurvey (1998–2008: 6.55 °C, 745 mm). The landscape around the mire is dominated by forests that are mainly composed of Norway spruce (*Picea abies* (L.) H. Karst.), with some Scots pine (*Pinus sylvestris* L.), pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.). Since the 1960s, the region has been exposed to high loads of wet deposition of nitrogen, which increased from 0.48 g m^{-2} year^{-1} (1947–62) to a maximum of 0.72 g m^{-2} year^{-1} (1962–76; Malmer & Wallén 1980), decreasing to 0.46 g m^{-2} year^{-1} in 1983–2008 (0.44 g m^{-2} year^{-1} from 1998 to 2008; Swedish Environmental Research Institute, http://www.ivl.se; see Appendix S1.2). This temporal trend is similar for sulphur, with wet deposition increasing from 0.96 g m^{-2} year^{-1} (1947–62) to 1.28 g m^{-2} year^{-1} (1962–76) and declining to 0.68 g m^{-2} $year^{-1}$ from 1983 to 2008 (0.43 g m^{-2} $year^{-1}$ from 1998 to 2008). In comparison with the deposition rates in 1947–62 and 1962–76 (both around 1 g m^{-2} $year^{-1}$), calcium deposition was low between 1983 and 2008 (0.16 g m^{-2} $year^{-1}$). Apart from cattle grazing along the mire margin until around 1950, clear cutting in large parts of the surrounding forests around 1970 (Gunnarsson, Malmer & Rydin 2002), and some peat cutting in a part of the mire not used in this study or by Malmer in 1954 (personal observations), the mire has not been directly used by humans for at least 50 years.

The vegetation of Åkhult mire was described in detail by Malmer (1962). His study includes two types of vegetation analyses conducted in different areas within the mire. In one of these areas, the Stattute area, he investigated both species distribution patterns and vegetation types. The Stattute area (560 × 300 m), whose vegetation was re-investigated by us in 2008, is in the north-eastern part of the mire. It can be characterized as a wide topogenous fen, which is surrounded by spruce forest on mineral soil and gradually turns into an ombrotrophic bog towards the south-west. The fen and a row of brook pools are fed by groundwater coming from the north of the study site. The arithmetic mean pH of four samples in the Stattute area was 4.4 in 2008.

RE-SAMPLING OF VEGETATION DATA

Malmer's (1962) studies on mire vegetation within the Stattute area were conducted between 1952 and 1955 with the aim of mapping species distributions and of describing mire vegetation types using a phytosociological approach. The geographical distribution of vascular plants and bryophytes was mapped using a grid cell of 20 × 20 m (for a detailed description see Malmer 1962; chapter 4). This size of grid cell includes fine-scale topographic variation in hummocks, lawns, carpets and mud-bottoms within each grid cell. At this scale, Malmer recorded presence or absence of each species. Seven of the most common species were not mapped. This part of the 1954 inventory was resurveyed in 1997 by Gunnarsson, Malmer & Rydin (2002).

The second part of Malmer's study consisted of a detailed phytosociological description of the vegetation (vascular plants, bryophytes and lichens) in different areas of Åkhult mire. In this study, we only used samples from the Stattute area (see all tables on pp. 242–276 and tables B–F on pp. 286–290 in Malmer 1962). For this part of the vegetation analysis, Malmer used small squares of 0.5 × 0.5 m, which ensures a high degree of uniformity within the plot. In the Stattute area, small square plots were placed around different measuring points for water level, which were relatively evenly distributed over the mire expanse area (see map I.1 in Malmer 1962 for more details). Around these points, six vegetation types (called series) were distinguished and surveyed with small plots if they were present. In the mire margin, small square plots were placed in the different vegetation types found. Species abundances were estimated following the Hult–Sernander–Du Rietz abundance scale (Du Rietz 1921). In the Stattute area, Malmer recorded the vegetation in the two lower layers (field layer and ground layer) from 833 plots, which can be considered a very intense sampling of the 560 × 300 m area comprising the Stattute area. The small squares were not permanently marked in 1954 and therefore impossible to relocate. In July and August 2008 we re-recorded the mire vegetation (vascular plants and bryophytes) of the Stattute area by sampling in a stratified random way, and otherwise using the same methods and restrictions as those described in Malmer (1962, chapter 5). Sampling stratification was achieved by covering the whole area and covering the variation of vegetation types in the different areas. The same abundance estimates as in Malmer (1962) were used. The total number of plots sampled in 2008 is 278.

To test the two data sets for comparability, we investigated the range of variation in vegetation in both data sets using correspondence analysis (Legendre & Legendre 1998; see Appendix S2.1). This analysis found a similar distribution of sampling units of both data sets without any obvious outlier plots, indicating that a data set comparable to the 1954 data set was sampled in 2008 (see Appendix S2.1).

TAXONOMIC NOTES

The nomenclature follows Lid (2005) for vascular plants and Smith (2004) for bryophytes. Frahm & Frey (2003) was used for additional bryophytes. Since 1950, there have been several revisions in the taxonomy and nomenclature of the genus *Sphagnum*. To achieve a comparable taxonomy to the one that Malmer used, merging of some species was necessary. *Sphagnum rubellum* and *S. nemoreum* have been unified to *S. capillifolium*. *Sphagnum inundatum* and *S. auriculatum* have been treated together as *S. denticulatum*. Liverworts and lichens were not included in the re-sampling because they were present in low abundance and the different species could not be detected reliably with the available expertise.

STATISTICAL ANALYSES

Species optima for environmental gradients

The lack of permanently marked sampling units and plot-specific environmental measurements in the original study by Malmer prevents direct temporal comparisons. We therefore used an indirect approach to identify long-term vegetation change at a fine scale with regard to the potential drivers causing changes in vegetation composition. This was done by calculating the relative change of the species' realized optimum value for different environmental gradients using Hill's version of the Ellenberg indicator values for vascular plants (Hill *et al.* 2007) and mosses (Hill *et al.* 2000) as representatives of environmental gradients for light, soil moisture, pH and nutrients. For temperature indicator values we used Ellenberg *et al.* (1991).

Because of individualistic responses of species to environmental change, a change in environment may cause a species to appear with different associates. For instance, if pH has changed, some species will tolerate the change and stay 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 highly likely that the average pH-indicator value for the new associate species is different from the average pH-indicator value of the previous species. To detect such changes in species composition we compared the indicator value for co-occurring species of a focus species today and in the previous sampling, and used changes in the indicator value to indicate important drivers of community dynamics. Based on a weighted averaging technique, four steps were taken to estimate if a species had changed its associates in a non-random way with respect to the different indicator values (Fig. 1). The four main steps were: (i) estimate sample scores; (ii) standardize the two data sets; (iii) estimate changes in realized species scores (species optima); and (iv) test if the changes are random or not.

1. The *sample score* for an indicator value was calculated for each sampling unit of both inventories by weighted averaging (weighted on species abundance) of the species' indicator values present in the samples (see Goff & Cottam 1967; ter Braak & Barendregt 1986; Diekmann 2003; Hill *et al.* 2007).

2. The weighted average species score (optimum) will, to a certain extent, be dependent on the distribution of samples (ter Braak & Looman 1986), which may be a result of differential sampling during the

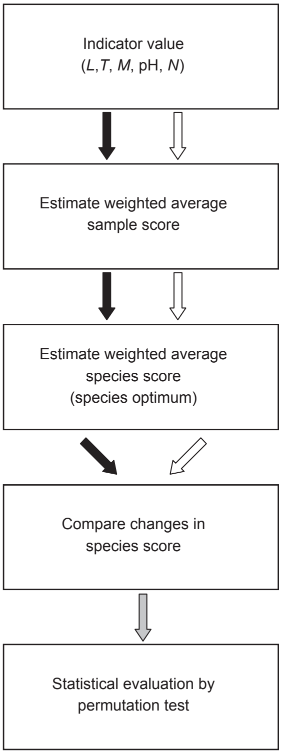

Fig. 1. Scheme for calculating change in species optima for different environmental gradients (L = light, T = temperature, M = moisture, pH, N = nutrients). Black arrows represent the species of interest in time 1, white arrows the comparison species in time 2 and the grey arrow the estimated change in the species optimum over the time period considered.

two time periods. To secure a similar distribution of the sample scores for the two inventories, the data sets were pruned prior to estimating the species optimum. This pruning was done separately for the different indicator values and in three steps. (i) Remove samples with extreme values of sample scores (both maxima and minima) for the two inventories. (ii) All outliers were removed from the data sets by deleting all samples that were outside the common remaining range for the two inventories. The result was two data sets with similar minima and maxima for the indicator values of interest. (iii) Based on this pruning, the sets of sample scores were divided into three equal sections along the indicator-value gradient. The relative number of samples in each section was equalized by randomly removing samples from the inventory with the most samples. The result is two data sets with equal range and frequency distribution of samples along the environmental gradient.

3. From the two pruned data sets, the species score for an indicator value (= *species optimum value*) was calculated for the two inventories separately. This was done by finding the average of the sample scores weighted by the species abundance. The estimated species optimum values of the two inventories were compared by simple subtraction of the 'old' from the 'new' value, and were divided by the standard deviation of sample scores of both inventories (= relative change in species optimum). This whole procedure was done separately for each species, and the species under study was excluded from the calculation of the initial sample score (1).

4. A restricted permutation test was used to test whether observed changes in the species optimum are greater than expected by random. For testing, samples from the two pruned data sets were randomized between time periods with the restriction that it can only be swapped within each of the three sections along an indicator value gradient as defined above. To avoid any bias in the random removal of samples during the pruning process both the observed (influenced by the random removal of samples in the pruning process) and randomized change was estimated in each permutation. An approximate P-value related to the change in the optimum value is given by counting the number of times the observed changes were larger than or equal to the randomized change. We chose the critical P-value of 0.05 and ran 1000 permutations for each species and for each indicator value.

These four steps were made for all species occurring in more than five plots in both time periods, reducing the total number of species of both data sets together from 85 to 47.

Species frequencies and richness

We calculated species frequencies of occurrence in the fine-scale plots for both the 1954 and the re-sampled data sets. This was done by relating the number of plots in which a species occurred to the total number of plots separately for the two inventories. For the comparison, frequencies in 1954 were subtracted from frequencies in 2008. Such a comparison is dependent on the sampling structure of the two inventories. If one vegetation type was sampled more in one inventory than in the other, this would have a large influence on the results. Significance levels for frequency changes were therefore tested by a restricted permutation test, randomizing the inventory identity and restricting the randomizations on the different vegetation types as identified by cluster analysis. For the cluster analysis, Ward's hierarchical clustering was applied including all species and both inventories in the same analysis, with the Bray & Curtis (1957) distance as the dissimilarity measure. We identified six clusters of sample units. When randomizing the data, the plots were shuffled between the two sampling times only within the same cluster. P-values were derived by counting the number of permutations (from 999 permutations) where the change in species frequency (absolute value) was larger or equal to the observed value. For this analysis, species occurring in more than five plots in the total data set were analysed (70 species).

We contrasted the results of our fine-scale study to those found by Gunnarsson, Malmer & Rydin (2002), who re-investigated broad-scale species distributions in the same area. In the broad-scale study, changes in species frequencies in permanent grid cells of 20 × 20 m were calculated for 245 plots between 1954 and 1997. We compared observed frequency changes between the studies using a Spearman rank-order correlation test. This analysis was based on the 70 species for which frequency changes were calculated in our study. For 8 of these 70 species no information about frequency change was given in Gunnarsson, Malmer & Rydin (2002), reducing the data set to 62 species for the comparison between broad-scale and fine-scale changes in species frequencies.

We calculated mean number of species per plot for both inventories. Changes in these were tested for statistical significance using the same randomization procedure as in the analysis of change in species frequencies.

All statistical analyses were conducted using R, version 2.11.1 (R Development Core Team 2010) and R package *vegan*, version 1.17.2 for ordination and classification (Oksanen *et al.* 2010).

Results

CHANGES IN SPECIES OPTIMA

Of 47 species tested for shifts of their optimum value, 36 species (21 vascular plants, 15 mosses) showed a significant change for at least one of the environmental gradients examined (Table 1). The numbers of species which showed significant changes along an environmental gradient are: 21 (temperature), 16 (pH), 14 (soil moisture), 13 (nutrients) and 10 (light).

Of these species, significant changes in the species' realized optimum predominantly towards one direction (positive or negative change) are for lower moisture values (86%), higher nutrient values (77%) and lower light values (67%). Predominant significant optimum change towards higher or lower indicator values is weak for the temperature gradient, with lower temperature values identified for 57% of the species (Table 1). For the pH gradient no predominant direction of optimum changes is found.

CHANGES IN SPECIES RICHNESS AND FREQUENCY

The total number of species (vascular plants and mosses) found in the Stattute area on the fine-scale plot basis was 75 species in both 1954 and 2008 (39 vascular plants and 36 mosses each). Of these, 10 species were found only in 2008 and 10 species were found only in 1954 (Table 1). Mean species number per plot has increased significantly from 8.2 species in 1954 to 9.1 species in 2008 ($P = 0.001$).

From the 70 species tested for changes in frequency, 30 (43%) showed a statistically significant change in frequency between the two inventories. Of these, 20 species had significantly increased in frequency (Fig. 2), including every tree species (*Betula pubescens*, *Picea abies*, *Pinus sylvestris*), a conspicuous number of dwarf shrubs (*Calluna vulgaris*, *Empetrum nigrum*, *Vaccinium* spp.) and sedges (e.g. *Carex nigra*, *Eriophorum* spp.) and several *Sphagnum* species (e.g. *S. pulchrum*, *S. papillosum*). In contrast, 10 species showed a statistically significant decrease (e.g. *Trichophorum cespitosum*, *Rhynchospora alba*, *Drosera* spp., *Carex limosa*) or were not re-found at all (e.g. *Scheuchzeria palustris*, *Rhynchospora fusca*, *Carex canescens*).

A Spearman rank correlation test found a statistically significant positive correlation between changes in species frequencies noted in the broad-scale study by Gunnarsson, Malmer & Rydin (2002) and our fine-scale study ($r_S = 0.67$, $P < 0.001$; Fig. 3). Of the 62 species included in this comparison, 30 species in the fine-scale study and 36 species in the broad-scale grid significantly changed in frequency. Changes in the same direction (significant and non-significant) in both studies were found for 43 species (24 in positive and 19 in negative direction). Sixteen species significantly changed in the same direction in both studies; eight species changed their frequency in positive and eight species in negative directions. Opposite trends (significant change in opposite direction) were identified for one species (*Carex panicea*). However, the result of the latter species may be influenced by its few occurrences as it occurred in only five plots in 2008 and was not recorded at all in the fine-scale plot survey in 1954.

Discussion

Our fine-scale comparison of mire vegetation in the Stattute area of the Åkhult mire found that species optimum values for different environmental gradients had changed significantly since 1954 for the majority of the tested species. A change in a species' optimum value indicates a shift in species composition at a fine scale, as the species of interest was found in combination with species of a different indicator value for the environmental factor in 2008 compared with the 1954 survey. The changes in species composition indicated by changes in optimum values first of all confirm that species respond individualistically to an environmental change shown for species in different vegetation types (see e.g. review by Walther *et al.* 2002; Le Roux & McGeoch 2008). Significant optimum changes were found for species in the Stattute area regardless of vegetation type and species commonness, reflecting an overall turnover in species composition independent of vegetation type.

Our fine-scale study found that the total number of species in the Stattute area was constant, but that species number per plot had increased and species frequencies had changed significantly. Several species, which were, however, present outside the Stattute area in the Åkhult mire, were not re-found or found for the first time within the Stattute area on the basis of fine-scale plots, again indicating a dynamic vegetation over the last 54 years. Even though a species changes its frequency, it does not necessarily change its companion species and thus its optimum if it just becomes more (or less) common in the vegetation type it used to be found in. However, species that show a change in frequency may have changed associates too, by expanding into new vegetation types or out-competing other species (e.g. *Sphagnum pulchrum*, *S. papillosum*) or retreating from habitats in which they had a tenuous hold (e.g. *Trichophorum cespitosum*, *Rhynchospora* spp.).

The observed changes in mire vegetation composition and species frequencies, as well as the observation of species' individualistic responses are consistent with other studies on vegetation dynamics described for several mires in northern Europe (e.g. Chapman & Rose 1991; Hogg, Squires & Fitter 1995; Gunnarsson, Håkan & Hugo 2000; Nordbakken 2001; Gunnarsson, Malmer & Rydin 2002).

We had expected discrepancies between the findings of our fine-scale study and the broad-scale study of Gunnarsson, Malmer & Rydin (2002), as any determination of vegetation change (composition and structure, species co-occurrence patterns, patterns of diversity) is scale-dependent (Levin 1992; Dengler, Lobel & Dolnik 2009). Thus, drivers of change in *Sphagnum*-dominated peatlands may range from broader to finer scales resulting in different patterns of change (Lang *et al.* 2009). Scale dependency may be most obvious for species of low frequency at a fine scale, because they may erroneously be

Table 1. Species frequency of occurrence in plots in the Stattute area in 1954 ($n = 833$) and 2008 ($n = 278$), relative changes in frequency of occurrence from 1954 to 2008 and from 1954 to 1997 (see broad-scale study of Gunnarsson, Malmer & Rydin 2002) and changes in species optimum for different environmental gradients (indicator values for light L, temperature T, soil moisture M, pH and nutrients N). $^{*}P \le 0.05$, $^{**}P \le 0.01$, $^{***}P \le 0.001$; n.s., not significant; n.p., statistical test not performed. Significant change values are printed in bold.

	Frequency (%)		Frequency change		Change in species optimum				
					1954–2008				
	1954	2008	1954–2008	1954–1997	*L*	*T*	*M*	pH	*N*
Agrostis canina	1.0	1.1	0.1n.s.	**−4.5****					
Andromeda polifolia	56.8	61.9	5.1n.s.		−0.04n.s.	0.05n.s.	**−0.19****	0.04n.s.	0.03n.s.
Betula pubescens	1.6	6.8	**6.4*****	**44.1*****	0.12n.s.	0.07n.s.	0.07n.s.	0.02n.s.	0.12n.s.
Calluna vulgaris	34.8	46.0	**11.2*****		0.21n.s.	**0.71*****	−0.10n.s.	0.05n.s.	−0.04n.s.
Carex canescens	0.8	0.0	−0.8n.s.	0.4n.p.					
Carex echinata	3.2	1.4	−1.8n.s.	**−20.0*****					
Carex lasiocarpa	11.9	11.5	−0.4n.s.	**−13.9*****	**−0.49***	−0.13n.s.	−0.25n.s.	−0.02n.s.	0.42n.s.
Carex limosa	14.4	1.8	**−12.6*****	**−34.3*****					
Carex nigra	0.8	8.3	**7.4*****	−1.2n.s.	−0.58n.s.	−0.15n.s.	−1.25n.s.	−0.37n.s.	−0.57n.s.
Carex panicea	0.0	1.8	**1.8****	**−6.5*****					
Carex pauciflora	7.6	0.7	**−6.8*****	**−19.6*****					
Carex rostrata	4.9	7.9	3.0n.s.	5.3n.s.	0.51n.s.	**0.80****	−0.55n.s.	**−0.61***	**−1.43*****
Comarum palustre	2.3	2.5	0.2n.s.	−3.3n.s.	0.48n.s.	**0.56***	−0.32n.s.	**0.75***	0.06n.s.
Drosera longifolia	8.3	4.0	**−4.3****	**−42.0*****	**−1.10*****	−0.16n.s.	**0.32***	**1.01*****	**1.04*****
Drosera intermedia	17.5	5.4	**−12.1*****	**−40.0*****	−0.35n.s.	**−0.59*****	0.08n.s.	0.25n.s.	0.27n.s.
Drosera rotundifolia	50.9	55.4	4.5n.s.		0.05n.s.	**0.17****	0.05n.s.	**0.19*****	0.09n.s.
Empetrum nigrum	8.4	11.9	**3.5***		−0.28n.s.	**0.88*****	**−0.96*****	0.13n.s.	0.39n.s.
Equisetum fluviatile	0.5	0.4	−0.1n.s.	**−6.9*****					
Erica tetralix	8.0	11.9	3.8n.s.	**11.0***	0.09n.s.	−0.12n.s.	0.01n.s.	**0.28****	−0.01n.s.
Eriophorum angustifolium	47.2	60.1	**12.9****	**15.1*****	−0.02n.s.	−0.05n.s.	−0.09n.s.	**−0.18***	−0.13n.s.
Eriophorum vaginatum	44.4	55.4	**11.0*****		**0.27***	**0.42*****	0.07n.s.	0.16n.s.	0.02n.s.
Galium palustre	0.5	0.0		0.0n.p.					
Lycopodiella inundata	1.1	0.4	−0.7n.s.	**−7.3*****					
Menyanthes trifoliata	19.6	18.0	−1.6n.s.	−4.1n.s.	−0.17n.s.	0.11n.s.	−0.05n.s.	−0.10n.s.	0.12n.s.
Narthecium ossifragum	41.1	44.2	3.2n.s.	4.5n.s.	**0.17****	−0.11n.s.	0.00n.s.	0.11n.s.	−0.06n.s.
Oxycoccus palustris	62.8	77.7	**14.9*****		−0.04n.s.	0.03n.s.	−0.06n.s.	**0.20****	**0.16***
Picea abies	0.0	2.5	**1.8****	6.5n.p.					
Pinus sylvestris	1.4	21.2	**2.9***	**34.3*****	0.03n.s.	0.13n.s.	−0.19n.s.	−0.28n.s.	−0.42n.s.
Potentilla erecta	0.6	0.7	0.1n.s.	2.9n.s.					
Rhynchospora alba	46.9	26.6	**−20.3*****	**−22.4*****	**0.29****	**−0.40*****	−0.07n.s.	**−0.42*****	**−0.29*****
Rhynchospora fusca	2.8	0.0	**−2.8****	**−10.6*****					
Rubus chamaemorus	5.9	6.5	0.6n.s.	**−11.0***	−0.19n.s.	**1.03*****	**−0.82***	**0.45***	**0.55***
Salix aurita	0.0	1.1		0.4n.s.					
Salix repens	8.5	5.4	−3.1n.s.	−9.4n.s.	−0.34n.s.	**−0.48***	**−0.58*****	−0.02n.s.	−0.13n.s.
Salix rosmariniifolia	0.0	0.4							
Scheuchzeria palustris	17.6	0.0	**−17.6*****	−41.6n.p.					
Trichophorum cespitosum	36.3	14.0	**−22.2*****	**−10.6****	**−0.21***	0.04n.s.	**−0.39*****	−0.10n.s.	**0.23*****
Utricularia intermedia	4.7	2.2	−2.5n.s.	**−14.3*****	−0.90n.s.	−0.34n.s.	**−1.03***	**−1.35*****	−0.53n.s.
Utricularia minor	4.7	6.1	1.4n.s.	**−11.8*****	−0.61n.s.	−0.25n.s.	**−1.61*****	**−1.06*****	**−0.97*****
Vaccinium myrtillus	0.8	4.0	**3.1****	**4.5***	0.09n.s.	0.20n.s.	−0.49n.s.	0.18n.s.	0.94n.s.
Vaccinium uliginosum	0.4	4.7	**4.3*****	**4.9***					
Vaccinium vitis-idaea	1.1	3.6	2.5n.s.	3.3n.s.	−0.67n.s.	0.44n.s.	−0.59n.s.	0.80n.s.	**1.37***
Viola palustris	1.2	0.7	−0.5n.s.	1.6n.s.					
Aulacomnium palustre	7.4	10.8	3.3n.s.	**42.9*****	**−0.53***	**0.87*****	**−0.42***	0.18n.s.	0.16n.s.
Bryum sp.	0.0	0.4	0.4n.s.						
Dicranum bergeri	4.1	2.2	−1.9n.s.	**27.3*****	0.59n.s.	**0.93****	−0.29n.s.	**−0.57***	−0.39n.s.
Dicranum bonjeanii	0.6	1.1	0.5n.s.	−0.4n.p.					
Dicranum fuscescens	0.0	0.4		0.4n.p.					
Dicranum polysetum	0.2	0.4							
Dicranum scoparium	1.3	0.4	−1.0n.s.	−3.3n.s.					
Hylocomium splendens	0.4	0.7	0.4n.s.	0.8n.s.					
Hypnum cupressiforme	0.0	0.7		2.4n.p.					

Table 1. (Continued)

	Frequency (%)		Frequency change		Change in species optimum				
					1954–2008				
	1954	2008	1954–2008	1954–1997	*L*	*T*	*M*	pH	*N*
Pleurozium schreberi	3.4	9.4	6.0**	23.3***	−0.27n.s.	0.65n.s.	−0.41n.s.	0.20n.s.	0.10n.s.
Pohlia sphagnicola	2.3	0.4	−1.9*						
Polytrichum commune	1.0	5.4	4.4***	2.0n.s.	0.09n.s.	0.74n.s.	0.79n.s.	0.32n.s.	−0.18n.s.
Polytrichum strictum	3.4	4.0	0.6n.s.	37.6***	0.18n.s.	1.27***	−0.12n.s.	−0.07n.s.	−0.15n.s.
Racomitrium lanuginosum	0.0	0.4							
Sphagnum affine	1.4	2.9	1.4n.s.	1.2n.s.	−0.05n.s.	−0.02n.s.	−0.51n.s.	−0.45n.s.	−0.55n.s.
S. angustifolium	2.9	10.4	7.6***	−2.9n.s.	0.28n.s.	0.61n.s.	1.50**	1.33**	1.12**
S. austinii	1.3	2.2	0.8n.s.	0.0n.p.	0.29n.s.	0.36n.s.	0.27n.s.	0.06n.s.	0.02n.s.
S. balticum	16.3	19.4	3.1n.s.	16.3***	−0.30***	−0.12n.s.	−0.41***	0.10n.s.	0.34***
S. capillifolium	24.1	32.7	8.6***		0.02n.s.	0.22*	−0.08n.s.	−0.05n.s.	0.00n.s.
S. compactum	4.1	0.7	−3.4**	−8.2**					
S. cuspidatum	19.9	19.8	−0.1n.s.	9.0*	−0.12n.s.	−0.48**	−0.67***	−0.23n.s.	0.12n.s.
S. denticulatum	16.0	12.2	−3.7n.s.	−11.0*	−0.53***	−0.48*	0.04n.s.	−0.16n.s.	0.08n.s.
S. fallax	10.6	9.7	−0.9n.s.	−5.7n.s.	−0.33n.s.	−0.27n.s.	−0.49n.s.	−0.30n.s.	−0.09n.s.
S. fimbriatum	0.1	0.0		0.8n.p.					
S. flexuosum	0.0	0.4							
S. fuscum	5.5	6.5	1.0n.s.	18.4***	0.14n.s.	1.20***	0.33n.s.	0.30n.s.	−0.03n.s.
S. girgensohnii	0.0	0.7		2.0n.p.					
S. lindbergii	1.2	2.5	1.3n.s.	3.7n.s.	−0.37n.s.	−0.73n.s.	−0.54n.s.	−0.72n.s.	−0.07n.s.
S. magellanicum	33.9	41.7	7.9**	−1.2n.s.	−0.12n.s.	−0.27**	−0.22***	0.06n.s.	0.19***
S. majus	5.2	15.1	9.9***	17.6***	0.39n.s.	−0.71**	−0.17n.s.	−1.11***	−0.44n.s.
S. molle	0.5	0.0		−1.2n.p.					
S. palustre	1.1	0.0	−1.1n.s.	1.6n.p.					
S. papillosum	24.2	45.0	20.7***	3.3n.s.	−0.22*	−0.53***	−0.40***	−0.10n.s.	0.05n.s.
S. pulchrum	7.3	29.9	22.5***	17.6***	0.30n.s.	−0.32n.s.	−0.14n.s.	−0.60**	−0.56**
S. russowii	0.7	0.7	0.0n.s.	0.8n.p.					
S. squarrosum	0.4	0.0		−0.4n.p.					
S. subnitens	0.1	0.0		−2.0n.p.					
S. subsecundum	0.2	0.0		−1.2n.p.					
S. tenellum	24.1	30.6	6.4n.s.	25.7***	−0.02n.s.	−0.23**	−0.03n.s.	0.08n.s.	0.03n.s.
Straminergon stramineum	10.1	13.7	3.6n.s.	−17.6***	−0.26n.s.	−0.15n.s.	−0.29n.s.	0.47**	0.52**
Warnstorfia exannulata	0.6	0.7	0.1n.s.	0.0n.p.					
Warnstorfia fluitans	1.8	0.7	−1.1n.s.	6.5**					

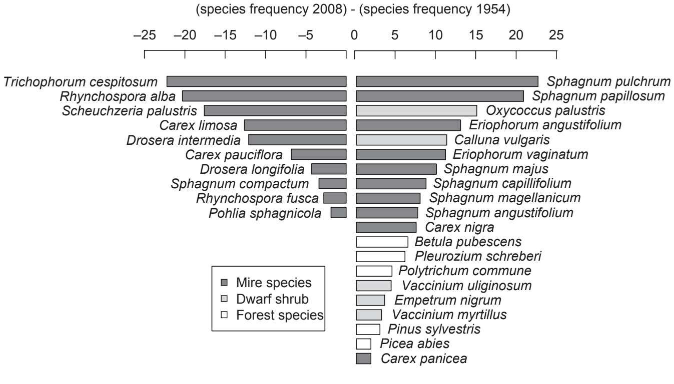

Fig. 2. Significant ($P \leq 0.05$) changes in species frequency of occurrence in plots from 1954 to 2008. Only species occurring in more than five plots in the two data sets together (= 70 species) were considered for calculation of frequency change.

assumed to have become extinct due to their scattered occurrences. On the other hand, changes in frequency might not be detected for widespread species at a broader scale. However, despite focusing on different spatial scales, both Gunnarsson, Malmer & Rydin (2002) and our study found the same trends in vegetation in the Stattute area since 1954.

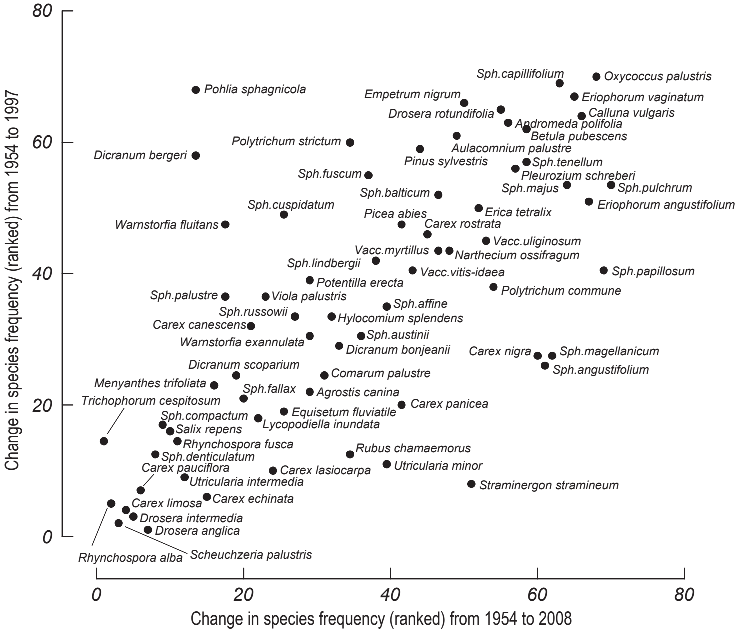

Fig. 3. Spearman rank correlation ($r_S = 0.66$, $P < 0.001$) of observed frequency changes of 62 species between 1954 and 2008 (present study) and between 1954 and 1997 (Gunnarsson, Malmer & Rydin 2002). Sph. = *Sphagnum*, Vacc. = *Vaccinium*.

Our fine-scale study on changes in species frequencies also demonstrated analogous changes to those found in the broad-scale study of Gunnarsson, Malmer & Rydin (2002), indicating that the species composition in the Stattute area has changed at different spatial scales over the times considered. The general trend in the fine-scale comparison is that typical mire species have decreased or not been re-found in the study site in 2008, whereas species of trees and dwarf shrubs have expanded, which matches the trend noted by Gunnarsson, Malmer & Rydin (2002). Species of high conservation value have not been recorded in 2008, including rare mire species such as *Hammarbya paludosa*, *Rhynchospora fusca* and *Scheuchzeria palustris*, the latter is a species typically growing in nutrient-poor bogs and sensitive to long dry periods (Tallis & Birks 1965). Missing species such as these and other wet-growing species that have decreased (e.g. *Carex limosa*, *Drosera* spp.) might partly have been substituted by species of higher competitiveness (e.g. *Sphagnum pulchrum*, *S. papillosum*, *S. magellanicum*), or of widespread species such as *Eriophorum angustifolium* (Gunnarsson, Malmer & Rydin 2002). Increasing *Calluna vulgaris* or *Sphagnum magellanicum* might have caused a decrease in species such as *Carex pauciflora* and *Trichophorum cespitosum* in the corresponding vegetation types (see also Malmer *et al.* 2003).

In our fine-scale study, species optimum changes were mainly in one direction for one environmental gradient but in a different or no dominant direction for other gradients. Predominantly unidirectional changes were found clearly for moisture, nutrients and light. This means that more species are now found together with species with a lower moisture optimum (i.e. the optimum for moisture has shifted towards lower values for the majority of species) and with more shade-tolerant species than they used to be, and also with more species with a higher demand for nutrients. This suggests the mire is tending towards drier conditions, lower light supply and higher nutrient availability. Soil pH and particularly temperature can also explain some of the observed changes in species composition, but for these factors species optimum changes are more evenly balanced in direction. Regardless of the direction of optimum change, which always depends on which species is being considered in relation to another, any significant change in species optimum in either case indicates a corresponding change of the underlying gradient towards altered conditions and an individualistic response to the changes. Our study found temperature to be the most important gradient for which 21 species have changed their realized optimum since 1954. Thus, effects of recent changes in the (local) climate might be of particular importance for the observed changes in the Stattute area.

Mire hydrology (depth of water-table, water content in mire surface) is strongly related to the local climate both seasonally and in the long term. Higher air temperature would lead to a drier mire surface and would lower the water-table, with significant changes in water supply for the species as a result. Recent changes in the hydrology may be assumed in the mire studied here, as mean annual temperature in the investigation area has increased significantly since 1980 from 5.4 °C (1903–80) to 6.1 °C (1980–2008; $P = 0.006$). This increase might be the reason for the observed changes in the mire vegetation of the Stattute area in favour of species with higher indicator values for temperature, as indicated by a significant correlation of the latter with optimum changes for temperature (Pearson $r = -0.57$, $P = 0.02$). A drying process as a consequence of raised temperatures might explain the relatively high percentage of mosses having increased their frequency since 1954 in comparison with those that decreased (eight moss and 12 vascular plant species increased, whereas two moss and eight vascular plant species decreased), since mosses (in particular *Sphagnum*) are physiologically adapted to dry periods and recover and regenerate quickly after desiccation (van Breemen 1995). Moreover, since *Sphagnum* moss absorbs water directly via the whole plant surface and grows as long as it is not frozen, its growth period exceeds that of vascular plants, which is restricted to a few months in the growing season (Malmer *et al.* 2003). The increased frequencies of tree species (*Betula pubescens*, *Pinus sylvestris*) and dwarf shrubs as a response to a drying process has also been documented by several recent studies on mire vegetation in northern Europe (e.g. Gunnarsson & Rydin 1998; Frankl & Schmeidl 2000; Gunnarsson, Malmer & Rydin 2002).

The observed vegetation changes towards higher nutrient availability may be the result of changes in nutrient supply. Increases in wet deposition of nutrients have been used to explain recent vegetation changes in mires in north-western Europe along with a trend towards more nutrient-rich conditions (Linderholm & Leine 2004; Gunnarsson & Flodin 2007). However, fertilization experiments on the Åkhult mire have shown no significant effects on the growth of either the vascular plants or *Sphagnum* (Aerts *et al.* 2001; Malmer *et al.* 2003), but Malmer & Wallén (2005) suggest that the decrease in *Sphagnum* growth is related to the increased concentration of N in the plant tissue since the 1950s. Regarding vascular plants, other nutrient sources might contribute to the vegetation changes found here. For instance, changes in the decay and mineralization rates of (plant) organic matter might be more important in supporting the growth of vascular plants, while the mosses have access to atmospheric supplies only (Aerts *et al.* 2001; Malmer *et al.* 2003). This might have caused changes in the vegetation of the Stattute area, as a lower water level creates more oxic conditions in the peat, and thus increases mineralization rates (Malmer *et al.* 2003).

The increased frequencies of dwarf shrubs and trees in the two lower layers of the Stattute area, possibly due to higher nutrient availability and drier conditions, may have caused altered light conditions for several low-statured plants. According to the changes in species optimum values, irradiance at ground level might have been reduced in different parts of the Stattute area, indicated by the predominant negative change in optimum for light for species independent of vegetation type (e.g. *Trichophorum cespitosum*, *Carex lasiocarpa*, *Drosera longifolia, Sphagnum balticum, S. denticulatum*, *S. papillosum, Aulacomnium palustre*). In association with increased frequency of tree species in the two lower layers, both drying processes (Gunnarsson & Rydin 1998; Frankl & Schmeidl 2000; Gunnarsson, Malmer & Rydin 2002; Linderholm & Leine 2004; Murphy, Laiho & Moore 2009) and shading may have caused an increased growth of species such as *Vaccinium* spp. or *Pleurozium schreberi*, which are associated with drier and shadier conditions (Laine, Vasander & Laiho 1995; Gerdol *et al.* 2004). However, in *Sphagnum*-dominated mires, site conditions are rather unfavourable for the growth of vascular plants, as *Sphagnum* creates acidic, anoxic, nutrient-poor and cold conditions (van Breemen 1995; Ohlson *et al.* 2001). In this regard, the combined effect of increased air temperature, drying of the mire surface, a lowered water-table and increased nutrient availability may have facilitated the successful establishment and an increased growth of competitive woody plants.

Changes in the pH value of the mire may have contributed to changes in species composition in the Stattute area. Impacts of acidification processes in terrestrial ecosystems after human-induced pollution (acidifying deposition) over wide parts of central and northern Europe have been of concern since the 1970s (Gorham 1976), and acidification effects on the vegetation in the Stattute area have also been discussed by Gunnarsson, Malmer & Rydin (2002). In our study, acidification effects are suggested by changes in pH optimum values, which have been found to be greater for several species growing in the wetter parts of the Stattute area (e.g. *Utricularia* spp., *Carex rostrata*, *Sphagnum majus, S. pulchrum*), which are now found together with acid-tolerant species (e.g. *Sphagnum balticum*, *S. cuspidatum* and *S. tenellum*) more often than they used to be. The latter species have the lowest indicator values for pH and are also found by Gunnarsson, Malmer & Rydin (2002) to have expanded since 1954. These observations, together with the effects reflected by species of several other microforms in the Stattute area, might indicate a trend towards more acidic site conditions with the effect being more pronounced in the wetter parts of the mire such as in the pools and lawns (see also Gunnarsson, Malmer & Rydin 2002).

Natural succession as an autogenic internal factor causing changes in species composition and vegetation types without any external change in climate or other environmental factors has been discussed by Gunnarsson, Malmer & Rydin (2002) and is suggested to have partly caused vegetation changes in the Stattute area. This was indicated, for instance, by high species mobility and increased frequencies of species typical of the surrounding forests. However, disentangling the effects of natural succession from those of external driving factors is difficult, as both would cause changes, for example, in light conditions and in the nutrient budget over the time period considered, and would show up as changes in indicator values and species optimum values in the two resurveys.

Using species optimum values as an indirect approach to identify change in vegetation in relation to the environment enables a temporal comparison at the local scale on the basis of non-permanent plots, and gives an indication of the amount of species turnover and which drivers may be important for the changes in local vegetation types. It allows the analysis of historical data sets with non-permanent plots, which, up to now, have only been used to a limited extent for studying vegetation dynamics, and thus unlocks a valuable archive for detecting vegetation change in the last 50–100 years.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Air temperature, precipitation and wet deposition rates in south Sweden over the last century.

Appendix S2. Data visualization of correspondence analysis (CA) and cluster analysis.

Figure S1.1. Air temperature and precipitation rates from 1901 (precipitation) and 1903 (temperature) to 2008.

Figure S1.2. Estimated mean annual wet deposition of nutrients from 1947 to 2008.

Figure S2.1. Biplots of distribution of samples in 1954 and 2008, vegetation as grouped by Ward's hierarchical clustering and species of highest axis scores for the first two CA axes.

SUPPORTING INFORMATION

Appendix S1 Air temperature, precipitation and wet deposition rates of nutrients in south Sweden over the last century.

Appendix S2 Graphical representation of the results of correspondence analysis and cluster analysis.

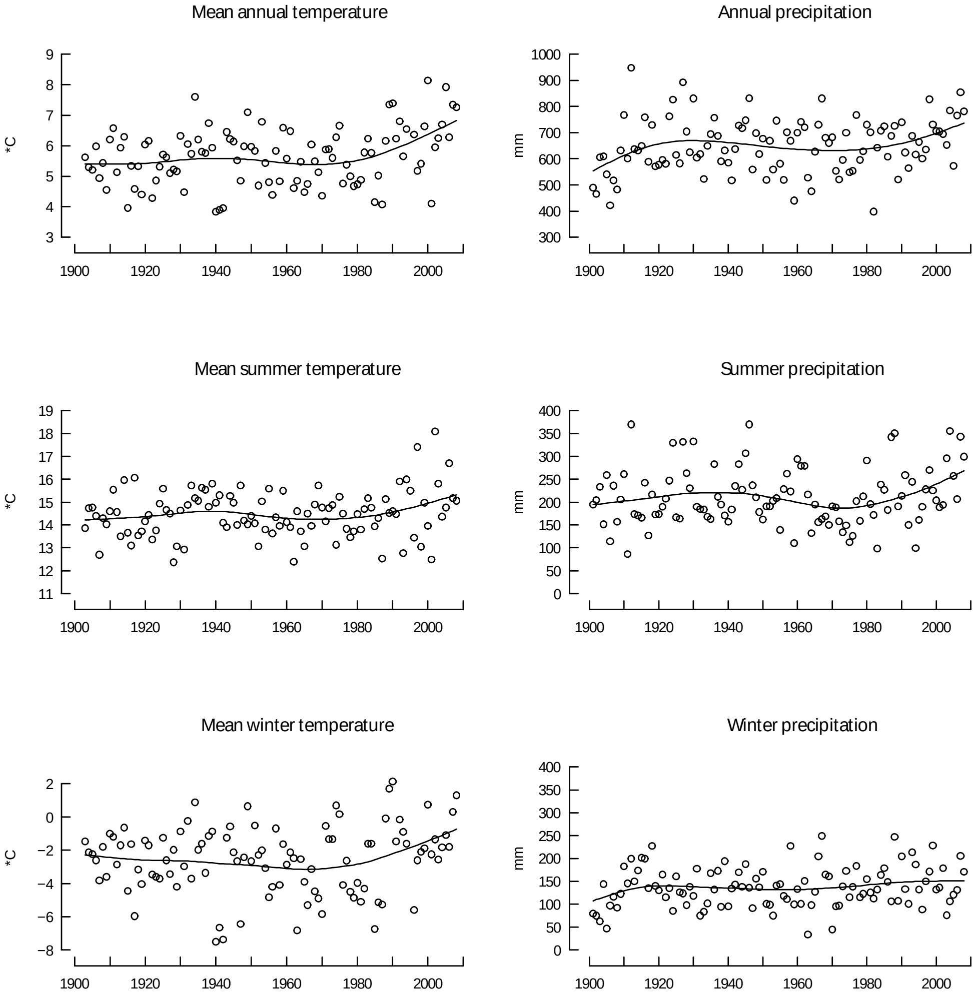

Figure S1.1 Air temperature and precipitation rates from meteorological stations in Lannaskede (1901/03-1958: 210 m a.s.l.) and Nävelsjö (1958-1988: 215 m a.s.l.; 1988-2008: 230 m a.s.l.) about 38 km NE of the mire from 1901 (precipitation) and 1903 (temperature) to 2008. Values are fitted with a smoother (degrees of freedom = 5). Data were provided from SMHI (Swedish Meteorological and Hydrologic Institute; http://www.smhi.se).

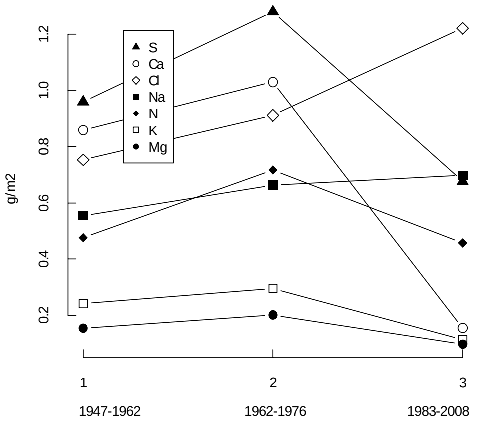

Figure S1.2 Estimated mean annual wet deposition (g/m^2) in Aneboda (200 m a.s.l.) of sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), nitrogen (N), chloride (Cl) and sulphur (S). Mean values for the period 1947 to 1976 refer to Malmer & Wallén (1980). Mean values for the period 1983 to 2008 were calculated from the Swedish Environmental Research Institute (http://www.ivl.se). Values for between 1977 and 1983 were not available.

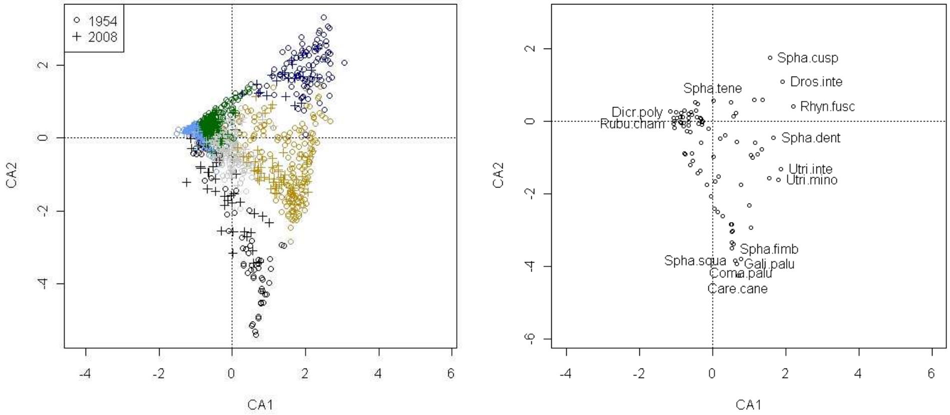

Figure S2.1 Graphical representation of the results of correspondence analysis (CA; Legendre & Legendre 1998) and cluster analysis as used for assessing similarity in the range of variation in vegetation sampled in 1954 and 2008. Eigenvalues for the unconstrained axes: CA1 0.63 (proportion explained 0.11), CA2 0.53 (proportion explained 0.09). Left: CA biplot showing distribution of samples from 1954 and 2008. The colours symbolise the vegetation as grouped by Ward's hierarchical clustering using the Bray-Curtis (1957) distance as the dissimilarity measure. Right: Species of highest axis scores for CA axis 1 and 2.

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Paper III

Changes in arctic vegetation on Jan Mayen Island – a comparison of two time-scales

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Abstract

Questions: Can recent vegetation changes on an isolated, grazer-free island be explained by recent climate change? Are observed changes consistent when focusing on two different time-scales?
Location: Jan Mayen, an arctic volcanic island in the North Atlantic Ocean.
Methods: We resurveyed two botanical studies conducted 19 and 80 years earlier to explore changes in species frequency, abundance, and co-occurrence with other species. The observed changes were statistically evaluated by restricted permutation tests and were compared for the two time-scales considered using Pearson correlation tests.
Results: Total number of species has not significantly changed over the two time periods considered. One species (*Botrychium lunaria*) was found new to the island. Dwarf-shrub *Salix herbacea* and several graminoids have increased in frequency or abundance, or both, whereas species linked to snow-beds (e.g. *Saxifraga* spp., *Oxyria digyna*, *Cerastium cerastoides*) have decreased. Changes over 19 years were significantly correlated with 80-year changes considering species frequency, but not when comparing changes in abundances and species co-occurrences. Observed changes were more pronounced in the 80-year comparison.
Conclusions: Longer growing season, altered soil moisture conditions, and increased nutrient availability due to warmer temperatures might explain the observed changes in arctic vegetation composition on Jan Mayen. 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.

Introduction

Climate is a major determinant of the abundance and distribution of species, and changes in climate may have considerable effects on terrestrial ecosystems (Walther 2003, IPCC 2007). Recent climate warming has caused ranges of plant species to expand polewards along the latitudinal gradient and upwards along the altitudinal gradient (Grabherr et al. 1994, Chapin et al. 1995, Tape et al. 2006, Danby & Hik 2007, Lenoir et al. 2008, Wilson & Nilsson 2009), which is also well documented for alpine habitats in the temperate and north-temperate region (Theurillat & Guisan 2001, Root et al. 2003, Walther 2003). In arctic and alpine areas, summer temperature and spatial and temporal distribution of snow are the most important factors determining the growth and survival of plants (Körner 2003, Post et al. 2009). The impacts of climate change may therefore be especially obvious in arctic-alpine areas, where vegetation is limited by low temperatures and short growing seasons (Körner 2003, Walther 2003, Post et al. 2009). Arctic plant species have been observed to respond to recent climate warming by shifting species distributions northwards (Post et al. 2009). Other studies report of changes in arctic vegetation such as increased growth and biomass of those shrub and graminoid species with the greatest abilities to respond to increases in temperature and nutrient availability (Serreze et al. 2000, Sturm et al. 2001, Tape et al. 2006, Meltofte et al. 2008, Hudson & Henry 2009, Tømmervik et al. 2009, Wilson & Nilsson 2009, Hallinger et al. 2010).

Most of the studies observing changes in species composition or distributions explain the observed changes as a consequence of recent climate warming. However, it may often be difficult to separate the effect of climate warming from the effect of other important factors driving vegetation dynamics in high alpine and arctic vegetation such as changes in land-use and grazing pressure (Virtanen et al. 1997, Pajunen et al. 2008, Post & Pedersen 2008, Olofsson et al. 2009, Vittoz et al. 2009, Virtanen et al. 2010, Walther 2010). In the Scandinavian low and high Arctic, both short- and long-term effects of reindeer grazing and trampling may have important effects on plant species richness, vegetation composition, nutrient cycling, and plant growth (Pajunen et al. 2008, Olofsson et al. 2009). As these effects may confound the effects of climate change (Dormann et al. 2004, Olofsson et al. 2009) this may easily lead to misinterpretation of observed changes in vegetation. Areas that are not affected by grazing animals today, and have not been historically, or where the effects of herbivory have remained stable and the effects of changes in grazing regime on vegetation changes can be ruled out are rare. However, Jan Mayen Island is such a unique place providing the opportunity for this type of study. The vegetation on the island is virtually undisturbed by grazers and direct human land-use is minimal. Moreover, due to its isolated geographic position in the North Atlantic Ocean, the vegetation on this island is hardly affected by invasions of new species.

Changes in vegetation are most commonly analysed by comparing species frequencies and abundances to identify shifts in species dominance and distributions (e.g. Gunnarsson et al. 2002, Klanderud & Birks 2003, Pajunen et al. 2008, Daniëls et al. 2011). If species respond individualistically to changes in environment, new community constellations will arise, and species will occur together with different species than before. Studying how species change in their co-occurrence with other species may be used to describe changes in vegetation composition, but so far has never been done for this purpose. We here study changes in co-occurrences and species frequency, abundance, and richness over short and long time-scales, which will give new insights into the predictability of vegetation assemblages at different time periods.

Resurveying historical studies is an excellent way to study and describe changes in vegetation over long time periods in relation to environmental change. However, vegetation studies in the Arctic exceeding time periods of 20 years are rare and mainly focus on *in situ* changes (Wilson & Nilsson 2009), changes in productivity (Hudson & Henry 2009, Hill & Henry 2011), or on comparisons with historical maps (Cannone et al. 2007, Prach et al. 2010) or repeat photography (Sturm et al. 2001, Tape et al. 2006). Comparing phytosociological data-sets containing detailed descriptions of species abundances in plots of restricted areas give valuable insights into long-term dynamics in vegetation composition and diversity (Wilson & Nilsson 2009, Virtanen et al. 2010, Daniëls et al. 2011). On Jan Mayen Island, two vegetation surveys of high quality and repeatability were conducted during the past 100 years enabling the study and comparison of changes in vegetation composition over two different time-scales. One of these surveys is the study by Lid (1964) conducted in 1930, which consists of a quantitative description of different vegetation types (synedria) distributed over the island. The other study was conducted in 1991 by Virtanen et al. (1997), who recorded vegetation composition along an altitudinal gradient (0 - 600 m a.s.l.). We repeated these two studies in 2010 using the same methods with the aim to detect, describe, and compare changes in vascular plant composition over 80 and 19 years and discuss whether observed changes may be linked to recent climate change. Most arctic species are long-lived perennials and, hence, vegetation dynamics are probably slow. Comparing how vegetation has responded over these two time-scales is a unique opportunity to increase our knowledge of how arctic ecosystems will cope with climate warming.

MATERIAL AND METHODS

Investigation area

Jan Mayen is a 57 km long and 3 to 15 km wide volcanic island in the North Atlantic (70° 50′ to 71° 10′ N, 7° 80′ to 9° 15′ W). The coastline is relatively long, and the coast is in large parts formed by steep cliffs colonised by sea birds. In the north of the island is the worlds' northernmost active and glaciated volcano, Mt. Beerenberg (2277 m a.s.l.). The non-glaciated peaks in the south of the island do not exceed 800 m a.s.l., and the centre is relatively flat and low-lying. Trachybasalt is the most common rock (Wordie 1926). Since this rock type is highly resistant to weathering, soil development is limited and drainage is rapid as lavas are naturally porous (Russell & Wellington 1940). Trachite, andesite, and, at the southern flank of Mt. Beerenberg, basaltic tuffs can also be found. The arithmetic mean pH of 35 soil samples from different localities taken in the course of the re-sampling of Lid (1964) was 6.73 in 2010 (minimum: 6.25, maximum: 7.13, median: 6.73).

Climate data over the last century are available from Jan Mayen meteorological station at 11.5 m above sea level (station number 99950; www.eklima.no; see Appendix Figure S1 in Supporting Information) for temperature (since 1921), precipitation (since 1921), wind speed (since 1956), and growing degree days (since 1943). The station has been moved a few times before 1962 but was always situated in the centre of the island at similar altitudes (see Appendix Table S1). The climate of Jan Mayen is arctic and oceanic with cold summers (4.0°C, 1921-2010) and relatively warm winters (-4.7°C, 1921-2010). Fog and clouds are common, especially during the summer months, and the sky is almost constantly overcast. Precipitation falls mostly in the form of mist and light rain, heavy rain is rare. Mean annual temperature is -0.6°C (1921-2010), and annual precipitation is 628 mm (1921-2010).

Temperatures have changed between the sampling periods. Both growing season and annual temperatures showed a cooling trend until the 1960-80s and a warming trend in the 1990-2010s, with the latter period prior to our resurveys in 2010 being clearly warmer than in the 1920s. Growing degree days, a close proxy to vegetation productivity in the Arctic, increased significantly since the 1980s. Annual precipitation has increased since the 1920s and remained stable over the last five decades.

When comparing climate measures in the periods prior to each of the three dates of vegetation sampling (i.e. Lid 1930, Virtanen et al. 1991, our resurveys in 2010), the following trends were observed: mean annual temperatures were -0.2°C in the decade prior to the first inventory (1921-30) and were significantly lower prior to the sampling on Mt. Beerenberg in 1991 (1982-91: -0.9°C), followed by a clear increase in the last decade (2001-10: 0.6°C). The same trend was found for summer temperatures (1921-30: 4.4°C; 1982-91: 4.0°C; 2001-10: 5.3°C). Annual precipitation was 391 mm prior to the first survey (1921-30) and it reached a maximum in the period prior to the sampling on Mt. Beerenberg in 1991 (698 mm), decreasing to 630 mm in the period prior to our study in 2010. Growing degree days (i.e. number of days with average temperature above 5°C) during the summer months were fewer between 1982 and 1991 (14.1 degree days) than between 2001 and 2010 (33.2 degree days). Annual average wind speed is 6.7 m/s and has not significantly changed since the measurements started in 1956.

Unfavourable environmental conditions, such as poorly developed soil, rapid drainage and exposure to frequent strong winds, limit the growth of vascular plants on Jan Mayen (Russell & Wellington 1940). Large areas are almost exclusively comprised of bryophytes, with *Racomitrium lanuginosum* (Hedw.) Brid., *R. ericoides* (F. Weber ex Brid.) Brid., and *Anthelia juratzkana* (Limpr.) Trevis forming the most important vegetation types on exposed sites, wind protected sites, and in depressions (Virtanen et al. 1997). With the exception of *Empetrum nigrum* L., *Salix herbacea* L., and one observed individual of *Salix arctica* Pall., the island is tree- and shrub-free. *Salix herbacea*, *Beckwithia glacialis* (L.) Á. & D.Löve, and *Saxifraga cespitosa* L. are very common and occur in almost every vegetation type. Lava fields consisting of loose blocks and hollows are usually poor in species. *Racomitrium lanuginosum* may be dominant here, being accompanied by *Luzula confusa* Lindeb. and species of *Cerastium* and *Saxifraga*. On exposed hillsides, *Saxifraga oppositifolia* L. and *Bistorta vivipara* (L.) Delarbre are frequent and grow also among *Racomitrium* moss. In addition to dry exposed sites, *Silene acaulis* (L.) Jacq. is often found on open rocky ground within sparse vegetation composed of e.g. *Luzula* spp. and *Cerastium* spp. Typical species on sandy beaches are *Mertensia maritima* (L.) Gray, *Honckenya peploides* (L.) Ehrh., and *Carex maritima* Gunnerus. Several species of the genus *Taraxacum* are endemic on Jan Mayen (e.g. *T. torvum* Hagl., *T. recedens* (Dahlst.) Hagl.).

The island is virtually grazer-free, with no grazing mammals and only occasional visits of Greylag Goose (*Anser anser*) and Pinkfooted Goose (*A. brachyrhynchus*), both of which are uncommon annual breeders, and Barnacle Goose (*Branta leucopsis*), which is a scattered breeder on the island (http://www.svalbardbirds.com/artsliste-jm.htm). The most dominant nesting birds are Northern Fulmar (*Fulmarus glacialis*), Common Eider (*Somateria molissima*), Arctic Tern (*Sterna paradisaea*), Brünnichs and Black Guillemot (*Uria lomvia*, *Cepphus grylle*), Little Auk (*Alle alle*), and Atlantic Puffin (*Fratercula arctica*). Thus, bird trampling and droppings rather than grazing may locally impact vegetation by increasing nutrient supply and compacting vegetation cover (especially mosses) with changes in the local microclimate as a possible consequence. However, direct influence of both grazing animals and humans (e.g. tourism, land-use) is low and restricted to areas on the island which are not used for the comparisons in our study.

Taxonomic notes

The nomenclature follows Lid (2005) for vascular plants, Rønning (1996) for high arctic species not covered by Lid, and Lid (1964) for endemic species of *Taraxacum*. To achieve a comparable taxonomy to the ones used in Lid (1964) and Virtanen et al. (1997), several species were merged. *Luzula confusa* and *Luzula arctica* were merged with *Luzula arcuata*, and *Cerastium alpinum* was merged with *C. arcticum*. Because the flowering season of *Draba* was largely over when doing the sampling in 2010 and identification of several individuals (including possible hybrids with *D. norvegica*) to species level proved difficult in the field, we unified *Draba oxycarpa*, *D. norvegica*, and *D.* sp. to *D. norvegica*. *Festuca richardsonii* was not distinguished in Lids study and was therefore merged with *Festuca rubra*.

Vegetation re-sampling

In the early 1930s, Lid (1964) investigated the vegetation on Jan Mayen with the aim to map the regional distribution of vascular plants and to describe the coexistence of species in restricted areas on the island (so-called synedria). To describe the synedria around 36 selected vascular plant species Lid recorded vegetation using 1 m x 1 m plots distributed over about 15 different localities. For each plot, coverage of vascular plants, bryophytes, and lichens was estimated using the Hult-Sernander-Du Rietz five-point scale (Du Rietz 1921). Usually ten plots were examined for one species if the distribution area was of sufficient size. In 2010, we re-sampled the synedria around the different focal species at the given localities using the same methods and restrictions as described in Lid (1964). Because plots were not permanently marked in the 1930 inventory, we placed the plots randomly in homogenous vegetation around the focus species at the different localities described in Lid (1964). In 2010, we recorded vegetation from a total of 254 plots to be used for the comparison with those collected by Lid in the 1930s. The numbers of plots sampled within each synedria is made equal for both inventories by randomly deleting samples from the synedria from our survey in areas where more samples were taken in 2010 than in the 1930 survey (i.e. in total 21 plots).

In 1991, Virtanen et al. (1997) sampled vegetation along an altitudinal transect (0 600 m a.s.l.) on the southwestern slope of Mt. Beerenberg with the aim to describe the different plant communities. They applied a systematic nested sampling design using 15 m transect lines at intervals of 25 altitudinal metres, where eight plots of 0.8 m x 0.8 m size were placed at regular distances ideally following a gradient from hillock to depression. A scale of 10 classes (Oksanen 1976) was used to estimate species coverage of vascular plants and bryophytes. As in Lids study, sampling units were not permanently marked by Virtanen et al. (1997) and the position of the transect could therefore be relocated only approximately in the resurvey in 2010 using a sketch-map of the approximate position of the transect. Apart from this inaccuracy, the re-sampling of vascular plant vegetation was conducted as in the previous study following the same systematic sampling design. The total number of plots sampled was 200 in 1991 and 2010.

Statistical analyses

All statistical analyses were conducted using R, version 2.11.1 (R Development Core Team 2010).

Species frequency, abundance, and richness

To get an indication of change in vegetation over the time periods 1930-2010 (synedria) and 1991-2010 (Mt. Beerenberg) we calculated and compared changes in vascular plant species frequency, abundance, and richness for each of the two inventories compared.

Vascular plant species frequencies of occurrence in plots were calculated by dividing the number of plots in which a species occurs by the total number of plots sampled in each inventory. Changes in species frequencies were estimated by subtracting frequencies of the previous study from the frequencies of the corresponding resurvey in 2010. Whether observed changes were random or not was tested by a restricted permutation test. We randomised the inventory identity by restricting the randomisations to the different synedria in the comparison with Lid's study and to the altitudinal intervals in the comparison with Virtanen et al.'s study. In these randomisations, plots were mixed between the two datasets compared only within the same vegetation type (synedria) or within the same altitude level. Significance levels were derived by counting the number of times where the change in species frequency (absolute value) of the observed value was smaller or equal to the randomised absolute value. In these analyses, tests were run for 46 or 20 non-rare species (occurring in more than five plots) in the 1930-2010 or 1991-2010 contrasts, respectively, and 999 permutations were run.

To calculate changes in species abundance and to test the changes, we used an identical approach to the one used for calculating change in species frequencies described above, but using species mean cover values instead of species frequencies. To make the data-sets of the two (re)surveys comparable, species cover values used in Lid (1964; 5 categories), Virtanen et al. (1997; 10 categories) and in the respective resurveys in 2010 were converted into corresponding geometric mean cover values (i.e. 71.6, 35.6, 18.6, 9.3, 4.6, 2.3, 1.2, 0.6, 0.3 and 0.15 %; after Oksanen 1976) before calculating changes in vascular plant species abundances.

When testing the changes in species richness per plot the same restrictions as described above (i.e. on synedria and on altitudinal levels for the short- and long-term comparison) were applied in the randomisation procedure.

Co-occurrence of species

To identify whether species have significantly changed their associates over time we selected one focus species at a time. We counted the number of plots where the species in focus co-occurs with another species and divided this by the total number of plots containing the focus species. This was done separately for the data-sets of the old surveys and the resurveys. Next, the change in co-occurrence was calculated by subtracting the co-occurrence frequency of the older inventory from the new inventory. The resulting values range between +1 when it was found more often together with the focus species or was new in 2010 and -1 when it was found less often together with the focus species or was not re-found in 2010, with no change in co-occurrence = 0. Again, a restricted randomisation test was applied to test observed changes in the co-occurrence of species for randomness, having 999 permutations in each randomisation test of the different synedria or the altitudinal levels for the long-term or short-term comparison. Change in co-occurrence was considered statistically significant if the observed value was significantly larger or smaller than 95% of the permuted values.

The analysis of change in co-occurrences considers only species occurring in more than ten plots in the old and new inventory together, reducing the number of species from 53 to 45 for the long-term comparison and from 25 to 18 species for the short-term comparison. To evaluate if there have been similar changes between the two resurveys we correlated the observed changes using Pearson correlation for each focus species separately. For the correlation test only species in common for the two surveys were used, i.e. 16 species were available for this comparison.

RESULTS

Changes in species frequencies

Of the total of 46 tested vascular plant species in the synedria studied, the frequency of occurrence in plots significantly decreased for 14 species and increased for 9 species over the past 80 years (Figure 1). *Salix herbacea*, *Carex maritima*, and *Honckenya peploides* increased most in frequency since 1930. Greatest negative changes were found for *Saxifraga rivularis*, *Poa alpina*, and *Sagina cespitosa*.

At Mt. Beerenberg over the past 19 years, two of the 20 tested species significantly increased in frequency (*Salix herbacea*, *Poa glauca*) and three species significantly decreased (*Saxifraga cespitosa*, *Cerastium arcticum*, *Saxifraga rivularis*; Figure 1).

The Pearson correlation test found a significant positive correlation between changes in vascular plant species frequency on Jan Mayen over 80 years (Lid's synedria) and over 19 years at Mt. Beerenberg ($r = 0.53$, $p = 0.023$).

Changes in species abundances

Vascular plant species abundances in the different synedria studied (80-year comparison) significantly decreased for 20 of the 46 species tested, with *Carex bigelowii*, *C. maritima*, *Taraxacum torvum*, and *Poa alpigena* showing the greatest changes (Figure 2). Increased abundances were found for 17 species (e.g. *Honckenya peploides*, *Cochlearia groenlandica*, *Salix herbacea*, *Sibbaldia procumbens*).

At Mt. Beerenberg, five of the 20 testable species changed abundances significantly (Figure 2). Three species (*Trisetum spicatum*, *Oxyria digyna*, *Luzula arcuata*) significantly decreased, and two species (*Saxifraga rivularis*, *S. tenuis*) significantly increased in abundance in comparison with the 1991 survey.

Changes in vascular plant species abundances in the synedria over 80 years were not statistically significantly correlated with the 19-year changes found at Mt. Beerenberg ($r = 0.38$, $p = 0.146$).

Changes in species richness and turnover

In the sample plots (synedria) studied, the total number of vascular plants observed was 49 species in 1930 and 50 species in 2010. In 2010, three species found in 1930 were not re-found (*Minuartia biflora*, *Omalotheca supina*, *Taraxacum brachyphyllum*), whereas four new species, namely *Euphrasia wettsteinii*, *Poa arctica*, *Poa glauca*, and *Botrychium lunaria*, were found in 2010. The mean number of species per plot decreased since 1930 from 9.5 species to 8.9 species (randomisation test, 999 permutations, $p = 0.016$).

At Mt. Beerenberg, the total number of vascular plant species decreased from 23 species in 1991 to 20 species in 2010. As in the resurvey of Lid's synedria, two species *Euphrasia wettsteinii* and *Poa glauca* were found only in 2010. Five species (*Cerastium cerastoides*, *Draba nivalis*, *Koenigia islandica*, *Minuartia rubella*, *Taraxacum acromaurum*) were not re-found in

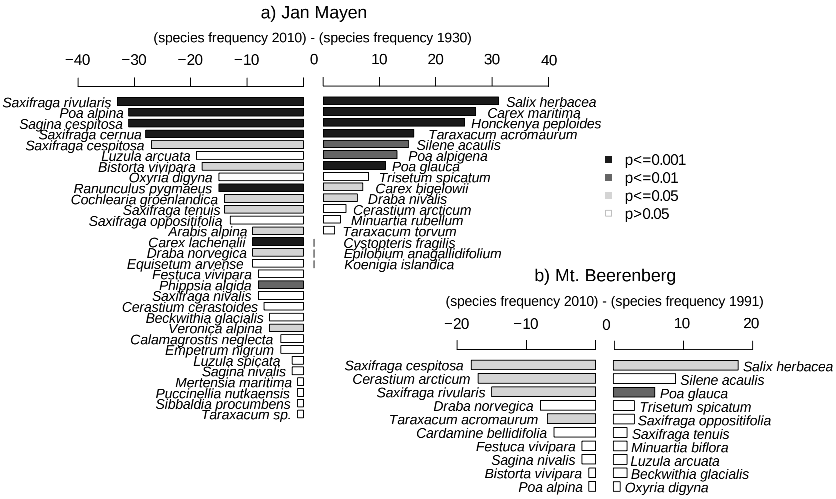

Figure 1: *Change in species frequency of occurrence in plots a) in Lid's synedria (1930-2010, 46 species testable) and b) at Mt. Beerenberg (1991-2010, 20 species testable).*

the 2010 sampling. The mean number of vascular plant species per altitudinal level significantly decreased from 9 species to 7.6 species since 1991 (randomisation test, 999 permutations, $p = 0.007$).

Changes in species co-occurrences

In the synedria studied, of the 45 tested species, average co-occurrences increased for 16 species (e.g. *Calamagrostis neglecta, Draba nivalis, Empetrum nigrum, Mertensia maritima, Puccinellia nutkaensis, Sagina cespitosa, Taraxacum torvum*) and decreased for 27 species (e.g. *Arabis alpina, Beckwithia glacialis, Bistorta vivipara, Draba norvegica, Festuca vivipara, Oxyria digyna, Poa alpina, Sagina nivalis, Saxifraga tenuis, Salix herbacea*; see Appendix Figure S2a). All species growing together with *Poa glauca* or *Honckenya peploides* were found to co-occur more frequently with these two species in 2010 than in 1930. Species co-occurrences with *Koenigia islandica* and *Phippsia algida* did not change.

At Mt. Beerenberg, the frequency of co-occurrence increased for 12 of 18 tested species (*Beckwithia glacialis, Bistorta vivipara, Cardamine bellidifolia, Draba norvegica, Festuca vivipara, Poa alpina, Sagina nivalis, Saxifraga cespitosa, S. rivularis, S. tenuis, Silene acaulis, Trisetum spicatum*) and decreased for *Cerastium arcticum, Luzula arcuata, Minuartia biflora, Oxyria digyna, Salix herbacea*, and *Saxifraga oppositifolia* (see Appendix Figure S2b).

Changes in species co-occurrences found for the period 1930-2010 (synedria) were significantly correlated with the changes found since 1991 at Mt. Beerenberg for the species *Draba norvegica* ($r = -0.78$, $p = 0.003$) and *Luzula arcuata* ($r = 0.60$, $p = 0.014$; Table 2). For the other 14 species tested, the directions of correlations varied, and no statistically significant correlation of the changes in co-occurrence was detected.

DISCUSSION

This study found clear changes in species frequency, abundance (cover), and species co-occurrence at the fine scale, indicating new arrangements between species within the vegetation types studied. The main trend observed was that dwarf-shrub and graminoid species have increased, whereas species linked with snow-beds have decreased. In contrast to these fine-scale observations indicating compositional turnover,

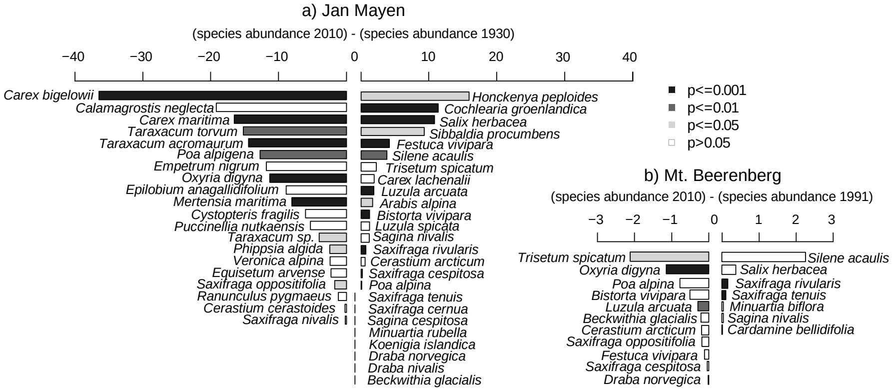

FIGURE 2: *Absolute change in species percent cover (abundance) a) in Lid's synedria (1930-2010, 46 species testable) and b) at Mt. Beerenberg (1991-2010; because Poa glauca was not found in 1991 and Taraxacum acromaurum was not found in 2010, only 18 out of 20 species could be tested for change in species abundance).*

the total species list in the plots resurveyed on Jan Mayen Island is relatively unchanged, both when focusing on 19-year (1991-2010) and 80-year changes (1930-2010). The total number of species has remained virtually stable and species turnover is low at the broad scale.

The observed low species turnover might reflect the remoteness of the island, lowering the chance of arrival and establishment of new species despite the clear climatic changes on the island. Besides dispersal by wind and drift wood, the arrival of new plant species relies mainly on birds as vectors, which under violent storms happen to be blown onto the island, or on the introduction by humans. However, since the frequency of these vectors is low on Jan Mayen in comparison with the mainland and environmental conditions are unfavourable for the growth of vascular plants, the probability of frequent and successful establishment of new plants may be assumed to be low. Accordingly, the only species found new to the island in 2010 by means of fine-scale plots is *Botrychium lunaria*, growing under a nutrient-rich bird cliff in more abundant and richer vegetation compared to the surrounding areas. All the other species, which were either found new or were not re-found in 2010 by our fine-scale plot sampling, were observed at different localities on the island outside the plots. Hence, species richness may be considered virtually stable over both 19 and 80 years, with species recorded for the first time or not re-found in 2010 being a result of the random placement of plots in the different vegetation types rather than species extinction or new arrivals to the island. This relative stability despite a clear warming during the last decades is contrary to the conclusion by Alsos et al. (2007), who infer that dispersal will not be the limiting factor for species establishment with climate warming. In our study, the observed vegetation changes in the course of the past 19- and 80-years of climate warming indicate that dispersal may be an important factor limiting new occurrences of species and that dispersal limitation may restrict species turnover with future climate change.

The significant increase of *Salix herbacea* in both the 19- and 80-year comparison is consistent with the common trend reported by several experimental and observational studies in the Arctic that several species of shrubs have significantly increased (Sturm et al. 2001, Bret-Harte et al. 2002, Dormann & Woodin 2002, Tape et al. 2006, Walker et al. 2006, Hudson & Henry 2009, Wilson & Nilsson 2009). On Jan Mayen, winter precipitation has increased since 1930 (non-significant trend of 1.4% per decade, Øseth 2010) whereas both growth degree days (www.eklima.no) and spring temperature increases have accelerated particularly since the 1970s (Øseth 2010). Changes in rain- and snow-fall patterns, and in particular the earlier onset of snow melting lengthening the growing season of plants, are considered the most important factors causing changes in arctic vegetation

(Sturm et al. 2001, Hinzman et al. 2005, Walker et al. 2006), with snow-bed vegetation assumed to be particularly sensitive (Totland & Alatalo 2002, Björk & Molau 2007). Klanderud & Birks (2003) report decreases in species of late-melting snow-beds, such as *Saxifraga species*, *Oxyria digyna*, *Cerastium cerastoides*, and *Ranunculus pygmaeus*. In addition to these species on Jan Mayen, we also found the snow-bed related species *Phippsia algida*, *Arabis alpina*, and *Epilobium anagallidifolium* to have decreased in frequency or abundance, or both. On the other hand, warmer temperatures have been shown to increase the growth of graminoids (Walker et al. 2006, Daniëls et al. 2011) and to drive the invasion of dwarf-shrubs and graminoids with higher competitive ability into snow-bed habitats (Björk & Molau 2007, Daniëls et al. 2011). Accordingly, our study found significant increases (frequency or abundance, or both) of *Salix herbacea* and several graminoids (*Poa alpigena*, *P. glauca*, *Trisetum spicatum*, *Luzula* spp.). Thus, the expansion of relatively high-statured plants (e.g. *Trisetum spicatum*), plants of dense growth form (e.g. *Salix herbacea*, *Silene acaulis*), or both (e.g. *Honckenya peploides*, *Poa* spp.) might explain the observed decrease of the less competitive species that are more-or-less closely linked with snow-beds, particularly those which are more light demanding and grow in open vegetation, as for instance *Saxifraga* spp. That species are invading new vegetation types is also indicated by our analysis of change in species co-occurrences, which found snow-bed species on average to occur less frequently together with other species in plots, whereas e.g. *Salix herbacea* and *Empetrum nigrum*, and several species of *Poa* and *Festuca*, and *Trisetum spicatum* were on average found to co-occur more often with the majority of the focus species (see Appendix Table S2).

A similar trend was found for species growing close to the shore on sandy beaches. We found that *Mertensia maritima* had significantly decreased in both frequency and abundance over the past 80 years, whereas its associated species *Honckenya peploides*, *Carex maritima*, and *Cochlearia groenlandica* have increased in frequency or abundance, or both. The increase in these sand-binding (*Carex maritima*; Russell & Wellington 1940), shady and wind protecting plants might locally have caused more stable ground and increased soil moisture. Thus, environmental conditions in these sandy habitats might have changed in favour of these species with superior ability to compete for light and space.

Further consequences of a warmer climate may also be important drivers of the observed changes in vegetation on Jan Mayen Island, in particular in wetter habitats such as snow-beds. It is likely that warming in addition to a potential drying-out of snow-beds has increased mineralisation rates (Björk & Molau 2007). This rise in nutrient availability in combination with a prolonged growing season might have led to the successful dispersal, establishment, and increased growth of more nutrient demanding species in snow-beds. The observed 19- and 80-year changes in the vegetation, in particular the increase of more competitive dwarf-shrub and graminoid species of taller and denser growth, and the decrease in snow-bed species, might signal an ongoing turnover from discontinuous to continuous vegetation, which is documented by several other studies in the high Arctic (Sturm et al. 2001, Tape et al. 2006, Prach et al. 2010).

We found the same trend in the observed changes in species frequency and abundance over the time periods considered. However, although differences in climatic conditions were more pronounced in the 19-year comparison than in the long-term comparison and temperatures have increased faster over the past 40 years with the coldest years noted in the late 1960s (Øseth 2010), our study found both magnitude of change and number of significantly responding species to be more pronounced when focusing on the 80-year comparison. This might indicate slow responses of arctic vegetation to changes in its environment such as climate, and changes will only become visible over longer time periods. Hence, it confirms the observation that arctic vegetation may resist climate warming over periods exceeding a decade as found by Hudson & Henry (2010). The observed modest changes on the arctic island of Jan Mayen are in line with the findings of e.g. Daniëls et al. (2011) and Prach et al. (2010), who found modest changes in vegetation composition in the Arctic over 40 years and 70 years, respectively. The overall vegetation stability seems to match with the observed negative relationship between vegetation change and productivity (Grime et al. 2008, Virtanen et al. 2010) indicating that in low productive communities slow-growing species lack the capacity for rapid responses to climatic shifts.

Consistency in 19- and 80-year trends in frequency was found for several species (e.g. *Salix herbacea*, *Silene acaulis*, *Trisetum spicatum*, *Saxifraga cespitosa*, *S. rivularis*), and little consistency was found for trends in species abundance (but see *Salix herbacea*, *Silene acaulis*), indicating that for these species long-term changes in frequency might be predictable from shorter-term observations. However, correlations of species co-occurrences were not consistent between the two time-scales suggesting that co-occurrence patterns across species are not predictable from short-term studies. Since both frequencies and abundances of several *Saxifraga* species with small rosettes (e.g. *S. cespitosa* and *S. rivularis*) decreased over both time-scales considered, whereas long-lived clonal species such as *Salix herbacea* and *Silene acaulis* increased frequencies, it is likely that growth form could to some extent explain the direction of vegetation response to warming climate trends.

When focusing on the two inventories separately, discrepancies in the observed trends in frequency and abundance were found for some species (e.g. *Honckenya peploides* and *Poa alpigena* in Lid's study). Opposite trends in the same species' frequency and abundance are likely to be a result of the sampling design applied in this study, where the lack of non-permanent plots meant that the vegetation in the different vegetation types could not be sampled from exactly the same plot as in the previous sampling. Effects of plot relocation such as these may also explain the conspicuous decrease in the abundance of *Carex bigelowii*, which is rather extreme in comparison with the negative trends found for other species. Although the distribution of *Carex bigelowii* might have become particularly reduced, both its low abundance and scattered growth (in comparison to high abundance observed at other localities not included in Lid's sampling) and the fact that it was the only species out of five that could be re-found at the given locality suggest that we have missed the main distribution area for this species at that specific site.

Conclusions

This study found modest changes in the vegetation composition on Jan Mayen Island over the past 19 and 80 years, which may be explained best by a prolonged growing season, as well as alterations in soil moisture, light conditions, and nutrient availability due to a warmer climate. These findings on Jan Mayen Island, which is virtually undisturbed by grazers and human land-use, are consistent with the observations and suggestions from vegetation studies on the arctic mainland, that increases in dwarf-shrub, shrub and (perhaps) graminoid species are a result of recent climate change. Moreover, our findings show that long-term studies are needed to identify recent changes in arctic vegetation, where responses to altered environmental conditions are slow. The comparison of changes over 19 and 80 years illustrates that predictions of long-term changes based on short-term findings are possible to some extent. However, the inconsistency at species level highlights the need to consider time-scales when making projections of vegetation change in recent decades, which could be less time-scale dependent when focusing on plant functional types such as growth form.

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Supporting Information

Table S1: Geographic positions of the meteorological station number 99950 on Jan Mayen since 1921 (Steffensen 1969).

Latitude	Longitude	Station height	Years of record
70°59' N	8°20' W	21 m	1921-27
70°59' N	8°21' W	23 m	1928-40
71°0' N	8°25' W	14 m	May - July 1941
71°0' N	8°21' W	30 m	July - September 1941
71°0' N	8°26' W	26 m	Oct. 1941 - Sep. 1943
71°0' N	8°26' W	18 m	Oct. 1943 - Aug. 1946
71°1' N	8°26' W	5 m	Sept. 1946 - Sep. 1949
71°1' N	8°26' W	40 m	Oct. 1949 - Sep. 1962
70°56' N	8°40' W	11.5 m	since Sep. 1962

Table S2: Average changes in species co-occurrences. Positive and negative values indicate that a species co-occurred more often or less often with other species in 2010 than in the previous sampling in 1930 or 1991. Species abbr. = species name abbreviation.

Species	**Species abbr.**	**1930-2010**	**1991-2010**
Arabis alpina	*Arab.alpi*	-0.14	
Beckwithia glacialis	*Beck.glac*	0.00	-0.06
Bistorta vivipara	*Bist.vivi*	-0.15	0.03
Botrychium lunaria	*Botr.luna*	0.14	
Calamagrostis neglecta	*Cala.negl*	0.13	
Cardamine bellidifolia	*Card.bell*		0.01
Carex bigelowii	*Care.bige*	0.07	
Carex lachenalii	*Care.lach*	-0.28	
Carex maritima	*Care.mari*	0.20	
Cerastium alpinum/arcticum	*Cera.arct*	-0.02	-0.08
Cerastium cerastoides	*Cera.cera*	-0.20	-0.29
Cochlearia groenlandica	*Coch.groe*	0.03	
Cystopteris fragilis	*Cyst.frag*	0.08	
Draba nivalis	*Drab.niva*	0.11	-1.00
Draba sp. (except *D. nivalis*)	*Drab.norv*	-0.03	-0.03
Empetrum nigrum	*Empe.nigr*	0.02	
Epilobium anagallidifolium	*Epil.anag*	-0.06	
Equisetum arvense	*Equi.arve*	-0.03	
Euphrasia wettsteinii	*Euph.wett*	0.15	0.27
Festuca richardsonii/rubra	*Fest.rubr*	0.01	
Festuca vivipara	*Fest.vivi*	-0.08	0.05
Honckenya peploides	*Honc.pepl*	0.19	
Koenigia islandica	*Koen.isla*	0.02	
Luzula arcuata/arctica/confusa	*Luzu.arcu*	-0.23	0.00
Luzula spicata	*Luzu.spic*	-0.03	
Mertensia maritima	*Mert.mari*	0.07	
Minuartia biflora	*Minu.bifl*	-1.00	0.03
Minuartia rubella	*Minu.rube*	0.13	-1.000
Omalotheca supina	*Omal.supi*	-1.00	
Oxyria digyna	*Oxyr.digy*	-0.05	-0.03
Phippsia algida	*Phip.algi*	-0.04	
Poa alpigena	*Poa.alpg*	0.09	
Poa alpina	*Poa.alpi*	-0.20	0.03
Poa arctica	*Poa.arct*	0.16	
Poa glauca	*Poa.glau*	0.23	0.26
Puccinellia nutkaensis	*Pucc.nutk*	0.10	
Ranunculus pygmaeus	*Ranu.pygm*	-0.23	
Sagina cespitosa	*Sagi.cesp*	-0.17	
Sagina nivalis	*Sagi.niva*	-0.03	-0.06
Salix herbacea	*Sali.herb*	0.11	0.05
Saxifraga cernua	*Saxi.cern*	-0.32	
Saxifraga cespitosa	*Saxi.cesp*	-0.21	-0.16
Saxifraga nivalis	*Saxi.niva*	-0.07	
Saxifraga oppositifolia	*Saxi.oppo*	-0.11	0.11
Saxifraga rivularis	*Saxi.rivu*	-0.03	-0.11
Saxifraga tenuis	*Saxi.tenu*	-0.18	0.15

Sibbaldia procumbens	*Sibb.proc*	-0.07	
Silene acaulis	*Sile.acau*	0.09	0.23
Taraxacum acromaurum	*Tara.acro*	0.16	-1.00
Taraxacum brachyrhynchum	*Tara.brac*	-1.00	
Taraxacum sp.	*Tara.sp*	-0.12	
Taraxacum torvum	*Tara.torv*	0.13	
Trisetum spicatum	*Tris.spic*	0.09	0.07
Veronica alpina	*Vero.alpi*	-0.17	

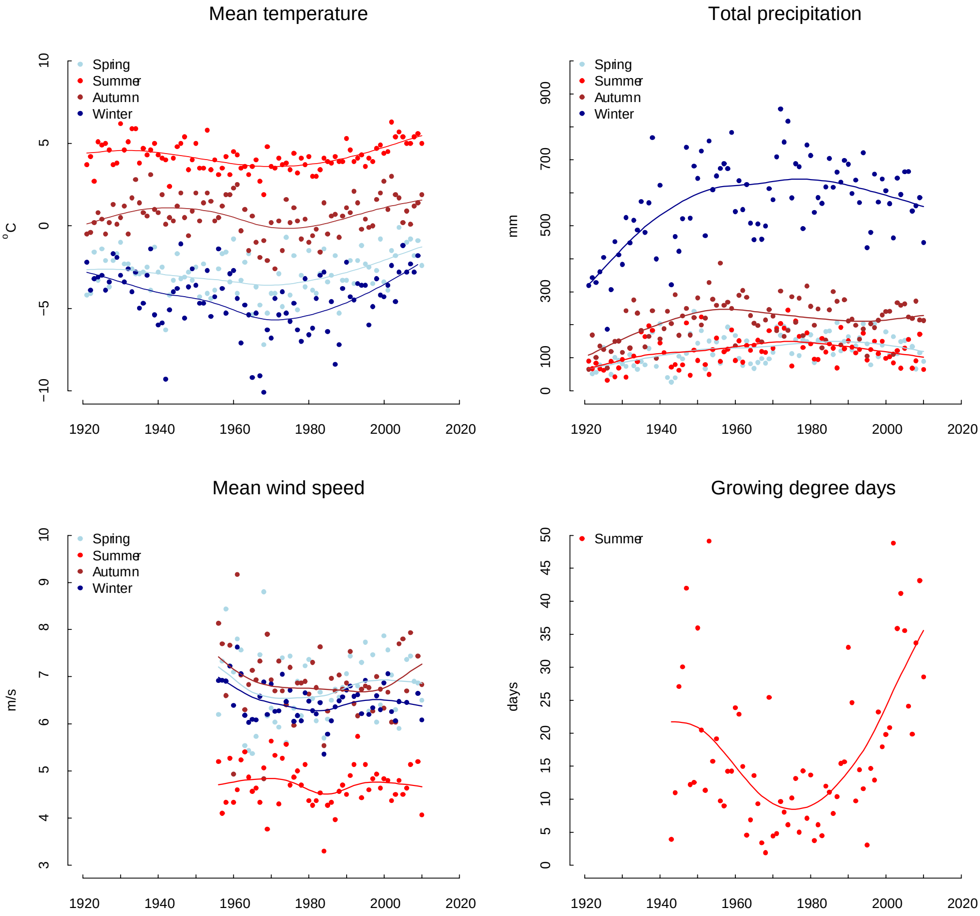
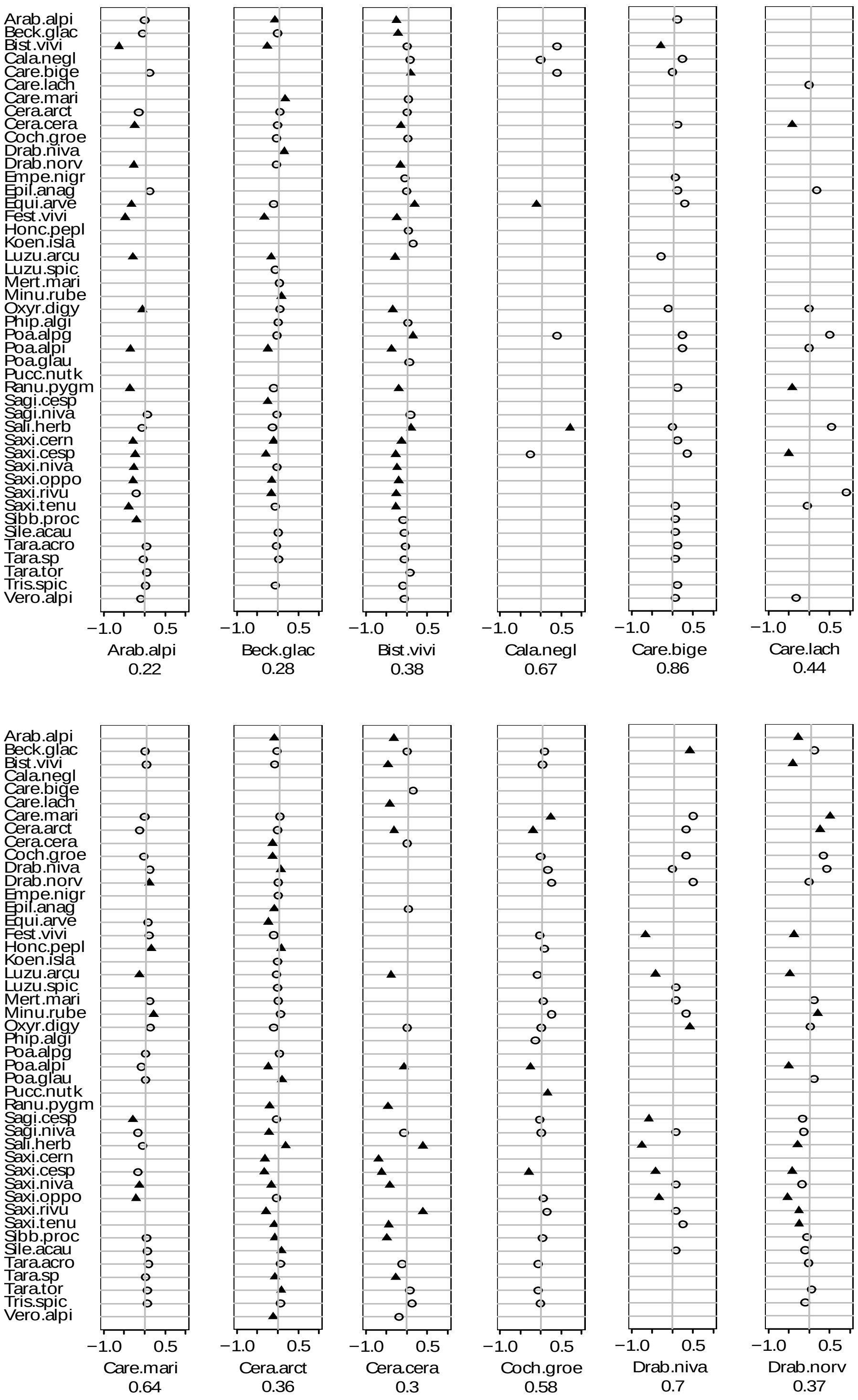
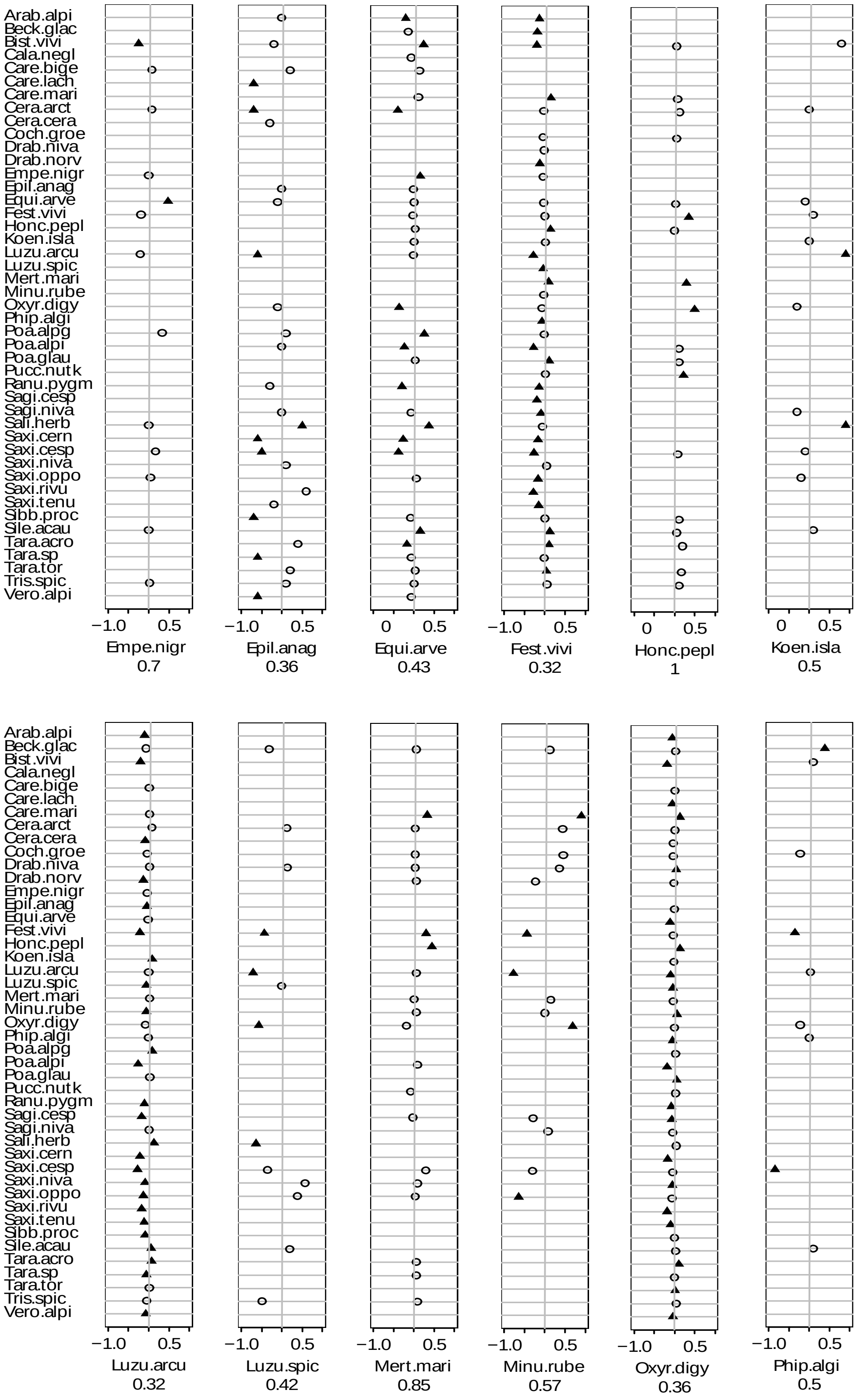


Figure S1: Last century climate chart for Jan Mayen. Values for mean seasonal temperature (1921-2010), mean seasonal precipitation (1921-2010) and growth degree days (1943-2010) are fitted with a smoother (degrees of freedom = 5; data source: www.eklima.no).

a) Jan Mayen, 1930-2010

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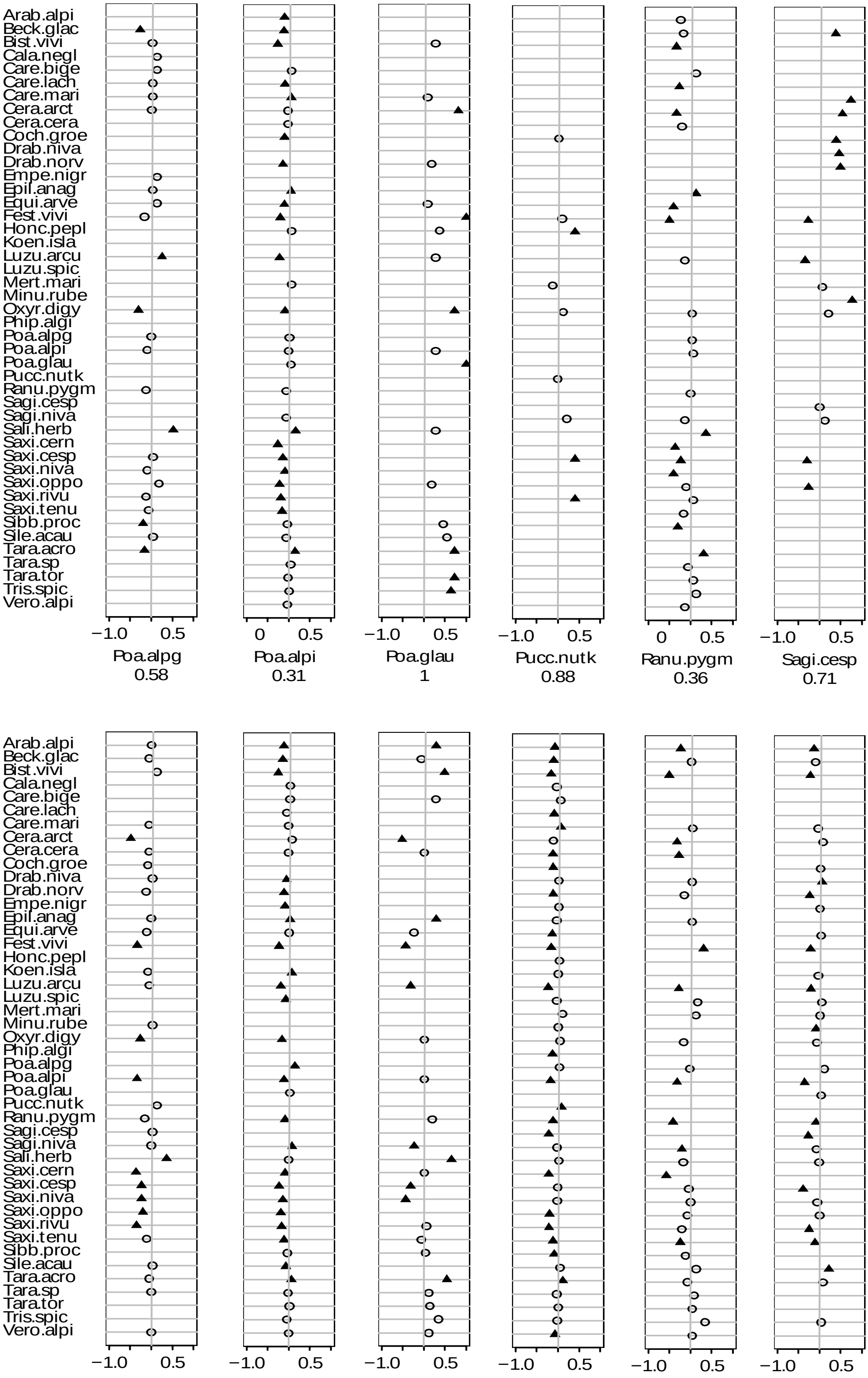
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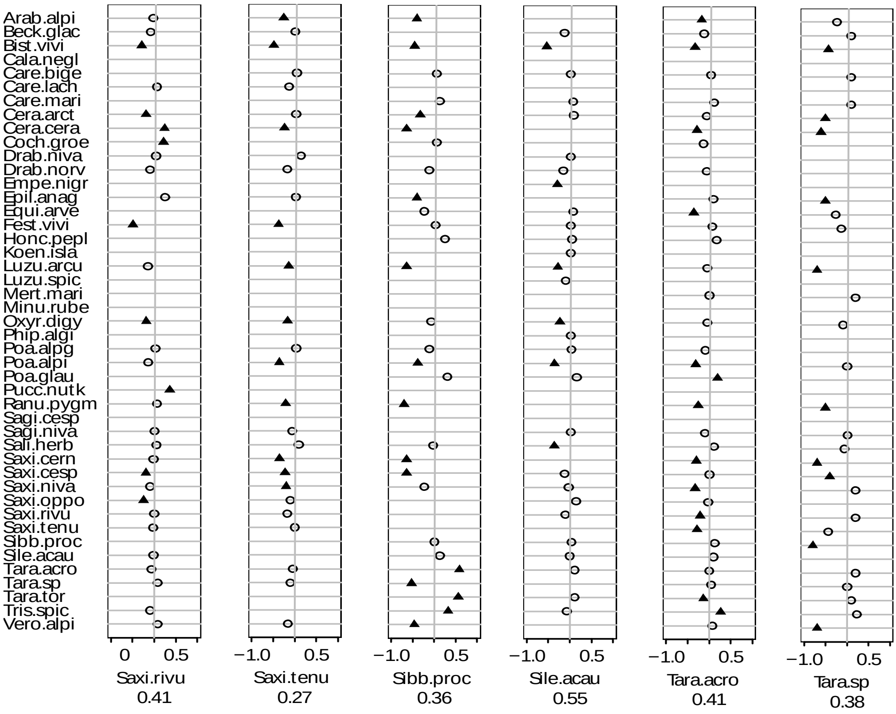
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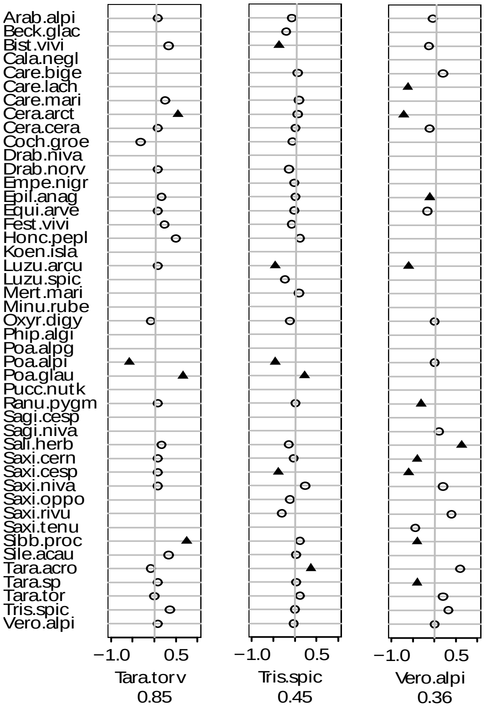
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Cala.negl
Care.bige
Care.lach
Care.mari
Cera.arct
Cera.cera
Coch.groe
Drab.niva
Drab.norv
Empe.nigr
Epil.anag
Equi.arve
Fest.vivi
Honc.pepl
Koen.isla
Luzu.arcu
Luzu.spic
Mert.mari
Minu.rube
Oxyr.digy
Phip.algi
Poa.alpg
Poa.alpi
Poa.glau
Pucc.nutk
Ranu.pygm
Sagi.cesp
Sagi.niva
Sali.herb
Saxi.cern
Saxi.cesp
Saxi.niva
Saxi.oppo
Saxi.rivu
Saxi.tenu
Sibb.proc
Sile.acau
Tara.acro
Tara.sp
Tara.tor
Tris.spic
Vero.alpi
−1.0
0.5
Tara.torv
0.85
−1.0
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Tris.spic
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Vero.alpi
0.36

b) Mt. Beerenberg, 1991-2010

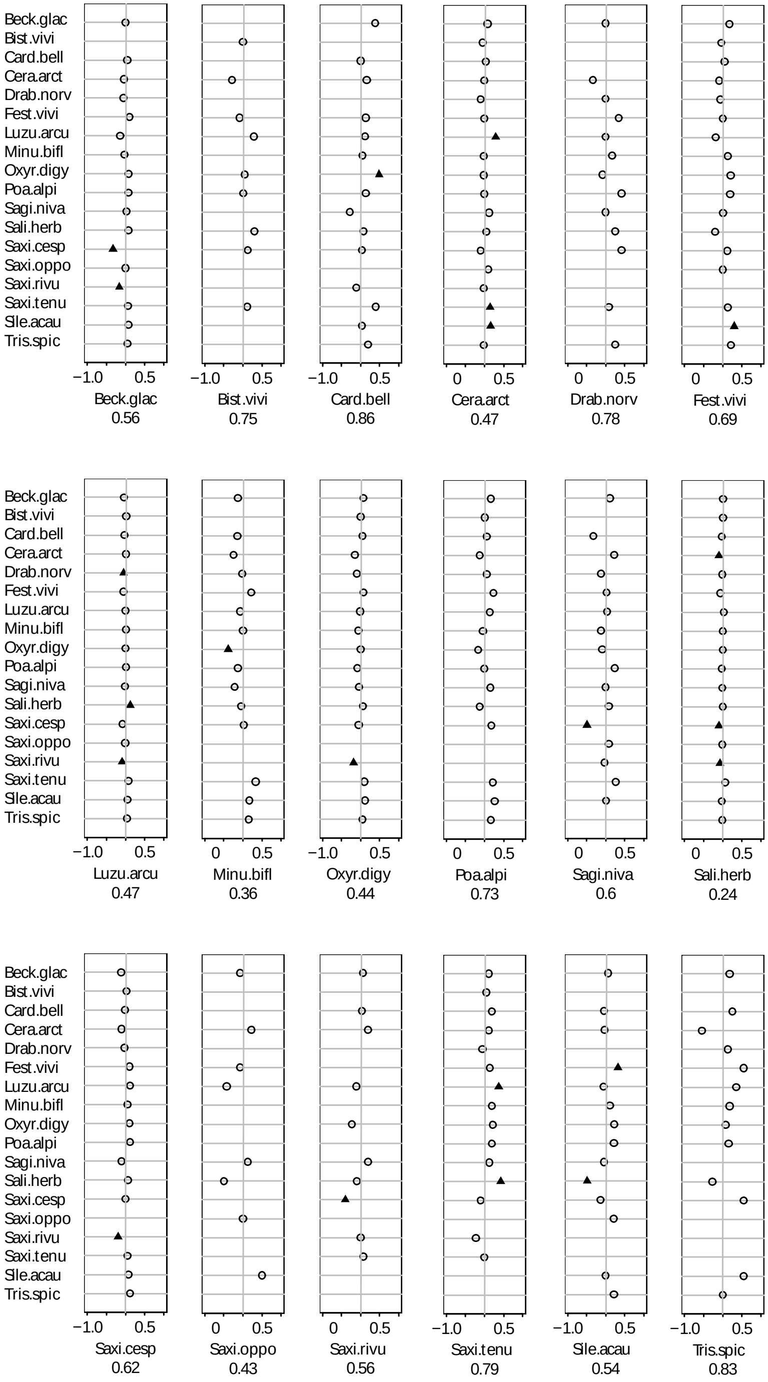

Figure S2: Changes in species co-occurrence in plots containing each of the species found a) in Lid’s synedria from 1930-2010 and b) at Mt. Beerenberg from 1991-2010. Values at the bottom of each individual plot indicate the ratio between positive and negative changes in species co-occurrences: 0 = only negative changes, 0.5 = 50% positive and 50% negative changes, 1 = only positive changes in species co-occurrence. Only species occurring in more than ten plots are considered for the calculation of change in species co-occurrence (1930-2010: n = 45 of 53 species, 1991-2010: n = 18 of 25 species). Circle = not significant, triangle = significant change in species co-occurrence ($p < 0.05$).

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Paper IV

Using species co-occurrences to quantify vegetation stability

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Abstract

Individualistic species responses to environmental change may lead to changes in species assemblages resulting in new arrangements of species composition and development of new plant communities through time. This study quantifies long-term vegetation changes in different habitats in northern Europe by exploring fine-scale changes in species co-occurrences, and tests if these changes are greater than would be expected by chance. We re-sampled vegetation in 15 arctic, alpine, and mire areas following the sampling protocols of the original phytosociological studies, which were done 20 to 90 years ago. To get an indication of vegetation stability at each site, we quantified the amount of change in species assemblages using species co-occurrences with other species. We tested if the observed changes are significantly greater than is expected by chance using a randomization test. This was done separately for vascular plants (n_{sites} = 15) and bryophytes (mosses and liverworts; n_{sites} = 4). Regression analysis was used to test if observed patterns in vascular plant stability can be explained by time-scale, plot number, or species diversity and productivity. Our results show that changes in the species arrangements of both vascular plants (at 13 of the 15 sites) and bryophytes (at all four sites) were significantly greater than is expected by chance. The observed patterns in stability were not found to be related to time-scale, plot number, or diversity and productivity. This study shows that fine-scale changes in the arrangement between species (vascular plants and bryophytes) over the past decades are not random. Our results suggest that site-specific factors other than diversity or productivity (e.g. grazing pressure, land-use, soil conditions, climate, species interactions) might be important drivers explaining the observed patterns in the stability of arctic, alpine, and mire vegetation in northern Europe.

Introduction

Recent climatic and other environmental changes may cause substantial changes in species abundances and distributions (Walther 2003). Examples come from studies of shifts in species distributions documenting general trends northwards in latitude (in the Northern hemisphere; (Sturm, Racine & Tape 2001; Tape, Sturm & Racine 2006; Tømmervik, Johansen, Riseth, Karlsen, Solberg et al. 2009; Wilson & Nilsson 2009) and upwards in altitude (Chapin, Shaver, Giblin, Nadelhoffer & Laundre 1995; Grabherr, Gottfried & Pauli 1994; Kullman 2002; Lenoir, Gègout, Marquet, de Ruffray & Brisse 2008; Wilson et al. 2009). Other examples come from wetter habitats, such as mires or snow beds, where the moisture regime may have changed. Here, the vegetation has been observed to have been invaded by species from surrounding areas and to have changed in favour of species of high competitive dwarf-shrubs, trees, and graminoids (Chapman & Rose 1991; Daniëls, de Molenaar, Chytry & Tichy 2011; Kapfer, Grytnes, Gunnarsson & Birks 2011; Klanderud & Birks 2003). Despite these general observations on species changes, observational and experimental studies also show that there is considerable variation between species, indicating that species respond individualistically to environmental changes (Arft, Walker, Gurevitch, Alatalo, Bret-Harte et al. 1999; Chapin & Shaver 1985; Daniëls et al. 2011; Kapfer et al. 2011; Klanderud 2008; Klanderud et al. 2003; LeRoux & McGeoch 2008). Individualistic species responses to an environmental change may lead to alterations in species assemblages, as some species may change in abundance and/or migrate whereas other species that are differently adapted to the new environmental conditions may persist unchanged or disappear. If species respond individualistically, this will result in new arrangements of species composition and unstable plant communities through time (Jackson 2006).

To detect long-term vegetational changes at a fine scale, studies commonly compare patterns in species richness or frequency and abundance of individual species (Daniëls et al. 2011; Kapfer et al. 2011; Pajunen, Virtanen & Roininen 2008). Changes in these may indicate changes in the composition and arrangement of species but even if species change their frequency or abundance they do not necessarily change their associated species as they, for instance, simply became more dominant within the same community. Thus, to detect changes in the assemblage of species a different approach is needed. In this study we examine the stability of plant communities by exploring patterns in species co-occurrences with other species and identify if species have changed their associated species over the past decades using data-sets from historical studies and corresponding recent resurveys. By calculating an index value specifying a species' co-occurrence with another species and comparing it over time, any positive or negative change will indicate that a species was found more often or less often in association with its companion species. Hence, the magnitude of changes in species co-occurrences with other species can be used as proxy for the stability of the vegetation within an area.

Stability of communities may depend on many different factors, both intrinsic (e.g. community productivity, diversity) and extrinsic (e.g. environmental change). The role of species richness for stability has been widely discussed, and species-rich plant communities are commonly viewed as being more resistant or resilient to environmental changes (e.g. disturbance) as they are also thought to be more diverse in traits that favour tolerance and recovery (Cottingham, Brown & Lennon 2001; Mikkelsson 2009; Mulder, Uliassi & Doak 2001; Tilman, Reich & Knops 2006; Yachi & Loreau 1999), whereas species-poor communities may be more sensitive to invasions by new species (Elton 1958; Tilman, Knops, Wedin, Reich, Ritchie et al. 1997). Productive sites are found to be more prone to climatic changes (Virtanen, Luoto, Rämä, Mikkola, Hjort et al. 2010) in accordance with predictions from plant-strategy theory (Grime, Fridley, Askew, Thompson, Hodgson et al. 2008). Low productive sites, such as at high latitudes and altitudes, are often considered to be more stable than sites with high productivity, as they mainly consist of stress-tolerant species that are resistant to external change (Grime 2001). In these nutrient-limited areas, competition for resources may be a more important driver for changes in community composition (Chapin et al. 1995; Tilman 1982, 1988). However, even if vegetation in arctic and alpine areas is known to respond slowly to changes in environment (Daniëls et al. 2011; Hudson & Henry 2010; Prach, Kosnar, Klimesova & Hais 2010), changes in vegetation may be expected to increase with time if environmental changes are unidirectional independent of which habitat is considered.

This study aims to quantify and compare community stability in vegetation of different arctic, alpine, and mire habitats and regions in northern Europe. To aid interpretations of the observed patterns in vegetation stability, different variables potentially important for species assemblages (e.g. site-specific vegetation diversity and productivity) are also analyzed for their relationship with the observed stability, or change.

Material and Methods

Data sources

To study trends in vegetation assemblages in northern Europe over the past decades, we have re-sampled several published and unpublished historical plant-sociological studies. In these historical studies, vegetation was sampled by the use of fine-scale sampling plots and from different vegetation types representative for a site or area. From each plot, all

Figure 1: *Location of the 15 alpine, arctic, and mire areas in northern Europe. Map source: http://www.mappinghacks.com/data/, provided by Bjørn Sandvik (thematicmapping.org).*

plant species of the plant group(s) studied were listed. By applying the same methods and restrictions as in the historical samplings, we re-sampled vegetation in 15 different areas (Table 1). These areas are distributed from west Spitsbergen (Svalbard) in the north (78° N, 15° E) via Greenland in the west (67° N, 50° W) to south-west Sweden (57° N, 14° E) in the south (Figure 1). Each site is classified as arctic, alpine, or mire. The original sampling for the 15 data-sets was conducted between 1924 and 1991, and the re-sampling was conducted between 1995 and 2010 with a time lapse between the two surveys varying between about 20 and 90 years.

Sampling methods of inventories in the same site or area (i.e. first survey and corresponding resurvey) are similar but they may differ slightly from studies at other sites concerning spatial scale and also if an effort was made to relocate approximately the original plots, the latter of which depends on the availability of information about the original plots. In most of the studies used for this analysis, vegetation was recorded using fine-scale plots of 0.5 m x 0.5 m or 1 m x 1 m. The number of plots may differ between the original survey and the corresponding resurvey and between the different studies.

Our final data-set includes floristic data from ten arctic, four alpine, and one mire site (Table 1). All data-sets consist of a comprehensive list of both the presence and the abundance of vascular plant species. Bryophytes were only recorded in four of the 15 studies (Table 1).

Statistical analyses

To quantify stability at each site we determined the amount of change in the species assemblages, i.e. to which extent species have changed their associated species over time. One focus species at a time was considered. We counted the number of plots where the focus species co-occurs with all the other species individually. This was done separately for the data-sets of the old and the new inventories, and only species occurring in at least five plots were considered in order to reduce the effects of rare species in the analysis. To account for the different number of plots sampled in the surveys, species co-occurrences were standardized by dividing the co-occurrence of the focus species by the total number of plots containing the focus species. Then, a change in species co-occurrence was calculated by subtracting the co-occurrence value of the older inventory from the new inventory (= observed change in species co-occurrence). Resulting positive change-values indicate that associated species were 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 (see Appendix Figure S2 in Supporting Information). To get an indication of the temporal stability of the different vegetation types considered, the absolute values of change in co-occurrence were calculated, and a site-specific average value was calculated from these absolute species co-occurrence change-values. This is taken as an estimate of the stability of the community at each site. A low value indicates a high stability of the species assemblages.

Even if changes in species co-occurrence in the vegetation of different habitats and sites may be observed, it is not clear what these changes mean, i.e. how big these changes are in comparison to what change may actually be expected by chance alone. We therefore used a null model and compared historical and re-sampled plots of randomly selected plots from both data-sets together for patterns in species co-occurrences (= expected change in species co-occurrence). The data-sets were then analyzed in

TABLE 1: *Summary of the characteristics of the study areas. Total no. species = total number of species in the historical sampling and re-sampling together. VP = vascular plants, B = bryophytes.*

Area	Type	Latitude/longitude	Original study and site description	Year(s) of 1. survey	Year of re-survey	Time scale	Vegetation studied
Svalbard, W Spitsbergen	arctic	77°50′ - 79°00′ N, 13°00′ - 18°00′ E	Lid 1967	1924	2009	85	VP
Svalbard, W Spitsbergen	arctic	77°50′ - 79°00′ N, 13°00′ - 18°00′ E	Hadac 1946	1939	2009	70	VP
Svalbard, W Spitsbergen	arctic	77°50′ - 79°00′ N, 13°00′ - 18°00′ E	Rønning 1965	1958/59/60	2009	50	VP
Jan Mayen	arctic	70°50′ - 71°10′ N, 7°80′ - 9°15′ W	Lid 1964	1930	2010	80	VP
Jan Mayen, Mt. Beerenberg	arctic	70°50′ - 71°10′ N, 7°80′ - 9°15′ W	Virtanen, Lundberg, Moen and Oksanen 1997	1991	2010	19	VP
N Finland, Saana	arctic	69°00′ N, 20°80′ E	Eskelinen and Oksanen 2006	1990	2010	20	VP, B
N Sweden, Kilpisjärvi	arctic	69°03′ N, 20°50′ E	Mikkola and Sepponen 1986	1982	2008	26	VP, B
N Norway, Finnmark, Rastigaissa	arctic	69°5′ - 70°10′ N, 25°50′ - 26°30′ E	Ryvarden 1969	1964	2008	44	VP
N Norway, Troms	arctic	68°22′ - 70°19′ N, 4°52′ - 12°12′ E	Lunde 1962	1954/55/56	2010	55	VP
W Greenland, Kangerlussuaq	arctic	67°01′01″ N, 50°41′22″ E	Böcher 1954	1946	2010	64	VP
C Sweden, Sylene	alpine	63°01′12″N 12°11′55″E	Nordhagen 1927	1927	1999	72	VP, B
C Norway, Rondane	alpine	61°53′ N, 9°50′ E	Dahl 1956	1940-50	2004	59	VP
C Norway, E Jotunheimen, Sikkilsdal	alpine	61°28′ N, 8°50′ E	Nordhagen 1943	1920s	2008	90	VP
C Norway, W Jotunheimen	alpine	61°28′ N, 8°10′ E	Jörgensen 1933	1930/31	1998	67	VP
S Sweden, SW Götaland, Åkhult	mire	57°10′ N, 14°30′ E	Malmer 1962	1954	2008	54	VP, B

the same way as for the observed changes (see above). If the observed changes are greater than the expected changes, this indicates that the observed trends in species co-occurrences are 'real' and have occurred due to other factors than chance. To test whether the observed changes were significantly greater than the expected changes, permutations of the null model were run 999 times and the exact *p*-value was calculated by counting the number of times the observed change was greater than or equal to the expected change. The expected changes were subtracted from the observed changes in species co-occurrence prior to relating it to the explanatory variables (= relative change in species co-occurrence). Regression analyses were conducted to explore the relationship between the observed variation in stability and different factors or drivers that might influence community stability and its detection, namely: (1) time between two surveys, (2) number of plots, and (3) vegetation diversity and productivity.

(1) We tested whether changes in species co-occurrences (stability) are dependent on the time elapsed between the two surveys in each of the studies included. Because the changes in stability may not be linear with time we tried two different transformations of time in addition to the non-transformed values when testing for the relationship between stability and time between surveys, namely a logarithmic and a square-root transformation. For some data-sets, the time-scale could not be defined exactly. Thus, if sampling had been conducted over more than one growing season, the year in the middle of the period was used to calculate the time between the original survey and the resurvey. If sampling was conducted over two years, the first year of sampling was used.

(2) As the different data-sets used in this study differ in the numbers of plots (both total number of plots and number of historical and re-sampled plots), we used regression analysis to test if plot number may explain statistically our estimates of stability. As the number of plots may merely affect the random change expected, we also used plot number as a predictor for the expected change.

(3) Regression analysis was further used to test to which extent stability may be explained by site-specific diversity and productivity. Different measures of species diversity were used, namely α-diversity (species richness per plot), γ-diversity (species richness per site), and β-diversity using all plots from both data-sets together. The latter was calculated using Sørensen dissimilarity index (Sørensen 1948). We further tested if plot number has an effect on the estimation of γ-diversity. This was done by randomly selecting a rarefied number of plots (i.e. 58 plot = total number of plots of the smallest data-set) from each data-set after plots from historical sampling and re-sampling had been randomized. Average γ-diversity was calculated from 1000 permutations. To obtain an indication of the productivity at each site we calculated weighted average Ellenberg indicator values (Ellenberg, Weber, Düll, Wirth, Werner et al. 1992; Goff & Cottam 1967) for temperature and nutrients, high values of whose indicate a high productivity. Indicator values were weighted by the number of plots a species occurred in at each site. A linear regression model was found to fit the data best (in comparison with logarithmic and square-root models) for all regressions. *F*-tests were used to test the relationships for statistical significance.

To get an indication about variation in stability between the different plant groups, the analyses of observed and expected change in species co-occurrence were run for vascular plants and bryophytes separately for those sites that had sampled both groups. Because of the low number of observations for bryophytes (four studies), regression analyses were run for vascular plant species only. All statistical analyses were made using R version 2.11.1 (R Development Core 2010).

RESULTS

Observed changes at the different sites were significantly greater than expected by chance (except for Hadač's sites on Svalbard and in Rondane; Figure 2), indicating a non-random turnover in species arrangements through time. Expected changes in species co-occurrences were positively and significantly correlated with observed changes (Pearson product-moment correlation; $r = 0.81$, $p < 0.001$).

On average for each main habitat type, relative changes in species co-occurrences (i.e. observed minus expected change) were relatively similar, but increased from 0.057 at alpine sites to 0.064 in the Arctic and 0.073 at the mire site (Figure 2), indicating a reduced stability in the vegetation of the latter. The difference between arctic and alpine stability was not statistically significant (two sample *t*-test, $p = 0.787$; the difference to mire stability could not be tested because of only one available observation). In the Arctic, the biggest turnover in species assemblages was found for Lid's and Rønning's study sites on Svalbard (0.114 and 0.105) and for Finnmark (0.111). On Jan Mayen (0.075, average for two sites), vegetation stability was lower than in Troms (0.058), Saana (0.045), Greenland (0.035), Kilpisjärvi (0.020), and Hadač's sites on Svalbard (-0.002, expected change > observed change), which were found to be most stable. In the alpine vegetation of the Sylene mountain area, highest vegetation turnover was found (0.122), whereas vegetation of the other alpine sites studied was stable (between 0.027 and 0.039). No significant relationships were found between changes in species co-occurrences and the predictor variables time-scale, plot number, or diversity and productivity (Figure 3, Appendix Figure S3, S5).

For the bryophytes, at all four sites, observed changes in species co-occurrences were significantly greater than the expected changes (Figure 2). In

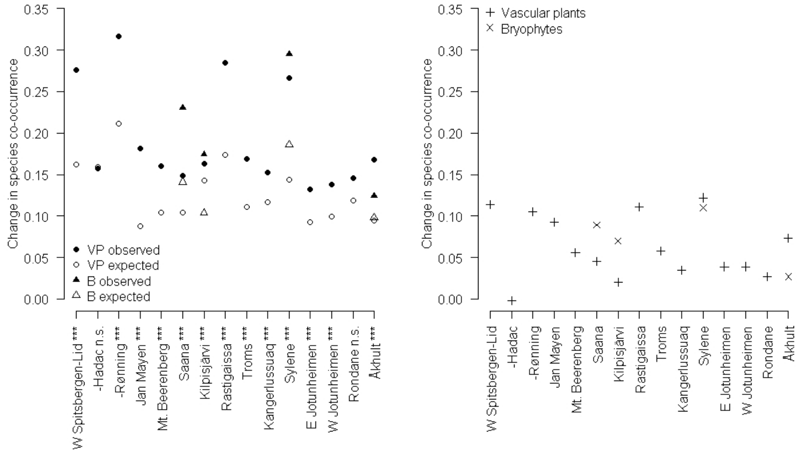

FIGURE 2: *Observed changes and changes as expected by chance (left) and relative changes in species co-occurrence (i.e. observed minus expected; right) per area. Change values are on average for absolute changes. Smaller change values indicate higher stability in species assemblages. Whether the absolute changes (both vascular plants and bryophytes) are significantly greater than the expected changes is indicated by significance levels: *** = p < 0.001, n.s. = not significant. VP = vascular plants, B = bryophytes.*

comparison with vascular plants, relative changes in bryophyte co-occurrences were greater in the vegetation at arctic sites (0.079 on average for Saana and Kilpisjärvi), whereas at alpine Sylene and the Åkhult mire, relative changes were found to be smaller than those in vascular plant species (0.110 and 0.027; Figure 2).

DISCUSSION

This is one of the first studies to quantify long-term stability in the vegetation of arctic, alpine, and mire habitats in northern Europe by exploring fine-scale changes in the arrangement of species using species co-occurrences. By focusing on 15 different sites, this study confirms that changes in plant community stability are greater than expected by chance alone, which is suggested by several studies observing species individualistic changes in response to environmental change (Chapin et al. 1985; Kapfer et al. 2011; Klanderud et al. 2003; LeRoux et al. 2008), but which has not been tested before. It is likely that site-specific factors explain observed non-random patterns in stability. This is supported, for instance, by the changes observed in the vegetation of eastern and western Jotunheimen. Although in these two areas vegetation was sampled using different sampling methods (W Jotunheimen: transect data sampling approximately the same plots, see Klanderud et al. 2003; E Jotunheimen: random placement of plots, ratio between historical and re-sample plots = 3/1, see Felde, Kapfer & Grytnes submitted), similar trends in vegetation stability were found indicating that similar vegetational changes have occurred across the area over past decades. Similar trends were also found in the vegetation of two of the three areas studied on Svalbard (Lid's and Rønning's sites). However, the relative constancy at Hadač's sites indicates that changes in the same area may not only be site-specific (e.g. due to similar changes in climate and soil conditions) but also time-specific, if, for instance, after the first sampling the vegetation is exposed to different changes in the environment (e.g. climate, grazing) than if it was sampled before or after being affected by these changes. However, the observed site-specific patterns in stability are also in accordance with other studies documenting vegetational changes of different extents. For instance, relatively large changes were found in the vegetation of the Åkhult mire (Gunnarsson, Malmer & Rydin 2002; Kapfer et al. 2011), whereas vegetational changes at the alpine area of Rondane were very small (unpublished data). This is reflected by our study, which found relatively large changes in the assemblage between species on the Åkhult mire, whereas in Rondane no significant changes were found.

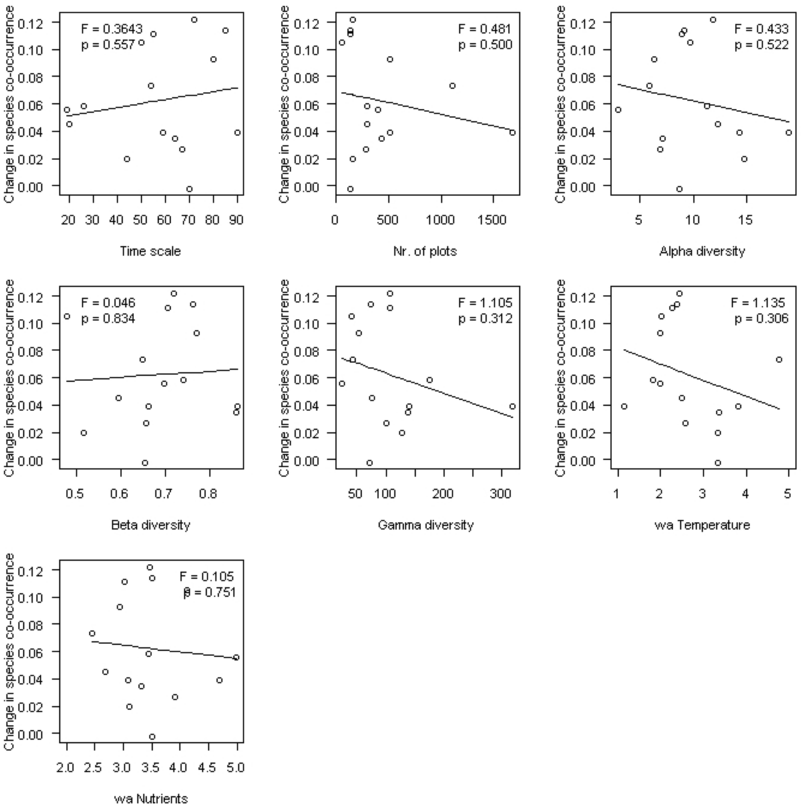

Figure 3: *Relationship between time-scale, number of plots, α, β-, γ-diversity, and weighted averaged (wa) temperature and nutrients as indicators for productivity on the relative changes in vascular plant species co-occurrence. F = F-value and p = significance level of the linear regression models.*

However, other than expected from suggestions of other studies (Bezemer & van der Putten 2007; Lehman & Tilman 2000; Tilman et al. 2006), site-specific species diversity and productivity in our study do not explain the observed patterns in stability at the 15 study sites. Hence, other factors (e.g. changes in abiotic and biotic conditions) may play a more important role in influencing stability in the species assemblages.

In this study, expected changes in species co-occurrences were found to have a high positive relation with the observed changes. It therefore may be assumed that effects internal to a data-set may influence our results. The data-sets used may differ in both time period between sampling and re-sampling and how many plots were sampled both within one data-set (i.e. historical sampling vs. recent re-sampling) and between different data-sets. Whereas time-scale was not found to explain the observed pattern in stability, differences in plot number between the different studies investigated may play a role in influencing the magnitude of change, with the effect becoming more pronounced when plot number decreases (see Appendix Figure S3). However, the differences caused by different plot number are marginal, and a clear effect of plot number on our results was only found when considering expected changes (see Appendix Figure S4). The lack of a significant relationship between the number of plots and the observed changes is independent of whether observed changes were corrected for expected changes (see Results) or not (see Appendix Figure S4). Moreover, plot number was found to be significantly positively correlated with γ-diversity suggesting that our results might be correspondingly biased. But even when accounting for plot numbers using a rarefied low but equal number of plots in the estimation of site-specific γ-diversity, the previously observed non-significant relation with change in species co-occurrence remains unchanged (see Appendix Figure S5). Hence, both these cases demonstrate that plot number does not satisfactorily explain the observed pattern in stability.

Species richness is often found to be positively related with plant community stability (Bezemer et al. 2007; Tilman et al. 2006). Different field observations and laboratory experiments have shown that higher species diversity in communities occurs in association with lower stability of individual species (Lehman et al. 2000; Tilman & Downing 1994; Tilman et al. 2006), which in our study is indicated by higher changes in species co-occurrences. The relative stability in the species assemblages over long time-scales as observed in this study (all change values < 0.3 of maximal 1.0) conforms with the assumption that low productive vegetation, such as high alpine, arctic, and boreal bog vegetation responds rather slowly to changes in the environment, as the vegetation is dominated by slow-growing species (Daniëls et al. 2011; Hudson et al. 2010; Körner 2003; Prach et al. 2010). This would also explain the relative stability in bryophytes observed in the *Sphagnum*-dominated Åkhult mire, in contrast to what is found at the arctic sites (Saana and Kilpisjärvi). However, contrary to the findings of other studies proposing a negative relationship between vegetation change and productivity (Grime et al. 2008; Virtanen et al. 2010), our results do not show that more productive sites (as represented by vegetation with high indicator values for temperature and nutrients) are more dynamic and, hence, less stable.

It is likely that the relationships observed in our study are rather weak due to a relatively low number of studies included (n = 15), and that a higher number of observations might strengthen the statistical significance of our results. However, other factors than (or in addition to) diversity and productivity that may have strong influences on species composition should not be ignored. The sites included in this study differ in both site-specific biotic (e.g. species interactions) and abiotic conditions. Thus, it is very likely that site- and habitat-specific factors such as sets of individualistically responding species and corresponding biotic interactions, as well as external factors such as local climate, soil conditions and land-use change, may explain some of the observed site-specific dynamics in the species assemblages, which is also suggested by other studies on alpine (Callaway, Brooker, Choler, Kikvidze, Lortie et al. 2002; Totland & Alatalo 2002; Totland & Esaete 2002) and arctic vegetation (Dormann, van der Wal & Woodin 2004; Shevtsova, Haukioja & Ojala 1997). In particular, grazing may have considerable effects on plant species richness, vegetation composition, nutrient cycling, and plant growth (Olofsson, Oksanen, Callaghan, Hulme, Oksanen et al. 2009; Pajunen et al. 2008). As grazing pressure differs greatly between the study sites included in this study, with this pressure being more pronounced on the northern Scandinavian mainland in comparison to the low or no pressure at other sites (e.g. Jan Mayen, Åkhult mire), this might be another likely reason for the stability patterns observed in our study.

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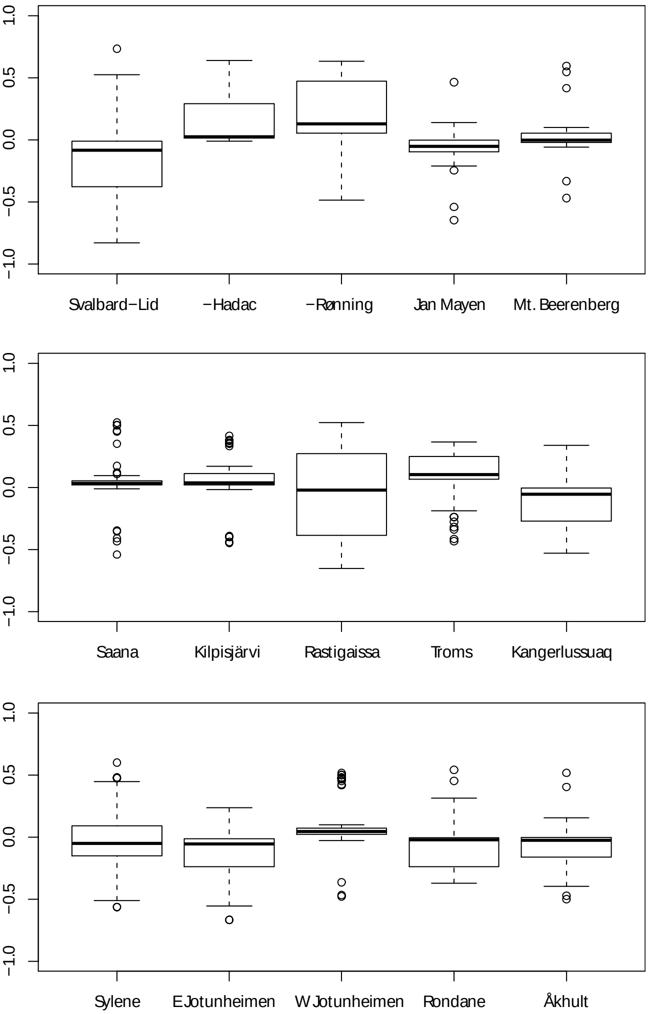
Supporting Information

(a) Vascular plants



(b) Bryophytes

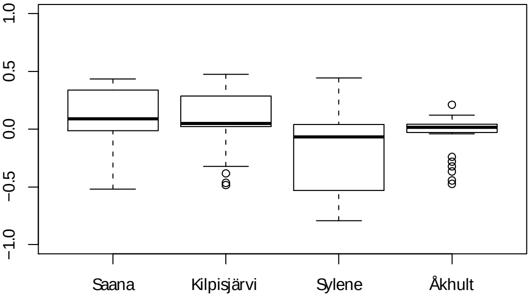


Figure S1. Changes in (a) vascular plant and (b) bryophyte species co-occurrence with other species per area averaged from the positive and negative values. Each plot is based on average change rates per species occurring in more than five plots at a site. Box-Whisker-plots: thick line = median, box = 50%, whisker = 90% of variation, points = outliers, notches are approximations of the 95% confidence interval of the median. See Table 1 in main document for area characteristics.

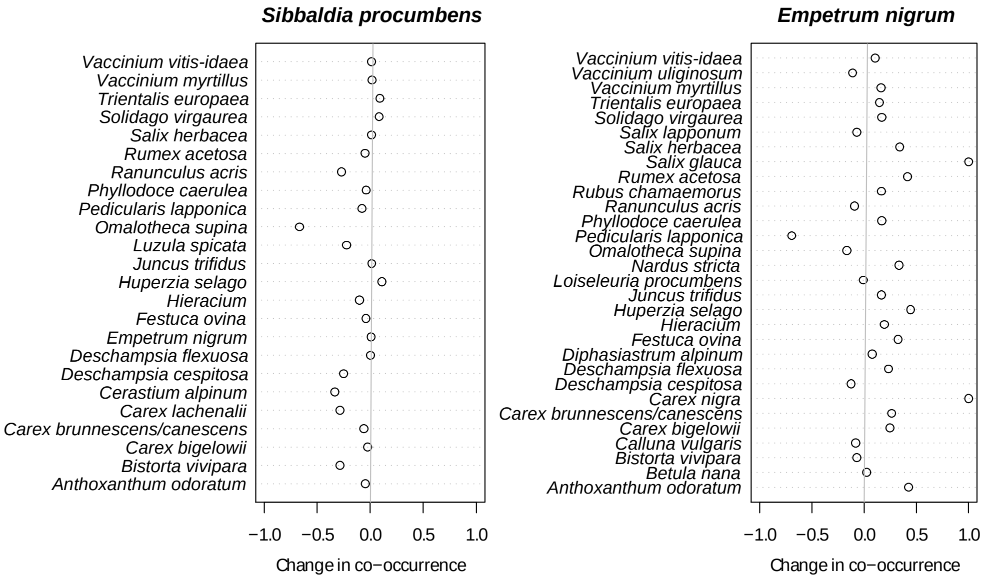


Figure S2. Examples of the temporal performance of *Sibbaldia procumbens* (left) and *Empetrum nigrum* (right) in their co-occurrence with other species in the Rondane alpine area. A positive change in co-occurrence indicates an increase in co-occurrence with the corresponding species, and vice versa for negative values. The graphs indicate that *Sibbaldia procumbens* has decreased whereas *Empetrum nigrum* has increased in the study area over the past 60 years. Based upon these species-specific change-values, a site-specific change in species co-occurrences is calculated by averaging the absolute change-rates as found for all species at a site.

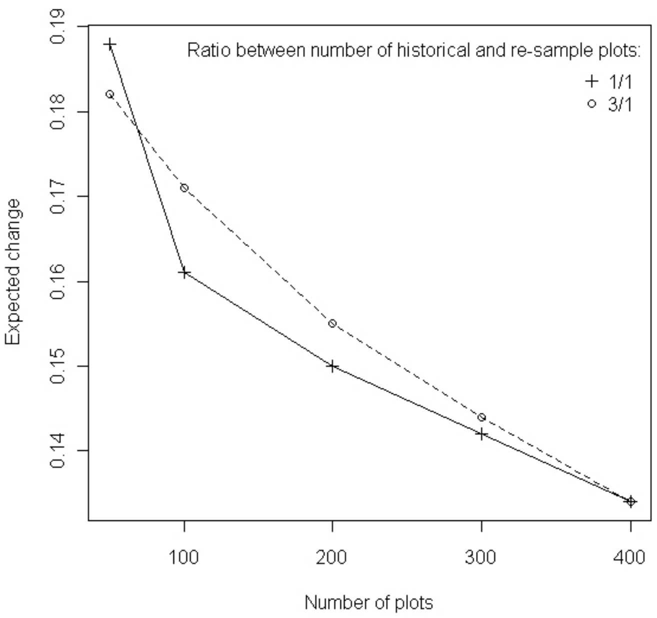


Figure S3. Example of patterns in the relationship between plot number used for calculating the expected change in species co-occurrence using the E Jotunheimen data-set ($n_{\mathrm{tot}} = 1684$).

Method: To get a clearer picture of the relationship between patterns in stability and plot number we explored patterns in expected changes in species co-occurrence using the data-set containing most plots (i.e. E Jotunheimen data-set, $n_{\mathrm{tot}} = 1684$). We therefore used (a) the same number of randomly selected plots from both the historical and the re-sampling data-sets (i.e. 400, 300, 200, 100, 50) and (b) a number of historical and replicate plots in a ratio of 3:1 (i.e. 1200:400, 900:300, 600:200, 300:100, 150:50), which conforms closely to the actual ratio between historical and re-sample plot numbers in the original E Jotunheimen data-set. Average values of 50 permutations each are shown.

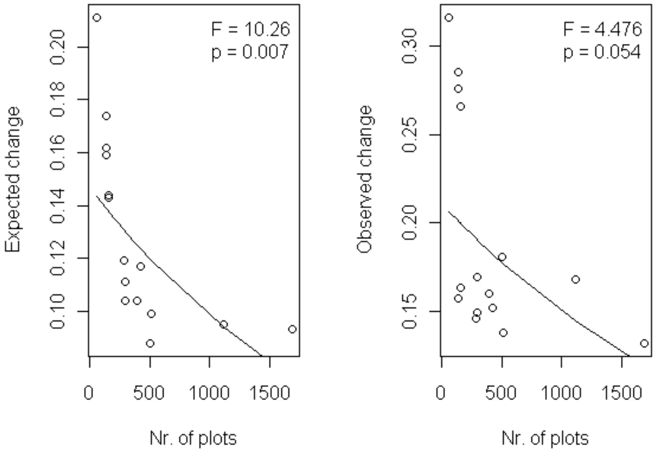


Figure S4. Relationship between the number of plots and the expected and observed change in species co-occurrence. F = *F*-value und p = significance level of the logarithmic regression model.

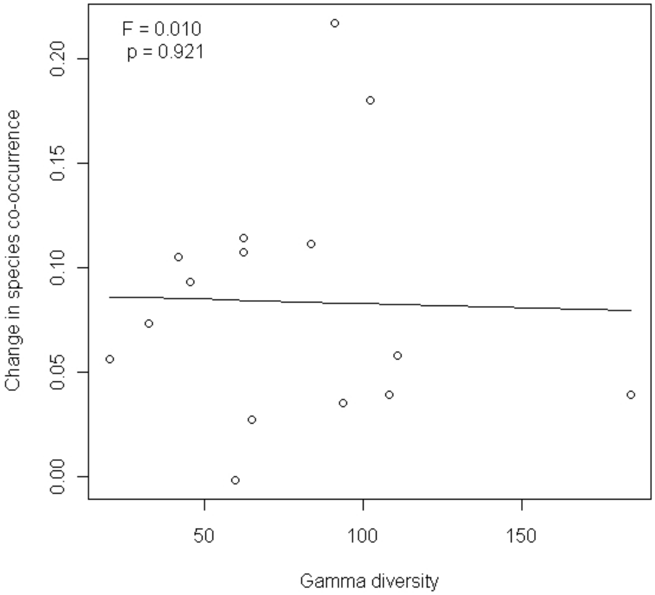


Figure S5. Relationship between γ-diversity and the change in species co-occurrence. γ-diversity is calculated using 58 plots (= total number of plots of the smallest data-set) selected randomly from both data-sets together. Values are averaged from 1000 randomizations. F = *F*-value and p = significance level of the linear regression model.

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