

Small-scale plant species distribution in snowbeds and its sensitivity to climate change

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Received: 12 November 2007 / Accepted: 29 April 2008 / Published online: 20 May 2008
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Abstract Alpine snowbeds are characterized by a long-lasting snow cover and low soil temperature during the growing season. Both these key abiotic factors controlling plant life in snowbeds are sensitive to anthropogenic climate change and will alter the environmental conditions in snowbeds to a considerable extent until the end of this century. In order to name winners and losers of climate change among the plant species inhabiting snowbeds, we analyzed the small-scale species distribution along the snowmelt and soil temperature gradients within alpine snowbeds in the Swiss Alps. The results show that the date of snowmelt and soil temperature were relevant abiotic factors for small-scale vegetation patterns within alpine snowbed communities. Species richness in snowbeds was reduced to about 50% along the

environmental gradients towards later snowmelt date or lower daily maximum temperature. Furthermore, the occurrence pattern of the species along the snowmelt gradient allowed the establishment of five species categories with different predictions of their distribution in a warmer world. The dominants increased their relative cover with later snowmelt date and will, therefore, lose abundance due to climate change, but resist complete disappearance from the snowbeds. The indifferents and the transients increased in species number and relative cover with higher temperature and will profit from climate warming. The snowbed specialists will be the most suffering species due to the loss of their habitats as a consequence of earlier snowmelt dates in the future and will be replaced by the avoiders of late-snowmelt sites. These forthcoming profiteers will take advantage from an increasing number of suitable habitats due to an earlier start of the growing season and increased temperature. Therefore, the characteristic snowbed vegetation will change to a vegetation unit dominated by alpine grassland species. The study highlights the vulnerability of the established snowbed vegetation to climate change and requires further studies particularly about the role of biotic interactions in the predicted invasion and replacement process.

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Keywords Global warming · Gradient analysis ·
Snowmelt date · Soil temperature ·
Species categorization · Swiss Alps

Introduction

Based on the global greenhouse gas emission scenario A2 established by the IPCC (Nagicenovic et al. 2000), the mean summer temperature will rise about 4°C in the Alps until the end of the twenty first century (Raible et al. 2006). In addition, Beniston et al. (2003) predicted an extension of the growing season of about 50–60 days for the period 2071–2100 at elevations above 2000–2500 m a.s.l. They further stated that the beginning of the snow season in fall is likely to remain the same as with the current climate, but that it will end much earlier than today. This is already confirmed by satellite observations of the snow coverage on high-elevation land areas in the Northern Hemisphere from 1972 to 2000 that showed an increasing snow-free period, particularly caused by an earlier snowmelt in spring (Dye 2002). The expected increase in winter precipitation in the form of snow at these elevations only slightly modulates the dominant effect of the +4°C warming on the snow cover duration (Beniston 2006). Consequently, climate change will alter two key abiotic factors controlling plant diversity in the alpine belt: snow cover duration and temperature (Kammer and Möhl 2002).

The snow-free period and daily maximum temperature 0.15 m above ground (together with soil pH) emerged to be characteristics of snowbed communities, which delimited snowbeds to several other alpine plant communities analyzed in the same investigation area in the Swiss Alps as the present study (Vonlanthen et al. 2006a, b). Snow regulates the key abiotic conditions in snowbeds. First, the start and the length of the growing season are determined by the date of snowmelt or the moment the snow cover almost disappeared. The time and duration of the snowmelt is controlled by the thickness of the snow pack, the quality of snow, and by climatic factors, such as air temperature and solar radiation. Second, the soil temperature during the growing season is also largely influenced by snow, i.e. the quantity of accumulated snow and the duration of the melting period regulate the amount and inflow of cold melting water, which keeps the soil humid and cool (Hiller et al. 2005). As shown above, both, the quantity of snow and the temperature are being altered by anthropogenic climate change. Therefore, snowbeds are among the alpine habitats with meso-climatic conditions most severely influenced by climatic factors sensitive to

global warming (see also Grabherr 2003; Heegaard and Vandvik 2004). Snowbeds may be considered as model vegetation unit for the research on the consequences of climate change on alpine vegetation, as suggested by Björk and Molau (2007).

Species typically growing in snowbeds, as for instance *Alchemilla pentaphyllea*, *Salix herbacea*, or *Gnaphalium supinum*, exhibit particular traits allowing to cope with a short growing season, for example a high relative growth rate, clonal reproduction, or a low carbon investment per unit of leaf area (Onipchenko et al. 1998; Körner 2003; Choler 2005). These specialized species show narrow habitat niches and high vulnerability to environmental changes (Björk and Molau 2007). Alterations of the key environmental conditions (e.g. snowmelt date) could therefore have direct and indirect effects on the vegetation in snowbeds (Galen and Stanton 1993; Stanton et al. 1994; Kudo et al. 1999).

Several studies have already revealed that climate warming has significant effects on the alpine vegetation (e.g. Walker et al. 2006). It is even supposed that alpine plant species are disproportionately sensitive to climate change (Guisan and Theurillat 2000; Thuiller et al. 2005b) and respond in a fast and flexible way (Cannone et al. 2007). The occurrence of several species is restricted to snowbeds, thereby characterizing this extreme alpine plant community (Holway and Ward 1963; Ostler et al. 1982; Stanton et al. 1994). Therefore, these highly specialized species may be particularly endangered by climate change because of the loss of their habitat (Theurillat and Guisan 2001). Grabherr et al. (1995) and Grabherr (2003) already observed an invasion process of grassland species in snowbeds of the alpine zone in the Central Alps. The start of this filling process could be traced by the oldest individuals and was probably triggered about 100 years ago by the more favourable climatic conditions after the Little Ice Age. It is likely that the warm years of the 1980s and 1990s have again favoured this invasion of the snowbeds (Grabherr 2003), leading to a replacement process which will have marked effects on the plant composition in snowbeds in the future (Björk and Molau 2007).

The distribution of alpine species along transects from ridges over slopes to hollows in relation to snowmelt date and temperature (or altitude) is well documented (e.g. Heegaard 2002). However, studies on the influence of the key abiotic factors sensitive to

anthropogenic climate change on the distribution of those highly adapted species living inside snowbeds and on species composition within snowbeds (Tomasselli 1991; Razzhivin 1994) are, as far as we know, rare. For example, there are no models based on the current distribution of species allowing predictions of small-scale shifts in species assemblages within the snowbed community and the determination of profiteers and losers of climate change.

High mountain regions contain a substantial part of global biodiversity. The conservation of this diversity provides the insurance for ecosystem stability (Körner 2002). In order to investigate the impact of climate change on plant species diversity in the Alps, we studied snowbeds, a sensitive indicator of the response of alpine vegetation to climate change (Björk and Molau 2007). In order to predict species distribution shifts in snowbeds with a changing climate, we used a correlative approach to the natural variability of species based on the realized niche, a so-called bioclimatic envelope model (Thuiller et al. 2005a). Its underlying principle is as follows: Reactions of species caused by changes in the environment will be predicted based on the current situation of plants in relation to the local variability of environmental variables. Hence, we studied the vegetation composition (presence/absence and relative cover of species) and measured soil temperature along the snowmelt gradient within snowbed vegetation in the Swiss Alps. The goals of this study were to analyze presence/absence and the relative cover (1) along the snowmelt gradient and (2) in response to soil temperature. On the basis of the observed dependencies of the vegetation to the respective climate change-sensitive environmental variables, we (3) established a species categorization according to their realized niche along the snowmelt gradient, and (4) formulated qualitative predictions about the impact of climate change on the species composition of snowbed vegetation in the future using a multiple linear regression model.

Methods

Study site

Fieldwork was conducted in the western part of the Central Swiss Alps at the Gemmi Pass, Leukerbad, Switzerland (2,400 m a.s.l., 46°25' N, 7°37' E).

Thirty spatially separated snowbeds were studied. In these snowbeds the vegetation was always visually classified as belonging to the class of *Salicetea herbaceae*-snowbed communities (according to Ellenberg 1996). The recorded snowbeds were located within an area of about 0.3 km² and had an average distance of 118 m ± 63 m *SD*. The snowbeds were situated in NE/SW-directed troughs where the predominating northwesterly winds (www.meteoswiss.ch) accumulated snow during wintertime. A variable microtopography caused by periglacial hummocks for example, another typical source of variability especially in arctic snowbeds, was not existent in the snowbeds under study. The total annual precipitation amounts to 2,100 mm (this and the following climatic data of the Gemmi area are from Döbeli 2000). The precipitation between July and September totals to 350 mm on average. The average annual temperature is close to 0°C. During the vegetation period from July to September, the average temperature is between 6°C and 9°C. The soil consisted of deep gleyed Brown Earths or gleyed Rendzinas, developed on silic limestone bedrock (Döbeli 2000; Vonlanthen et al. 2004). The fractions of sand, silt and clay in the mineral soil particles were 51%, 36%, and 13%, respectively, determined by the hydrometer method (Bouyoucos 1962) modified by Day (1965). The soil moisture conditions were mesic with low soil suction values (Vonlanthen et al. 2006a and personal observations). The snowbeds under study were occasionally grazed by sheep.

Environmental variables

In 2003, weekly visits to the study site during the snowmelt allowed the establishment of 52 square plots (0.16 m²) with four different snowmelt dates: 2nd June (snowmelt date I, six plots), 9th June (snowmelt date II, 20 plots), 16th June (snowmelt date III, 18 plots) and 23rd June (snowmelt date IV, eight plots). Each plot area was 50% snow-free at its corresponding snowmelt date. Plots within one snowbed had an average distance of 3.1 m ± 1.9 m *SD*. In order to minimize spatial autocorrelation, the number of plots per snowmelt date and snowbed was restricted to a maximum of one at the NW-facing slope and one at the SE-facing slope of each snowbed trough.

The process of snow melting in 2003 was unexpectedly fast because of unusually high temperatures,

especially in June (Bader 2004). Therefore, the snowmelt dates for the investigation area were about 23 days earlier in this year compared with the average snowmelt date of the previous five years (D. Mihajlovic, unpublished data). Also, in the years 2004–2007, the snowmelt dates were clearly later: 26 days in 2004, 15 days in 2005, 17 days in 2006 and 8 days in 2007 on average (C. Schöb, personal observations). Nevertheless, the snowmelt regime, i.e. the chronological ranking of the plots getting snow-free, was constant over the years. The inter-annual variability in the date of snowmelt is assumed to have negligible influence on species composition in snowbeds, because the composition of predominating perennial species in snowbeds is considered conservative (see Körner 2003). Therefore, the analysis of the effect of snowmelt on snowbed vegetation was restricted to the original 2003 snowmelt data only.

In 31 out of the 52 plots the soil temperature about 3 cm below ground was measured with UTL-1 data loggers (Geotest AG, Zollikofen CH). For soil temperature measurements the top layer of the soil was chosen because of the highest abundance of roots in the upper soil (Hiller et al. 2005). Furthermore, a small depth showed a higher sensitivity to changes in air temperature and no time lag to atmospheric temperatures (Körner 2003). The plots with temperature measurements were haphazardly distributed over every different date of snowmelt: four loggers for plots with snowmelt date I, eight loggers for II, 12 for III and seven for IV. The temperature measurements started in October 2004 and finished in September 2006. For analysis, the data during the vegetation period from the time of the snowmelt 2006 until 31st of August 2006 were taken into account. The data loggers stored temperatures at an interval of four hours, starting at midnight. For calculations of mean maximum temperatures (T_{\max}), the average of daily maxima was considered, and correspondingly, for mean minimum temperatures (T_{\min}), the average of daily minima. Furthermore, the average daily temperature (T_{mean}) was calculated.

Vegetation data

Within plots, in 2003 and 2004 all vascular plants were identified (nomenclature according to Aeschmann and Heitz 1996). Species richness was defined as the number of vascular plant species per plot. Furthermore,

the relative cover of each species and each functional type was estimated in late July 2003 and early August 2004, the time when most of the species were in flower. For this purpose, the 0.16 m² squares were subdivided into 25 subplots in order to increase the accuracy of species cover estimation. Relative cover of each species was estimated visually separately for each subplot. Then, the average relative cover value of the 25 subplots was calculated. Plant functional types were derived from the major vascular plant growth forms (shrubs, graminoids, and forbs), bryophytes, and lichens. In addition, for the analyses with regard to the number of species within the graminoids, the sedges (*Carex* sp.) were analyzed separately. For bryophytes and lichens no species data were observed.

Statistical analyses

Dependence of presence and absence of species from the snowmelt date in 2003 was determined by means of a two-way contingency table and a Fisher's exact test (two-tailed) based on a randomization procedure with 5,000 replicates using hypergeometrical distribution keeping the marginal sums (Agresti 1990). For detection of the direction of dependence and for comparability with linear regression methods, Kendall's Tau_b (τ_b) was calculated. Based on the observed distribution pattern of species along the snowmelt gradient, a categorization of species was established. The response of the species categories and functional types along the snowmelt gradient was analyzed with simple linear regression methods. Species richness and the relative cover of each category and functional type were tested for significant trends along the snowmelt gradient. Further, the relative cover of each individual species was tested in the same way.

The performance of the species categories and functional types in relation to the temperature gradient was also tested with simple linear regressions of species richness and relative cover on temperature. Further, the relation of the binomial-distributed presence/absence data of each species to temperature was determined by simple binary logistic regression. The fit of the originated model was tested with the likelihood ratio χ^2 statistic (Menard 2002). Goodness of fit was calculated with Hosmer–Lemeshow statistic (Hosmer and Lemeshow 1989). Two influential observations with deviance residuals less than -2 or greater than $+2$ and values >1 for the Hosmer and

Lemeshow's (1989) logistic regression equivalent of Cook's measure of influence (D_i) were treated as outliers and omitted for the analyses. The response of the relative cover of each species to temperature was tested with simple linear regression methods.

For each species category a multiple linear regression analysis was performed to explain the variance of the relative cover or the number of species with snowmelt date, temperature, and the interaction term of these two abiotic factors as independent variables. The continuous predictor variable T_{\max} was centered prior to analysis to reduce collinearity between the lower-order terms and their interaction. These analyses provided a model for qualitative predictions about the impact of altered environmental conditions due to climate change on the vegetation composition in snowbeds.

All species-number data were log-transformed and all relative cover values were square root-transformed to approximate normal distribution of residuals and homoscedasticity for linear regression analyses. Simple linear regression diagnostics on species cover data of single species along the snowmelt gradient showed three influential observations, and also three along the temperature gradient. They had large values for Cook's distance statistic D_i . Outliers with $D_i > 1$ were omitted for the analyses shown. However, our conclusions would not have changed markedly if these observations had been included.

In order to control the type I error inflation associated with multiple hypothesis testing, the false discovery rate FDR was performed over all statistical analyses (García 2003). As a positive FDR measure of significance for each statistic we calculated the adjusted P -value (the so-called q -value) for each P -value (Storey 2003). Calculations were performed with 'q-value' (Dabney et al. 2004), a software package based on the statistical software R (R Development Core Team 2007). Almost all q -values confirmed the conclusions done based on P -values.

All the other statistical analyses were carried out with SPSS 14.0 for Windows (SPSS Inc.).

Results

The temperature data gave a homogeneous pattern over the whole investigation area. T_{mean} during the vegetation period 2006 was $9.4 \pm 0.8^\circ\text{C}$ on average ± 1 SD,

with an average T_{\max} of $15.7 \pm 1.5^\circ\text{C}$ and an average T_{\min} of $5.1 \pm 0.6^\circ\text{C}$. All three calculated temperature variables showed highly significant correlations among each other. Due to the best performance of T_{\max} in explaining variance of dependent variables and missing collinearity with snowmelt date (variance inflation factor = 1.006, $r_s = -0.082$, $P_{\text{two-tailed}} = 0.66$), T_{\max} was used for subsequent analyses with temperature. T_{mean} ($r_s = 0.055$, $P_{\text{two-tailed}} = 0.77$) and T_{\min} ($r_s = 0.072$, $P_{\text{two-tailed}} = 0.70$) also showed no significant correlations with snowmelt date. In fact, we found a correlation between the temperature variables and the ordinal direction, i.e. the position of the plots within the troughs: the plots in south-east directed slopes of the troughs showed significantly higher T_{\max} -values than those in north-west directed slopes ($T = 6.05$, $df = 1$, $P_{\text{two-tailed}} < 0.001$). The temperature regime of the plots did not change from 2005 to 2006, i.e. the ranking of the plots in relation to their temperature values was constant over the years. In 2005 T_{\max} was, with 16.0°C on average, 0.3°C higher than in 2006.

Presence/absence and species richness per plot did not change between 2003 and 2004 and only five out of 70 species showed significant changes of the relative cover between the 2 years. Therefore, for subsequent analyses only the vegetation data from 2003 were taken into account. Summarized over all 52 plots, we found 70 different vascular plant species. The number of species/plot differed between 6 and 37 species (mean = 16.6 species/plot). The most frequently occurring plant species were *Gnaphalium supinum*, *Poa alpina*, *Salix herbacea* and *Alchemilla pentaphyllea* (Table 1). Vascular plant species covered 72% of the plot area on average, the remaining 28% comprises 15% bryophytes, 3% lichens, and 10% bare ground. Forbs were the most abundant vascular plant growth form with 55% relative cover, followed by shrubs with 12% and graminoids with 5%. The most covering species were *A. pentaphyllea*, *S. herbacea*, and *G. supinum*, which reached average relative cover values over all 52 plots of 21%, 12%, and 10% respectively.

Effect of the snowmelt date on species distribution patterns in snowbeds

The total number of species per plot decreased linearly along the snowmelt gradient from early

Table 1 Response of species variables along the snowmelt date and temperature gradients: Fisher's exact test on a two-way contingency table for analyses of presence/absence data along the snowmelt gradient and binary logistic regression for presence/absence on T_{\max} (measured 3 cm below ground). Linear regressions of square root-transformed relative species cover with each environmental variable

Species	C	n	Snowmelt date			T_{\max}						
			Presence/absence		Species cover		Presence/absence		Species cover			
			τ_b	$P_{\text{Fisher's exact test}}$	β	$P_{F\text{-test}}$	β	$P_{\text{likelihood ratio } \chi^2}$	β	$P_{F\text{-test}}$		
FO _{date}	FO _{T_{\max}}											
<i>Alchemilla pentaphylla</i>	D	48	30	0.250	0.225	0.073	0.518	n.c.	n.c.	n.c.	-0.414	0.037
<i>Gnaphalium supinum</i>	D	51	31	-0.082	0.516	0.085	0.490	n.c.	n.c.	n.c.	0.064	0.572
<i>Poa alpina</i>	D	51	30	-0.201	0.262	<0.001	0.658	n.c.	n.c.	n.c.	-0.106	0.501
<i>Salix herbacea</i>	D	50	30	0.007	0.658	0.599	< 0.001	n.c.	n.c.	n.c.	-0.338	0.093
<i>Cardamine alpina</i>	I	38	27	0.308	0.075	0.222	0.154	-0.688	0.225	-0.191	0.611	0.572
<i>Carex parviflora</i>	I	15	10	0.130	0.597	0.026	0.648	0.377	0.178	0.123	n.c.	n.c.
<i>Myosotis alpestris</i>	I	14	5	-0.238	0.214	-0.213	0.427	2.905	0.003	n.c.	0.024	0.648
<i>Potentilla brauneana</i>	I	8	6	-0.080	0.648	n.c.	n.c.	0.543	0.116	0.024	0.648	
<i>Ranunculus alpestris</i>	I	7	5	-0.165	0.521	-0.671	0.125	0.248	0.414	0.951	0.075	
<i>Sedum alpestre</i>	I	13	5	-0.046	0.129	-0.061	0.611	1.781	< 0.001	0.029	0.648	
<i>Sibbaldia procumbens</i>	I	17	10	0.037	0.611	-0.123	0.521	1.184	< 0.001	0.598	0.094	
<i>Silene acaulis</i>	I	9	6	-0.302	0.125	-0.366	0.320	0.504	0.137	-0.636	0.250	
<i>Soldanella alpina</i>	I	6	3	-0.287	0.088	-0.745	0.116	n.c.	n.c.	n.c.	n.c.	
<i>Taraxacum alpinum</i>	I	26	15	0.048	0.114	0.046	0.610	0.102	0.538	0.446	0.122	
<i>Arenaria biflora</i>	S	16	11	0.345	0.007	0.060	0.610	0.047	0.611	-0.458	0.178	
<i>Carex foetida</i>	S	26	17	0.095	0.003	0.141	0.196	0.319	0.102	0.017	0.322	
<i>Cerastium cerastoides</i>	S	28	21	0.433	0.008	0.239	0.445	-0.502	0.214	-0.413	0.648	
<i>Sagina saginoides</i>	S	32	22	0.356	0.049	0.335	0.226	-0.260	0.092	-0.013	0.090	
<i>Veronica alpina</i>	S	45	29	0.309	0.007	0.228	0.088	0.680	0.320	0.040	0.648	
<i>Campanula scheuchzeri</i>	A	19	8	-0.448	0.003	-0.092	0.562	0.384	0.190	0.602	0.138	
<i>Carex curvula</i>	A	16	5	-0.421	0.019	-0.121	0.527	0.518	0.152	n.c.	n.c.	
<i>Euphrasia minima</i>	A	41	22	-0.445	0.008	-0.082	0.516	0.824	0.021	0.190	0.373	
<i>Festuca violacea</i>	A	29	13	-0.417	0.003	-0.100	0.516	0.352	0.181	0.414	0.179	
<i>Homogyne alpina</i>	A	9	6	-0.514	< 0.001	-0.501	0.188	-0.089	0.588	-0.985	< 0.001	
<i>Leontodon helveticus</i>	A	22	10	-0.708	< 0.001	-0.079	0.572	0.205	0.398	0.100	0.594	
<i>Leucanthemopsis alpina</i>	A	15	6	-0.402	0.014	-0.604	0.028	-0.093	0.584	-0.569	0.242	
<i>Ligusticum mutellina</i>	A	31	15	-0.603	< 0.001	-0.315	0.112	0.507	0.076	0.128	0.526	
<i>Luzula alpinopilosa</i>	A	15	8	-0.437	0.008	-0.054	0.611	-0.087	0.583	-0.016	0.648	

Table 1 continued

Species	C	n	Snowmelt date				T_{max}			
			Presence/absence		Species cover		Presence/absence		Species cover	
			τ_b	$P_{\text{Fisher's exact test}}$	β	$P_{F\text{-test}}$	β	$P_{\text{likelihood ratio } \chi^2}$	β	$P_{F\text{-test}}$
<i>Phytuma hemisphaericum</i>	A	12	-0.438	0.005	-0.008	0.652	0.046	0.623	0.254	0.519
<i>Polygonum viviparum</i>	A	40	-0.554	< 0.001	-0.521	0.003	0.954	0.018	0.238	0.261
<i>Potentilla aurea</i>	A	10	-0.525	< 0.001	-0.182	0.516	0.191	0.475	0.551	0.321
<i>Viola calcarata</i>	A	12	-0.378	0.019	-0.839	0.003	1.643	0.005	n.c.	n.c.

Significant P -values at <0.05 in bold. Degrees of freedom for all regression analyses = 1. FO_{date} = frequency of occurrence in 52 plots along the snowmelt gradient, FO_{Tmax} = frequency of occurrence in 31 plots along the mean maximum soil temperature gradient. τ_b = Kendall's τ_{ab} , correlation coefficient, β = standardized regression coefficient (=correlation coefficient R for linear regression). n.c. = not computable. Species categorization (C) in five classes: D = dominants, I = indifferents to snowmelt dates, S = snowbed specialists, A = avoiders of late-snowmelt sites (transients (=38 species) are not shown)

melting sites to late melting sites ($F = 25.48$, $df = 1$, $P < 0.001$, Fig. 1a), whereas the total vegetation cover by vascular species was unchanged along the snowmelt gradient ($F = 0.01$, $df = 1$, $P = 0.65$; Fig. 1b). The occurrence patterns of the species along the snowmelt gradient allowed the establishment of five categories in order to summarize species with the same realized niche along the snowmelt gradient at present (Table 1). The component species of the snowbeds under study were classified according to Grime (1998) into the following three categories: dominants, subordinates and transients. Furthermore, the subordinates were subdivided into a category of species with a positive response to delayed snowmelt dates, a category of species with a negative response pattern to snowmelt dates, and a category with no significant response to the snowmelt date.

1. Dominants (D): very common and dominant species with a presence in more than 47 plots (>90% of all plots). The number of dominants showed no significant relationship to snowmelt date, and the presence of the individual species of this category was not dependent on snowmelt date. This category, responsible for the main part of the vegetation cover in the snowbeds, significantly increased in abundance from about 40 to about 80% of the total vegetation cover with later snowmelt dates ($F = 19.44$, $df = 1$, $P < 0.001$). A remarkable increase was found from snowmelt date II to snowmelt date III (Fig. 1b).
2. The three categories of the subordinates summarized species with an occupancy between 10 and 90% of all plots.
 - 2a. Indifferents to snowmelt dates (I): a category of subordinate species without a significant dependence of their presence on snowmelt date. This category showed no significant relationship of the species number to snowmelt date. However, in contrast to the dominants, their abundance was, with a range between 3 and 10% of the total vegetation cover on average, clearly smaller and independent of snowmelt date.
 - 2b. Snowbed specialists (S): subordinate species with significantly increasing presence with later snowmelt date and, therefore, favouring late melting snowbed sites. The number of specialist-species showed a significantly positive relationship

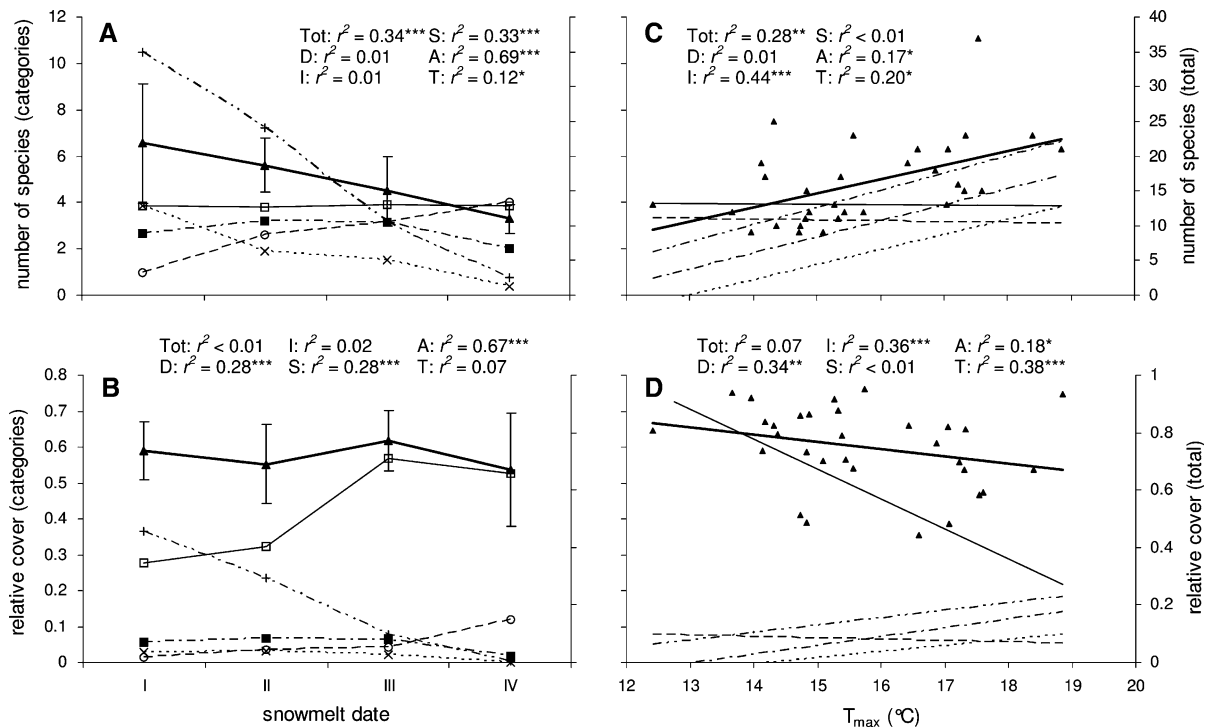


Fig. 1 Number of species and relative species cover along the snowmelt and temperature gradients: Linear regressions of log-transformed species number and square root-transformed species cover data for all species Tot (\blacktriangle -, right y-axis) and for the five categories (left y-axis): dominants D (\square -), indifferent to snowmelt dates I (\blacksquare -), snowbed specialists S (\circ -),

avoiders of late-snowmelt sites A ($\cdot\cdot\cdot$ - $\cdot\cdot\cdot$ -), and transients T (\times -). Error bars indicate ± 1 SD for each snowmelt date. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. n for snowmelt date I (02.06.2003) = 6, II (09.06.2003) = 20, III (16.06.2003) = 18, IV (23.06.2003) = 8. n for T_{max} = 31

to snowmelt date ($F = 24.25$, $df = 1$, $P < 0.001$). The relative cover of the snowbed specialists also significantly increased with later snowmelt date ($F = 19.79$, $df = 1$, $P < 0.001$) and showed the highest increase from snowmelt date III to the latest melting sites (Fig. 1b).

2c. Avoiders of late-snowmelt sites (A): subordinate species with a significantly decreasing occurrence with later snowmelt date and, therefore, avoiding the late melting sites. The number of avoiders significantly decreased with later snowmelt date ($F = 111.65$, $df = 1$, $P < 0.001$). Their relative cover also regularly decreased with later snowmelt date ($F = 99.92$, $df = 1$, $P < 0.001$).

3. Transients (T): occasional species with a presence in less than six plots (<10% of all plots). The number of transients significantly decreased with later snowmelt date ($F = 6.49$, $df = 1$, $P = 0.024$). The relative cover of the transients showed no response to snowmelt date.

With regard to the plant functional types, the number of species within forbs ($F = 15.69$, $df = 1$, $P < 0.001$) and graminoids ($F = 14.69$, $df = 1$, $P < 0.001$) significantly decreased with later snowmelt date. However, within graminoids, sedges showed no response in species richness to snowmelt date, as well as shrubs.

The linear regressions of the relative cover of the individual species gave four statistically significant results (Table 1): *Leucanthemopsis alpina*, *Polygonum viviparum* and *Viola calcarata* showed a decrease and *Salix herbacea* an increase in their relative cover with later snowmelt date. Due to the fact that the relative cover of shrubs is predominantly composed of *Salix herbacea*, this functional type also significantly increased in relative cover with later snowmelt date ($F = 21.07$, $df = 1$, $P < 0.001$). Graminoids ($F = 8.45$, $df = 1$, $P = 0.005$) and lichens ($F = 9.28$, $df = 1$, $P = 0.004$) decreased in cover with later snowmelt date, whereas bryophytes

and forbs had a constant abundance along the whole snowmelt gradient.

Effect of temperature on species distribution patterns in snowbeds

The total number of species significantly increased ($F = 11.28$, $df = 1$, $P = 0.005$) from about 11 species/plot with $T_{\max} = 13^{\circ}\text{C}$ to about 21 species/plot with $T_{\max} = 18^{\circ}\text{C}$ (Fig. 1c). The same pattern could be found with T_{mean} ($r^2 = 0.16$, $F = 5.44$, $df = 1$, $P = 0.027$), but not with T_{\min} ($r^2 = 0.05$, $F = 1.47$, $df = 1$, $P = 0.24$). The relative cover of all vascular species showed no dependence on temperature (Fig. 1d).

The number of species as well as the relative cover of the avoiders ($F_{\text{number}} = 6.12$, $df = 1$, $P = 0.031$ and $F_{\text{cover}} = 6.43$, $df = 1$, $P = 0.028$), the indifferents ($F_{\text{number}} = 22.57$, $df = 1$, $P < 0.001$ and $F_{\text{cover}} = 16.38$, $df = 1$, $P < 0.001$), and the transients ($F_{\text{number}} = 7.15$, $df = 1$, $P = 0.021$ and $F_{\text{cover}} = 18.10$, $df = 1$, $P < 0.001$) significantly increased with increasing T_{\max} (Fig. 1c, d), whereas the relative cover of the dominants significantly decreased with higher T_{\max} -values ($F_{\text{cover}} = 14.69$, $df = 1$, $P = 0.003$). The snowbed specialists showed no response to the observed variations in T_{\max} .

Logistic regressions of presence/absence data with T_{\max} resulted in six species with significant increases in presence with higher T_{\max} (Table 1): *Myosotis alpestris*, *Sedum alpestre*, *Sibbaldia procumbens*, *Euphrasia minima*, *Polygonum viviparum*, and *Viola calcarata*. No species significantly increased with decreasing T_{\max} . The same trend along the temperature gradient was found for the functional types: there were no decreases in the number of species with decreasing T_{\max} . However, forbs ($F = 9.14$, $df = 1$, $P = 0.005$) and graminoids ($F = 9.13$, $df = 1$, $P = 0.005$) significantly increased with higher T_{\max} , and within graminoids, also the sedges ($F = 9.53$, $df = 1$, $P = 0.004$).

Most of the species showed no significant change in relative cover with higher T_{\max} (Table 1). Only the relative covers of *Alchemilla pentaphyllea* and *Homogyne alpina* were significantly negatively associated with T_{\max} . Also for the relative cover of functional types, no dependences on T_{\max} could be found.

Multiple linear regression model of species distribution in snowbeds

The multiple linear regressions of the relative cover or the number of species of each category in relation to snowmelt date and T_{\max} (Table 2) were in accordance with the results of the univariate regressions. The four dominants of snowbeds were constantly found over the whole gradients and showed, therefore, no variance in their frequency distribution. About 53.4% of the observed variance in the relative cover of the dominants was explained by snowmelt date and T_{\max} . The avoiders of late-snowmelt sites showed the most marked relationship to the environmental variables observed: both, number of species as well as the relative cover were positively correlated to T_{\max} and negatively to the snowmelt dates. These two abiotic factors together could explain 82.5% of the variance in the number of species and 80.6% in the relative cover of the avoiders. Much less variance observed could be explained for the indifferents (48.3% of the number of species and 39.9% of the relative cover) and the transients (29.8% and 44.8%). Both of them increased in species number and relative cover with increasing T_{\max} , and were not dependent on snowmelt date. In contrast, the snowbed specialists were only dependent on snowmelt date and increased in species number as well as relative cover with later snowmelt date. The multiple linear regression model explained 34.9% and 25.6% of the species response data for this species category. The interaction between snowmelt date and T_{\max} was not significant for all analyses. Since no interaction was found, the regression model with the two main effects and without interaction term is presented.

Discussion

The present study revealed a high variability in the length of growing season (measured on the snowmelt date) as well as in the soil temperature within snowbeds. The variability in soil temperature was independent on snowmelt date, but significantly different between the SE- and NW-directed slopes within the troughs studied, which is most probably caused by different irradiance of the opposite slopes. Both environmental factors together could explain a

Table 2 Response of species categories along the environmental gradients: Multiple linear regressions of log-transformed number of species and square root-transformed relative cover for each category with snowmelt date (Date) and average daily maximum temperature T_{max} (measured 3 cm below ground) as explanatory variables

Species categories	ns	Number of species				Relative cover					
		β		P	r^2		β		P		
		Date	T_{max}		Date	T_{max}	Date	T_{max}			
Dominants	4	n.s.	n.s.	n.s.	n.s.	0.534	0.445	-0.546	<0.001	0.005	<0.001
Indifferents to snowmelt dates	10	0.483	-0.215	0.645	<0.001	<0.001	0.172	-0.196	0.586	0.003	0.235
Snowbed specialists	5	0.349	0.592	0.032	0.005	0.661	0.003	0.506	-0.010	0.033	0.705
Avoiders of late-snowmelt sites	13	0.825	-0.809	0.354	<0.001	<0.001	<0.001	-0.793	0.364	<0.001	<0.001
Transients	38	0.298	-0.318	0.420	0.016	0.027	0.095	-0.252	0.600	<0.001	<0.001
Total species	70	0.635	-0.598	0.483	<0.001	<0.001	<0.001	n.s.	n.s.	n.s.	n.s.

Significant P -values at <0.05 in bold. Degrees of freedom for all multiple regression analyses = 2. $n = 31$. ns = number of species included in the category. r^2 = coefficient of determination (part of the variance explained by the model), β = standardized regression coefficient. n.s. = model not significant. Negative β means a decrease in species number or relative cover with later snowmelt date or higher T_{max} , a positive β means an increase in species number or relative cover with later snowmelt date or higher T_{max}

substantial part of the variance in species data and significantly influenced species distribution and abundance in snowbeds. Therefore, our outcome corresponds with that found by Vonlanthen et al. (2006a, b). They showed that, besides soil pH, length of growing season and daily maximum temperature (measured 15 cm above ground) were important abiotic factors discerning snowbed communities from other alpine plant communities. Furthermore, the study of Vonlanthen et al. (2006b) as well as our study found that T_{max} and T_{mean} were highly correlated and that both significantly influenced floristic composition while T_{min} was of lower relevance in this regard. Our results, therefore, suggest that growing season length and T_{max} are not only relevant explanatory variables to discriminate among the alpine plant communities (Vonlanthen et al. 2006a), but also for small-scale vegetation patterns within alpine snowbed communities.

Within snowbeds, the number of species was reduced by approximately 50% along both environmental gradients. Stanton et al. (1994) could show that this decrease in species richness is not a consequence of historical inertia concerning limited dispersal of seeds and vegetative propagules, but of the physiological tolerance of the species to the prevailing environmental conditions. Short growing seasons and low temperature are well known alpine stress factors (e.g. Komárková 1993; Kammer and Möhl 2002; Vonlanthen et al. 2006b) delimiting the number of species able to grow under these conditions. Only well adapted plant species could grow and reproduce at the harsher end of the environmental gradients under study. The observed monotonic relationship between species richness and the environmental gradients reflect one leg of the unimodal relationship proposed by the intermediate stress hypothesis (Grime 2001). The observed decrease in species richness along the environmental stress-gradients (temperature and growing season length) on a very small spatial scale of a few meters in our study is also known for larger scales along elevational or latitudinal gradients (Körner 2002; Virtanen et al. 2002).

From the functional groups considered, all categories but bryophytes and shrubs (predominantly comprising of the dominant species *Salix herbacea*) favoured the early melting sites with respect to species richness and/or relative cover. These results

are not in line with an earlier study by Kudo and Ito (1992), who found an increased abundance of forbs, graminoids and bryophytes in the late melting sites. However, they studied a very different type of snowbed dominated by shrubs along a much longer gradient of about 70 days. However, the increase in species richness with higher summer temperature is consistent with the broad pattern of increasing diversity along natural gradients of increasing temperature in tundra communities (Walker 1995). However, we did not find the effect observed by Walker et al. (2006) in experimentally warmed plots in alpine tundra, where the vegetation changed from herbaceous to woody plants.

The distribution pattern of the vascular plant species led us to the identification of five different categories. Their separation was based on the different frequency of occurrence of the species among the snowbeds under study and on the different response pattern along the snowmelt gradient. Each category includes species with the same realized niche inside snowbeds in relation to the snowmelt gradient. Therefore, for each category a unique response pattern to climate change is assumed.

Under the predicted scenario of climate change until the end of this century, i.e. an extension of the growing season of at least 50 days (Beniston et al. 2003) and a considerable temperature increase (Rabib et al. 2006), at least the snowbed specialists in the investigation area will almost disappear if only the abiotic factors responsible for their occurrence are taken into account. They are the main losers of climate change in snowbeds, because this category consists of species with almost no occurrences outside late melting snowbeds. Their currently suitable habitats will become unsuitable due to an earlier start of the growing season. This will lead to a mortality which will exceed the local reproduction and will conclude, after a considerable time lag, with the loss of their habitat (Pulliam 2000). Further, the dominants, which build the matrix of the snowbed vegetation to date, will show a remarkable decrease in abundance (Table 2). However, even though these species will experience less favourable conditions in the future due to climate change, they will probably resist complete disappearance from the snowbeds in the investigation area. In contrast, the avoiders of late-snowmelt sites are assumed to be the main profiteers of climate change. Providing that they exhibit

phenological plasticity, as discussed below, they will benefit from climate change because of an extended growing season length as well as increased temperature and, therefore, more suitable habitats in the future. They will remarkably increase in species number and abundance and probably dominate the snowbeds of the investigation area at the end of the twenty first century. Also, the indifferents and the transients prefer warmer growing conditions and will, therefore, profit from a mitigating climate in the future. Therefore, it can be assumed that the existing characteristic snowbed vegetation will change to alpine grassland with frequently occurring and dominating species to date belonging to the category of the avoiders, as for instance *Carex curvula*, *Festuca violacea*, *Leontodon helveticus*, *Ligusticum mutellina*, or *Polygonum viviparum*, and other species from the regional species pool.

However, whether and to which extent the avoiders and, to a smaller extent, the indifferents or the transients really will benefit and whether and to which extent the snowbed specialists and the dominants will suffer from changed climatic conditions in the future is not only dependent on changed conditions in terms of the key abiotic factors, e.g. snowmelt date and temperature (Davis et al. 1998). Since, even if the explanatory power for each of the two environmental factors was statistically significant, an important part of the variance observed within snowbeds could not be explained by the explanatory variables under consideration. The real response to climate change depends to a great part on the specific phenological plasticity of the species involved (Galen and Stanton 1993, 1995), on biotic interactions (Totland and Nylén 1998; Choler et al. 2001), and on species resistance to an increased frequency of spring frost events due to the earlier melting of snow (Inouye 2000). Sørensen (1941) described two phenological patterns in tundra species from Greenland: (i) *periodic* species are characterized by a finite growing period controlled by genetic constraints; (ii) *aperiodic* species continue to function until the environment becomes unfavourable. Hence, if the length of growing season increases, periodic species should be at a disadvantage against competing aperiodic species that can take advantage of an extended growing season (Starr et al. 2000; Totland and Alatalo 2002). As a consequence of climate change, especially aperiodic species will compete for

space against established snowbed species, predominantly showing a periodic phenological pattern (C. Schöb, unpublished data). This may lead to a competitive exclusion of typical snowbed species from late-snowmelt sites by species that had their optima outside snowbeds so far (Heegaard and Vandvik 2004).

Therefore, projections just by bioclimatic envelope models implied by our spatial gradient research can be misleading if biotic interactions are strong and also poorly correlated with considered climatic variables (Davis et al. 1998; Pearson and Dawson 2003; Dunne et al. 2004). Consequently, in order to estimate the effect of climate change on the vegetation composition in snowbeds, studies are needed to investigate the competitive and facilitative ability of (i) the probably suffering species categories (i.e. the existing dominants and snowbed specialists) and (ii) the potential invaders and profiteers of climate change (i.e. the current avoiders of late-snowmelt sites, the indifferents and the transients) along the key environmental variables.

Conclusions

Snowbeds and their highly adapted inhabiting plant species are endangered due to the loss of suitable habitats as a consequence of climate change. The distribution of most of the characteristic snowbed species is limited to harsh environmental conditions occurring in snowbeds and significantly dependent on the respective snowmelt date and/or soil temperature. Both of the limiting abiotic factors are sensitive to anthropogenic climate warming and will therefore change to a considerable extent in the future. Several alpine grassland species with the ability to invade snowbeds will benefit from the mitigating climate and probably compete with the current specialized snowbed vegetation on site. Further investigations about the role of biotic interactions in snowbed vegetation are needed in order to assess the vulnerability of the established snowbed vegetation to invading species.

Acknowledgements This research was made possible by the “Stiftung zur Förderung der wissenschaftlichen Forschung” of the University of Bern. We thank the University of Teacher Education Bern and the Institute of Plant Sciences (University of Bern) for infrastructural and financial support. We are

grateful to W. and S. Loretan for accommodation at the Berghotel Wildstrubel, to C. Vonlanthen, Institute of Geography, University of Bern, for her contributions in the field, to M. Puscas, University Babes-Bolaii, Cluj, Romania, for the classification of *Carex curvula* by DNA-analysis, to D. Mihajlovic, Institute of Geography, University of Bern, for sharing his unpublished results with us, to J. Hüsler, Institute of Mathematical Statistics, University of Bern, for statistical advice, to N. Arn for language review, and to two anonymous reviewers for their helpful comments on an earlier version of the manuscript.

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