Contrasting impacts of climate change on the vegetation of windy ridges and snowbeds in the Swiss Alps

Loïc Liberati[1,2], Swanee Messerli[1,3], Magalì Matteodo[1,4] & Pascal Vittoz[1*]

[1] University of Lausanne, Faculty of Geosciences and Environment, Institute of Earth Surface Dynamics, Géopolis, 1015 Lausanne, Switzerland
[2] ETH Zürich, Institute of Integrative Biology, Department of Environmental Systems Science, Building CHN, Universitätstrasse 16, 8092 Zürich, Switzerland
[3] Route des Esserts 61, 1854 Leysin, Switzerland
[4] Chemin de Bonne-Espérance 28, 1006 Lausanne, Switzerland

Corresponding author: Pascal Vittoz, University of Lausanne, FGSE, Institute of Earth Surface Dynamics, Géopolis, 1015 Lausanne, Switzerland; +41 21 692 4367; pascal.vittoz@unil.ch

ORCID:
Magalì Matteodo: https://orcid.org/0000-0003-3813-5261
Pascal Vittoz: https://orcid.org/0000-0003-4218-4517

Abstract

The impacts of climate change on alpine summit floras have been widely investigated. However, only few studies included alpine grasslands and generally concluded that snowbeds, with a long snow cover duration and a short growing season, and windy ridges, with a short snow cover duration and strong winter frosts, are the most sensitive alpine grasslands. However, these habitats were mostly investigated in different regions, where local factors (e.g., nitrogen deposition, grazing) can co-vary with climate changes, potentially obscuring differences between habitats. Here, we focused on the Zermatt region (Swiss Alps) to investigate the impacts of climate change in snowbeds and on windy ridges.

Forty-three exhaustive historical plant inventories on windy ridges (acidophilic or basophilic) and 31 inventories in snowbeds (typical or wet) were repeated in quasi-permanent plots after approximately 23 years. Historical and recent records were compared with the Simpson index, Bray-Curtis dissimilarity, a PCA, ecological indicator values and the frequency and cover changes of species.

There was a general increase in α-diversity and a decrease in β-diversity (homogenisation). Most of the new species in the plots were generalists from surrounding grasslands. The plant composition tended to be more thermophilous on acidophilic windy ridges and in typical snowbeds. The flora of acidophilic windy ridges became more similar to that of basophilic windy ridges and more eutrophic. We interpreted this as possibly arising from fertilisation by the aeolian dust deposition coming from the expanding glacial moraine in the valley. In snowbeds, the species indicated increasingly drier conditions, especially in wet snowbeds. Warming climate induces lower snow fall and earlier snowmelt, leading to a shorter snow cover duration. Hence, wet snowbeds are certainly among the plant communities most threatened by climate change in the Alps.

Keywords: *Salicion herbaceae, Elynion*, snow cover, temperature, quasi-permanent plots, vegetation dynamics, Switzerland

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[*] Declaration of authorship: all authors designed the study, LL and SM inventoried the plots in the fields and analysed the data under the advices of MM and PV, all authors contributed to the manuscript.

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Introduction

Climate is one of the main drivers of the distribution of vegetation in the alpine and nival mountain belts. Human impact is low at these elevations, and the snow cover duration and the mean and minimum temperatures are among the most important factors controlling species distribution (Körner 2003). Consequently, the climatic changes recorded in the last decades (Stocker et al. 2013; Klein et al. 2016) have already had a strong impact on species distributions in alpine-nival belts, particularly on high mountain summits, with a general increase in species richness (e.g., Pauli et al. 2012; Matteodo et al. 2013; Steinbauer et al. 2018).

Snow cover extent and duration depend on elevation and on topography, with an important redistribution of snow by wind (Körner 2003). As a consequence, the differences in snow cover duration in spring can be up to 11 weeks between very close sites at the same elevation because of microtopography or aspect (Friedel 1961). It is well known that plant distribution in high mountains follows this snow pattern, as a long snow cover period reduces the growth season down to the limits of plant survival and, conversely, the short snow cover period on ridges exposes plants to deep frost in winter (Körner 2003). As the snow cover duration tends to decrease at all elevations with climate change (Klein et al. 2016), one can expect that plant communities in both extreme conditions, i.e. very long and very short snow cover periods, are particularly sensitive to climate change.

A few recent studies have indeed concluded that species composition in snowbeds, with a long snow cover duration, and on windy ridges, with a short snow cover duration, have already changed under climate change. Matteodo et al. (2016) concluded that these two vegetation types are among the most sensitive ones to climate change, with clear changes in the last 25-40 years, whereas calcareous and siliceous grasslands occupying intermediate conditions relative to snow cover did not change. Similarly, Gritsch et al. (2016) in Austria and Carbognani et al. (2014) in Italy observed that snowbeds are particularly sensitive to climate change, with a general colonisation of species from surrounding grasslands. These authors concluded that the shorter snow cover period, due to a decrease in snowfall and an earlier melt under warmer spring temperatures (Serquet et al. 2013; Klein et al. 2016), was the best explanation for the observed changes. Apart from the study of Matteodo et al. (2016), changes on windy ridges have been addressed only outside of the Alps, mainly at higher latitudes, and the conclusions of these studies are mixed. Elumeeva et al. (2013) noted only small changes in the Caucasus, while Virtanen et al. (2003) and Vanneste et al. (2017) recorded an increase of dwarf shrubs in Scandinavia, although the opposite was observed by Ross et al. (2012) in Scotland, where graminoids are replacing dwarf shrubs. All authors agreed on a general decline of lichens, an important component of windy ridges, but explained this pattern differently, attributing it to reindeer grazing (Virtanen et al. 2003; Maliniemi et al. 2018), nitrogen deposition (Armitage et al. 2014), competition with vascular plants, especially dwarf shrubs (Vanneste et al. 2017) or trampling and climate change (Ross et al. 2012). These different explanations show the importance of other local factors (e.g., grazing and nitrogen deposition) and how they can influence the impact of climate change on vegetation (Vittoz et al. 2009b; Maliniemi et al. 2018).

Until now, only a few studies have addressed the impact of climate change on these two habitats in a single region: Matteodo et al. (2016) in the Alps, but with a restricted data set, and Maliniemi et al. (2018) in Scandinavia. Moreover, the regions considered by these two past studies were still broad enough to allow local conditions to vary considerably. Only a restricted area, sharing similar land use and exposure to pollution, is likely to provide a good understanding of vegetation responses to climate change. The aim of this study was to assess climate change impact on snowbeds and windy ridges over more than 20 years with a large dataset in the same valley. For this, we repeated 23-year-old phytosociological relevés in 34 snowbeds and on 43 windy ridges, all situated in the Zermatt Valley in the Swiss Alps. Based on previous studies, we hypothesised a general increase of thermophilous species and grasses in both habitats and a flora indicating dryer conditions in snowbeds.

Materials and methods

Study site

The study was performed in the central Alps of Switzerland, in the Zermatt valley (Fig. 1). This site is characterised by a large variety of geological materials, such as gneiss, granite, calcschists, marble and ophiolite (Käsermann et al. 2003). The lower slopes are mostly covered by glacial moraines or colluvial and aeolian deposits. This diversity induces a large range of soil pH. Due to the 29 peaks exceeding 4000 m a.s.l. around the valley, it is one of the most continental and dry places in the Alps given its elevation (Richard 1991). The mean annual temperature is 4.4°C in Zermatt (1638 m; between -4.2°C in January and 13.4°C in July), and has been increasing by 0.25°C per decade for the last 30 years (Fig. 2a). The annual sum of precipitation amounts to 639 mm, including 274 cm of fresh snow per year. In winter, snow covers the ground for an average of 142 days in Zermatt, disappearing between mid-March and the beginning of May, with a mean advance of 3 days per decade (Fig. 2b; www.meteoswiss.ch).

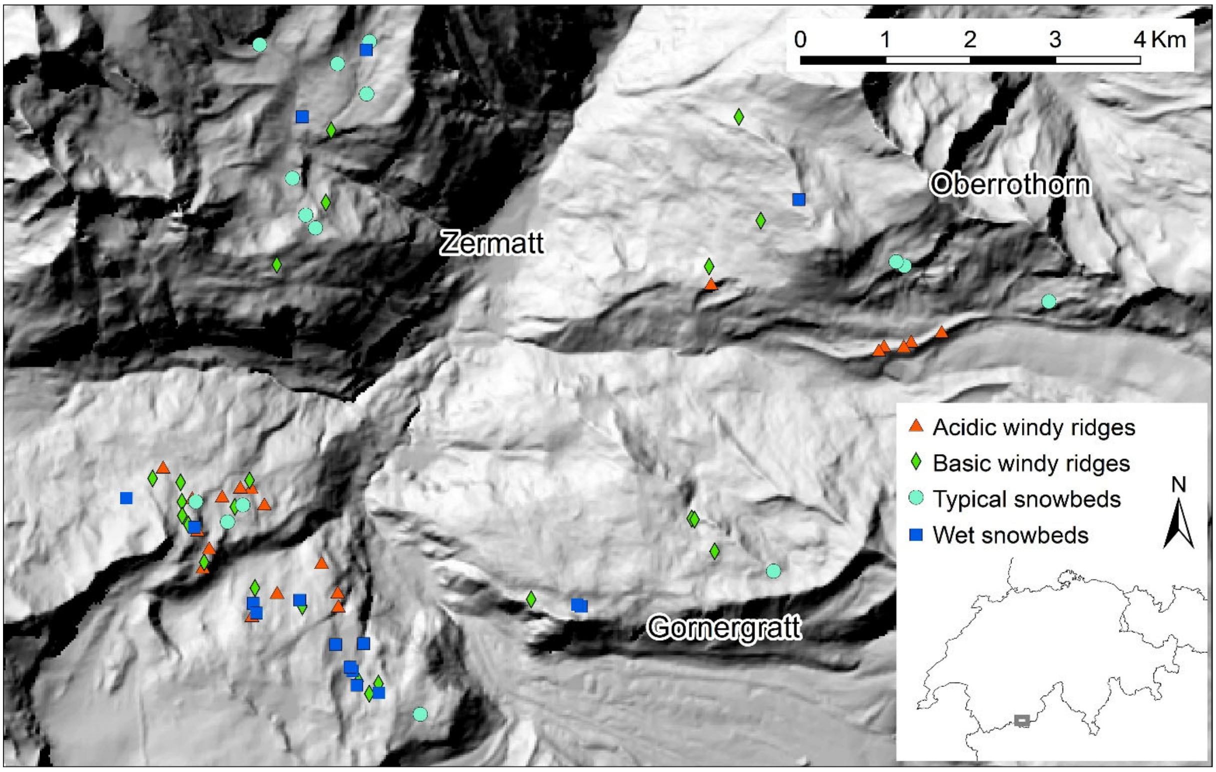

Fig. 1 The distribution of the 74 relevés in the Zermatt Valley. The grey rectangle in the inset shows the location of Zermatt in Switzerland.

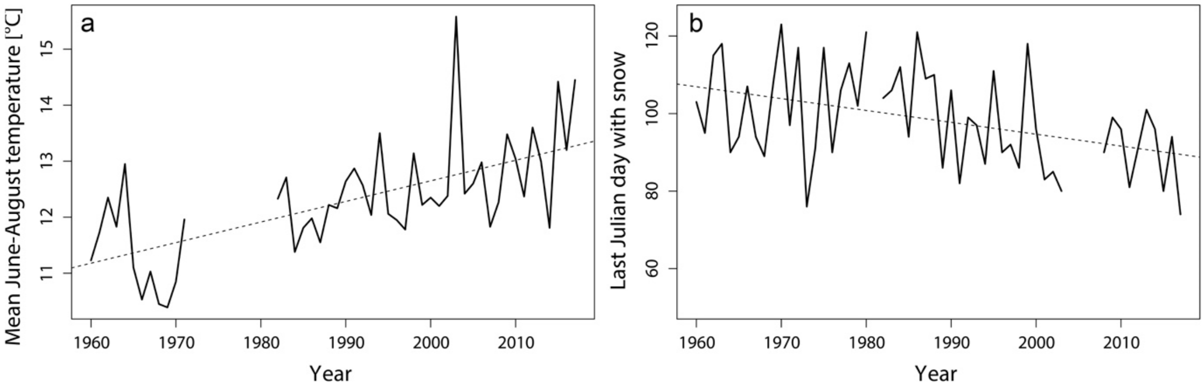

Fig. 2 (a) Summer (June-August) mean temperatures between 1960 and 2017 and (b) last day (counted from the 1st of January) with snow in Zermatt (1636 m a.s.l.; data www.meteoswiss.ch). Both trends are significant ($p < 0.001$ for summer temperature, $p = 0.002$ for the last day with snow cover).

Vegetation data

Hundreds of exhaustive floristic inventories (relevés) were conducted by several botanists around Zermatt between 1970 and 1995 and were classified into community types by Steiner (2002). Historical relevés of windy ridges (n = 186) and snowbeds (n = 65) were extracted from this dataset. To obtain a broad perspective on the dynamics of these vegetation types, we selected historical plots covering contrasting soil pH for windy ridges (acidophilic and basophilic) and soil humidity for snowbeds (typical and wet). Windy ridges are generally classified in the phytosociological alliance *Oxytropo-Elynion* (Prunier et al. 2017); they correspond to locations where strong winds regularly sweep out the snow in winter, exposing species to deep frosts during most of the winter (Körner 2003). Two plant associations were retained: the *Elyno-Caricetum rosae* on basic substrate and the *Elynetum myosuroidis* on acidic substrate (Prunier et al. 2017). Conversely, the snowbeds are characterised by a very long snow cover duration, reducing the growing season to less than 3 months. The typical snowbeds are in hollows, on north-facing slopes or on the leeward side of ridges. They belong to the alliance *Salicion herbaceae*, in which three associations were retained: *Salicetum herbaceae* (middle conditions), *Caricetum foetidae* (depressions with short waterlogging) and *Polytrichetum sexangularis* (very long snow cover duration). The wet snowbeds are continuously irrigated by melt-water from a firn, small river, or lake throughout the short growth season. The two retained associations were the *Salici herbaceae-Caricetum lachenalii* (in *Salicion herbaceae*), on soil rich in organic matter, and the *Junco triglumis-Caricetum bicoloris* (in *Caricion bicoloris-atrofuscae*), in pioneer conditions (Prunier et al. 2017). The main species of the respective associations are listed in the Appendix (Table S1).

Only plots with precise location information were retained, generally a point on a topographic map (1:25'000), mostly completed by field notes (describing exposure, slope, surface) and, in a few cases, by a photograph. For windy ridges, plots with a historical inventory of lichens were also preferentially selected. In the field, once the plot was approximately located, the surface with a species composition most similar to the historical relevé was selected for a conservative approach. When no surface corresponded correctly to the historical data (vegetation or site description), the site was discarded. For snowbeds, as historical relevés were often small (1-4 m^2), when different surfaces were possible in the same site, two or three new plots with similar conditions to the historical relevé were selected and inventoried. Thereafter, all new inventories were compared to the historical one with the Bray-Curtis dissimilarity, and the most similar one was retained for further analyses. Hence, the data can be considered as quasi-permanent plots (Kapfer et al. 2017). In total, 43 plots from windy ridges (21 to 36 years old, mean 23 years) and 31 plots from snowbeds (21 to 45 years old, mean 23 years) were re-inventoried throughout the Zermatt valley, from July to August 2016. They were located between 2410 and 2943 m a.s.l. for windy ridges and between 2455 and 2920 m a.s.l. for snowbeds (see Appendix, Table S2, for details).

All vascular plants were recorded (nomenclature according to Lauber et al. 2012), and complemented with terricolous lichen species on windy ridges (nomenclature according to Clerc & Truong 2012). We adopted the same method as for the historical dataset, with a visual cover estimation according to Braun-Blanquet's scale (1964). The inventoried area was identical to the historical relevé, and the new plot was marked with aluminium plates in the soil, and the precise coordinates of the four corners were recorded (± 1 m GPS Trimble GeoXH) for future inventories.

Data analyses

Data preparation and analyses were similar to Matteodo et al. (2016), with a conversion of the Braun-Blanquet scale to the median of the cover range (r → 0.05, + → 0.5, 1 → 3, 2 → 15, 3 → 37.5, 4 → 62.5, 5 → 87.5) to compare species cover between relevés, and a conversion to an ordinal scale (r → 0.1, + → 0.5, 1 → 1, 2 → 2, …) for the other analyses. Clustering using the Hellinger distance and the Ward aggregation algorithm was used to separate the data sets (windy ridges or snowbeds) into subunits. The Simpson index was used to investigate changes in α-diversity through time and the difference between historical and recent medians was tested with a pairwise Wilcoxon-Mann-Witney test. A possible homogenisation was addressed by calculating, within each vegetation type, the mean Bray-Curtis dissimilarity between each historical inventory and all other historical inventories, and between each recent inventory and all other recent inventories. The difference between medians of historical and recent dissimilarities was tested with a pairwise Wilcoxon-Mann-Witney test.

The differences in species frequency and cover between historical and recent relevés were tested by permutation tests following Kapfer et al. (2011), as detailed in Matteodo et al. (2016), with each randomisation being limited within one vegetation type. All the species were included in the frequency change analyses, but only the species present in at least 25% of the historical and recent surveys were considered for the cover change analyses.

We used the mean Landolt ecological indicator values (Landolt et al. 2010), calculated and weighted by species cover for each plot, to investigate potential associations between ecological factors and the observed vegetation changes. Significant changes in mean indicator values by vegetation type and period were checked using pairwise Wilcoxon-Mann-Witney tests for temperature (T), light (L), continentality (K), soil humidity (F), soil pH (R), nutrient content (N) and humus content (H).

Vegetation shifts between historical and recent inventories were assessed by principal components analysis (PCA, R *vegan* library), separately for windy ridges and snowbeds and based on the species cover, which had been submitted to Hellinger transformation (Borcard et al. 2011). For each vegetation type, the shift between historical and new relevés along the two first axes was tested with a MANOVA, applied to the differences of axis scores against the intercept (Vittoz et al. 2009b).

All data processing and analyses were performed using the R statistical software (version 3.4.3, R Core Team 2017).

Results

All pairs of historical and recent relevés were maintained in the same group following cluster analysis, very close to each other in the dendrogram, except one plot, which shifted from wet to typical snowbeds (Appendix, Fig. S1).

Diversity

Our data showed extremely strong differences in the frequency and composition of lichens between historical and recent data on windy ridges. Added to the fact that many occurrences in the historical data set were identified only at the genus level, we had to conclude that the historical data were most likely not complete enough for a valid comparison. Hence, lichens were not included in the analyses.

The α-diversity of vascular plants increased in 36 of 43 plots for windy ridges and in 27 of 31 plots in snowbeds from historical to recent inventories. The mean Simpson index increased significantly in snowbeds (+4.1 ± 2.8 for typical snowbeds, p < 0.001; +4.0 ± 3.7 for wet snowbeds, p < 0.001) and on windy ridges (+3.5 ± 4.0 for acidophilic ridges, p = 0.001; +2.2 ± 4.7 for basophilic ridges, p = 0.004; Fig. 3). At the same time, β-diversity (Bray-Curtis dissimilarity) decreased for 38 plots on windy ridges and for 18 plots in snowbeds. The mean index decreased significantly in acidophilic (-0.067 ± 0.035, p < 0.001) and basophilic windy ridges (-0.020 ± 0.037, p = 0.007) and in typical snowbeds (-0.049 ± 0.065, p = 0.005; Fig. 4), but was stable in wet snowbeds.

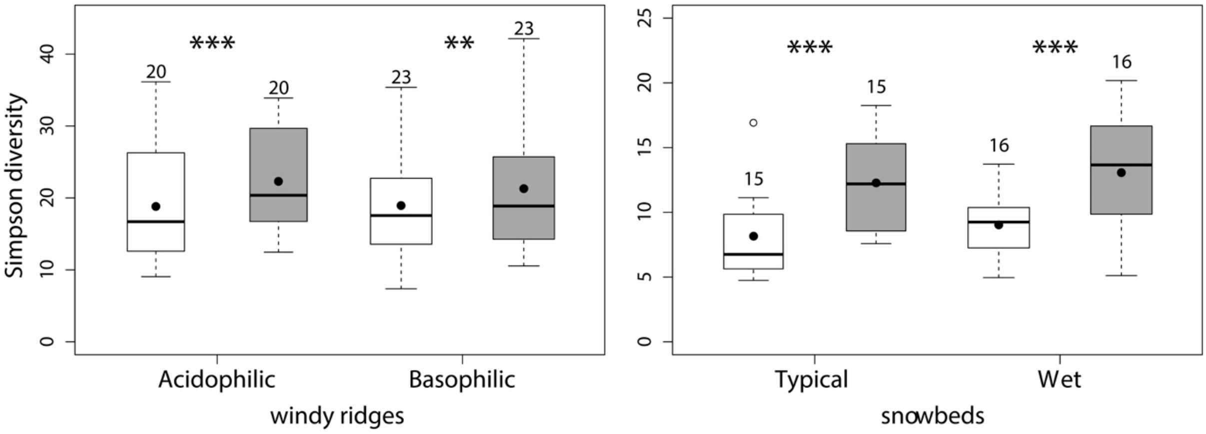

Fig. 3 Simpson diversity indices for historical (white boxes) and recent (grey boxes) inventories of vascular plant species on windy ridges and in snowbeds. Black dots represent the mean values, the black line is the median, and boxes delimit the 1st and 3rd quartiles. Stars above the boxes indicate a significant difference between historical and recent inventories, according to a pairwise Wilcoxon-Mann-Whitney test: *p < 0.05, **p < 0.01, ***p < 0.001. The numbers above boxplots are the sample sizes.

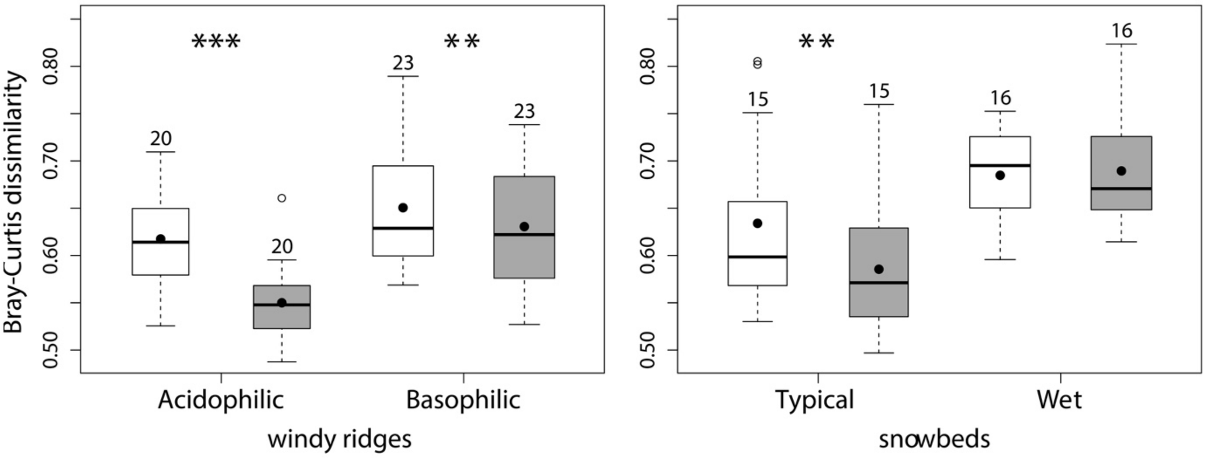

Fig. 4 Bray-Curtis dissimilarity indices, calculated for each inventory with all the other inventories of the same period and habitat, among historical (white boxes) and recent (grey boxes) inventories of vascular plant species on windy ridges and in snowbeds. Symbols are the same as in Figure 3.

Changes in species composition and cover

The first two axes of the PCA based on windy ridge inventories explained 13% of the total variance (PC1: 6.8%, PC2: 6.2%). Recent and historical relevés were almost always situated closely together, corresponding to a weak change in composition and cover (Fig. 5a). Nevertheless, the acidophilic windy ridges showed a significant mean temporal shift (p = 0.016 with a MANOVA) in the direction of basophilic windy ridges. These latter ones showed no significant change in species composition and cover. A significant shift was also detected for wet snowbeds towards typical snowbeds (p = 0.023; Fig. 5b) according to the PCA, whose first two axes explained 17.0% of the total variance (PC1: 11.8%, PC2: 5.2%). The typical snowbeds did not show any significant shift.

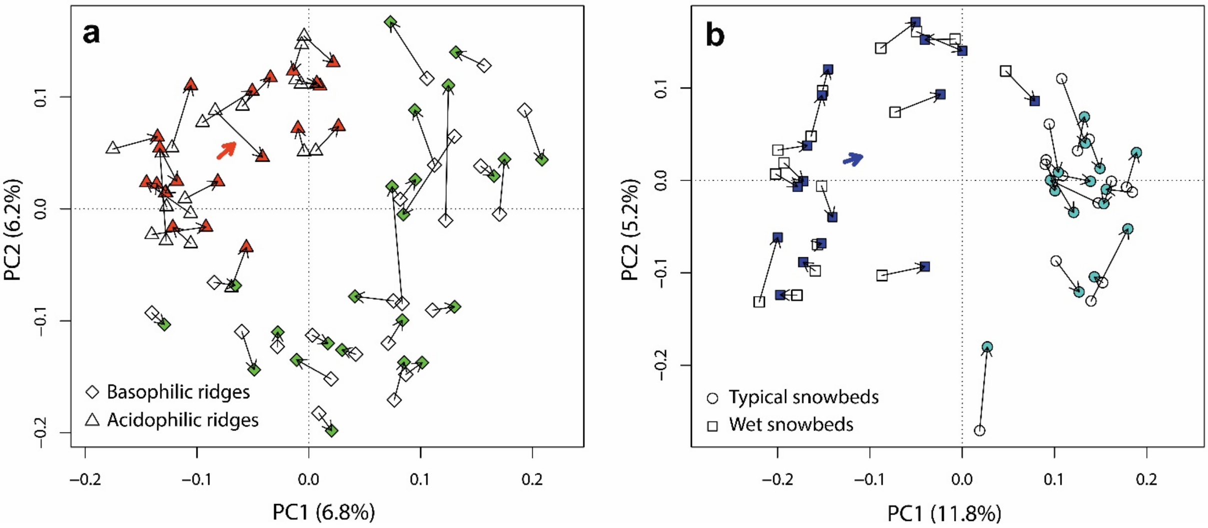

Fig. 5 Principal components analyses based on the composition and cover of vascular plant species (a) on windy ridges and (b) in snowbeds. Couples of historical (empty symbols) and recent (full symbols) surveys are connected with arrows. The thick arrows represent a significant shift of the plant community centroids, i.e. for (a) acidophilic windy ridges and (b) wet snowbeds.

Species frequency and cover changes

In both habitats, there were more species whose frequencies increased between inventories than species with a decreased frequency (Table S3-S6), and only increasing frequencies were statistically significant. On acidophilic windy ridges (Table S3), only the relative frequency of *Euphrasia minima* increased significantly (+47%, p = 0.002). As an annual species, its populations can fluctuate widely from year to year. On basophilic windy ridges (Table S4), the frequencies of a typical graminoid for this habitat (*Agrostis alpina*; +29%, p = 0.023) and of two generalists (*Euphrasia minima*; +38%; *Campanula scheuchzeri*, +29%) increased significantly (p = 0.004 and p = 0.009, respectively). In both habitats, several species from windy ridges (e.g., *Phyteuma hemisphaericum*, *Veronica aphylla, Salix serpillifolia*) and other grasslands (e.g., *Poa alpina*, *Leontodon helveticus*, *Erigeron uniflorus*, *Festuca violacea aggr.*) increased in frequency, but not significantly. *Sesleria caerulea* was the only species with a significant increase in cover (+6.7%, p = 0.030) on basophilic windy ridges. Conversely, *Carex ericetorum* decreased in frequency (-21%), although only marginally significantly (p = 0.099).

In typical snowbeds (Table S5), *Festuca halleri aggr*. and *Leontodon helveticus*, species from acidophilic alpine grasslands, increased in frequency (both +40%, p = 0.027 and p = 0.020, respectively). *Sagina saginoides*, a typical snowbed species, similarly increased (p = 0.003). Some snowbed species (e.g., *Veronica alpina, Gnaphalium supinum*), grasslands species (e.g., *Festuca violacea aggr., Agrostis schraderiana*) and *Cirsium spinosissimum* increased in frequency, although not significantly. Other snowbed species (*Carex foetida, Salix herbacea, Alchemilla pentaphyllea*) decreased in cover, but never significantly. On wet snowbeds (Table S6), only *Veronica alpina* and *Leontodon helveticus* increased in frequency (both +38%, p = 0.020 and p = 0.022), while increases of other grassland species were not significant in terms of frequency (e.g., *Campanula scheuchzeri, Carex sempervirens, Pedicularis kerneri*) or cover (e.g., *Carex capillaris, Festuca rubra aggr*.). Two typical species of this plant community decreased, but not significantly: *Carex lachenalii* decreased in frequency (-19%) and *Carex bicolor* in cover (-11%).

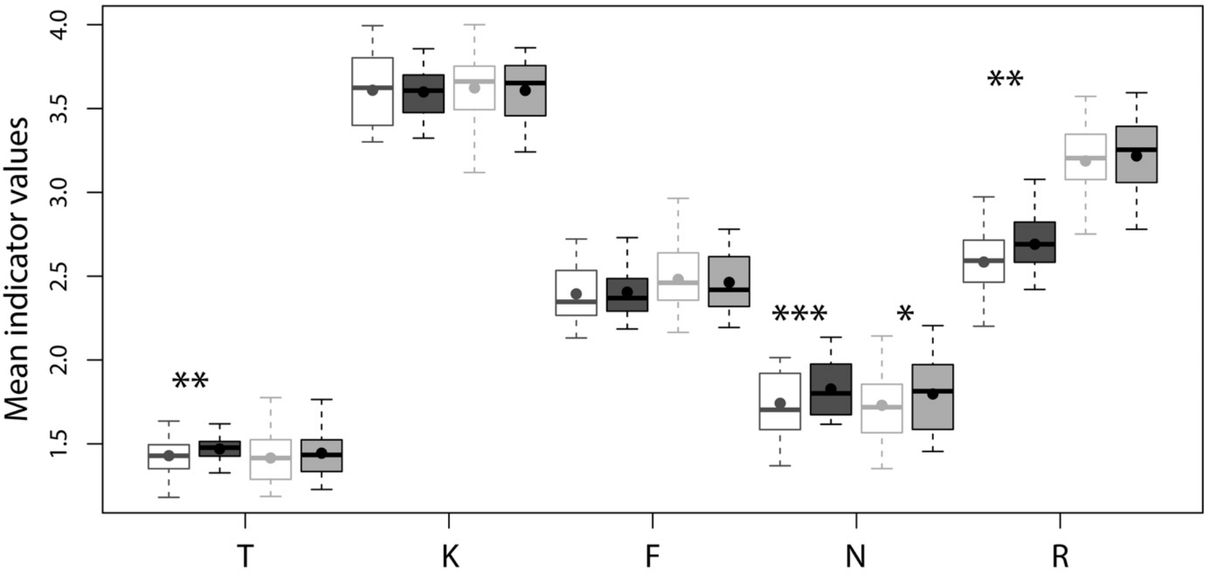

Fig. 6 Cover-weighted means of ecological indicator values (Landolt et al. 2010) for temperature (T), continentality (K), soil humidity (F), nutrient content (N) and pH (R) in historical (white boxes) and recent inventories of vascular plant species on acidophilic (dark grey) and basophilic (light grey) windy ridges. Symbols are the same as in Figure 3.

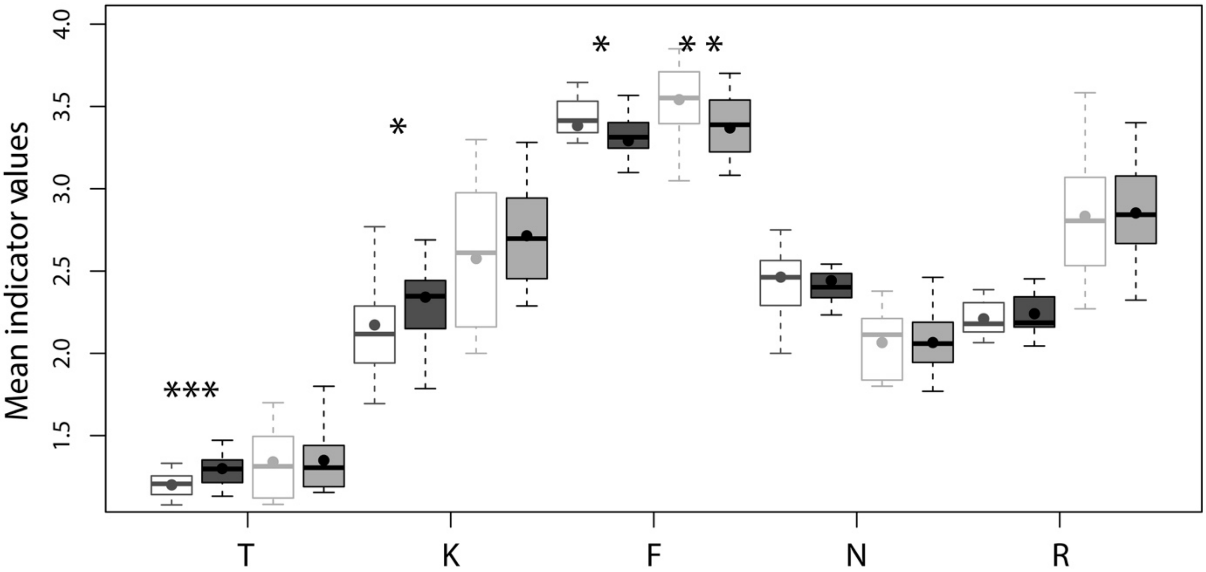

Fig. 7 Cover-weighted means of indicator values (Landolt et al., 2010) for temperature (T), continentality (K), soil humidity (F), nutrient content (N) and pH (R) in historical (white boxes) and recent inventories of vascular plant species in typical (dark grey) and wet (light grey) snowbeds. Symbols are the same as in Figure 3.

Ecological indicator values

Acidophilic windy ridges and typical snowbeds showed a significant increase in their mean ecological indicator values for temperature (T; $p = 0.014$ for acidophilic windy ridges, $p < 0.001$ for typical snowbeds; Fig. 6) between historical and recent surveys. Windy ridges and snowbeds also differed in terms of other ecological indicator values. The vegetation of windy ridges indicated a shift toward more eutrophic soils (N; $p < 0.001$ for acidophilic, $p = 0.015$ for basophilic windy ridges; Fig. 6). The values for soil pH of the two community types were coherent with their respective position along this ecological gradient, but acidophilic windy ridges showed a significant increase ($p = 0.008$), representing a shift towards basophilic windy ridges. The snowbeds showed no significant changes for these indicator values, but the mean continentality values (K) increased between the two inventories in the typical snowbeds ($p = 0.026$; Fig. 7). Simultaneously, the species composition of the snowbeds indicated a trend toward drier conditions ($p = 0.002$ for wet, $p = 0.041$ for typical snowbeds). The wet snowbeds now contain a vegetation indicating humidity conditions close to those of the typical snowbeds 23 years ago. No significant difference was observed for the other ecological indicator values (light, humus content) between historical and current surveys.

Discussion

We observed an increase in biodiversity and biotic homogenisation in snowbeds and on windy ridges, although these changes were not in the same direction. While both communities shifted towards a more thermophilous species composition, as frequently observed in mountains under climate change, the flora of windy ridges indicated more fertile conditions, whereas the snowbeds shifted towards a flora containing less hygrophilous species, preferring more continental conditions.

The α-biodiversity increase (Simpson index) and the homogenisation (decrease of β-diversity) confirmed, with a considerably larger data set, the findings of Matteodo et al. (2016). Both trends have also been observed by various authors in alpine plant communities (e.g., Britton et al. 2009; Carbognani et al. 2014) under climate change. Globally, the climatic changes recorded in the last decades have improved the conditions for plants in the alpine belt, with warmer summer temperatures and longer growing seasons (Rebetez & Reinhard 2008; Klein et al. 2016; CH2018; Klein et al. 2018). Generalist species or species from neighbouring alpine grasslands could colonise windy ridges and typical snowbeds. These new species are adapted to less extreme conditions in terms of winter temperature and growing season length and, consequently, have mostly higher ecological values for temperature (T) than the species previously growing in these plots. This could explain the observed significant thermophilisation (Gottfried et al. 2012) in two of the four communities that we considered. A similar trend has previously been observed in alpine grasslands (Vittoz et al. 2008; Matteodo et al. 2016) and by numerous authors on alpine summits (e.g., Pauli et al. 2012; Matteodo et al. 2013; Steinbauer et al. 2018) and corresponds to the monotonic relation between species richness and daily maximum temperature (Vonlanthen et al. 2006b). These newcomers increase the α-diversity but the more stress-tolerant species (adapted to cope with winter frost on windy ridges and short growing seasons in snowbeds) apparently have not yet been competitively displaced by the newly arriving species (extinction debt; Dullinger et al. 2012). At the same time, some missing specialists (e.g., *Agrostis alpina, Phyteuma hemisphaericum* on windy ridges; *Sagina saginoides, Veronica alpina* in snowbeds) colonized the plots, causing the decrease in β-diversity, as the communities contain more and more the same species (Matteodo et al. 2016).

Windy ridges

Windy ridges were characterised by a change of flora indicating more eutrophic conditions in both community types, and with less acidic conditions on the acidophilic windy ridges. The increase of N values can be explained by different factors. (1) It has often been demonstrated that nitrogen deposition induces eutrophication in grasslands (e.g., Stevens et al. 2010; Roth et al. 2015). But the deposition values are low (around 5 kg•ha•yr) in the study area (CFHA 2005; www.bafu.admin.ch) and tended to decrease over the last years, although a cumulative effect cannot be excluded (OFEV 2018). Moreover, eutrophication due to nitrogen deposition is often associated with acidification (Stevens et al. 2010), whereas we observed the opposite in Zermatt. (2) Generalist grassland species tended to increase in cover (*Sesleria caerulea*) or in frequency (*Campanula scheuchzeri, Poa alpina, Festuca violacea aggr., Potentilla aurea, Anthoxanthum alpinum*). These increases were rarely significant, but these species have higher N values than average and, all together, they influence the mean, probably without responding to a real eutrophication. For example, *Poa alpina* has an N value of 4 and was previously observed as an efficient colonizer of alpine summits, even in rocky conditions (Vittoz et al.

2009a; Matteodo et al., 2013). Moreover, species from lower elevations have, on average, higher N values than alpine species (Odland 2008; Güsewell et al. 2012). (3) Following the significant glacier retreat in the Zermatt region (Rastner et al. 2016), there is a potentially important aeolian dust deposit in the valley (Gisladottir et al. 2005). This loess can be quite nutrient-rich (Küfmann 2003) and might cause soils to evolve towards less oligotrophic conditions.

Aeolian dust deposition is probably an important cause of the observed eutrophication as it can be related to the simultaneous shift of acidophilic windy ridges towards basophilic ones. Indeed, acidophilic windy ridges were characterised by a recent species composition corresponding to less acid soil conditions. This dynamic of windy ridge vegetation has never been highlighted before and could be specific to the study area. The increasing area of glacial moraines and the corresponding increase in aeolian dust in the valley could potentially explain these changes. The geology of the Zermatt region is highly diverse, with numerous basic rocks (calcschists, ultramaphic rocks, marble, etc.) among acidic rocks (Service géologique national 2005). This rock variability is also reflected in the moraines from which the aeolian dust originates. The deposition of aeolian dust, potentially rich in basic cations, on the topsoil of the Zermatt region could be favourable for the establishment of basophilic species. Such dust deposition has been measured in the Central Austrian Alps, where they amounted on average to ~100 $g \bullet m^{-2} \bullet a^{-1}$ (Gruber 1980 in Körner 2003) and were considered as an important buffer of the natural acidity of alpine soils (Küfmann 2003). Indeed, dense clumps of graminoids (e.g., *Elyna myosuroidis, Carex sp.*), often important in ridge communities, are highly efficient traps for aeolian dust (Steiner 2002; Küfmann 2003).

Snowbeds

We found that plants originating from neighbouring alpine grasslands had colonized snowbeds (*Leontodon helveticus*, *Festuca halleri aggr., Campanula scheuchzeri*), while some of the typical snowbed species tended to decrease in cover over time (*Carex lachenalii*, *C. bicolor, Luzula alpinopilosa*). As already observed in previous studies (Carbognani et al. 2014; Sandvik et Odland 2014; Matteodo et al. 2016; Maliniemi et al. 2018), snowbeds have become more similar to alpine grasslands than they were 23 years ago, with a flora indicating drier and more continental conditions than in the past.

The snow cover period, which is the most important environmental filter for snowbeds (Vonlanthen et al. 2006a), has become shorter (Klein et al. 2016) because of lower snowfall (Serquet et al. 2013) and higher spring temperatures. This shorter snow cover duration has several consequences for snowbed vegetation: (1) The growing season is longer, opening the snowbeds to species that require longer periods for growth and reproduction, such as generalists or the typical species of surrounding communities (Braun-Blanquet 1964; Vonlanthen et al. 2006a). One can expect that the colonisation of these species is facilitated by the close proximity of alpine grasslands and snowbeds, which are often distributed as a mosaic in the landscape, depending on the microtopography. (2) Water availability decreases in quantity, and water is available over a shorter period in summer. This particularly affects wet snowbeds, which are mostly irrigated by the melt-water further upslope. A similar trend towards drier conditions were recorded with a smaller data set by Matteodo et al. (2016), and these new conditions are probably the cause of the cover decrease of some typical species of wet snowbeds (*Carex bicolor, C. lachenalii*). (3) Snow also occurs as a protection against cold nights. With a shorter snow cover period, plants have less protection and have to cope with larger temperature shifts. This corresponds to the increase of the indicator value for continentality, indicating more contrasted temperatures between nights and days. However, according to Klein et al. (2018), the risk of frost after snowmelt has not increased in the last decades.

Conclusions

Snowbeds and windy ridges in the Zermatt region are both influenced by climate change. Although situated in the same valley, often close to each other, the mechanisms driving their plant community changes are different. While increasing temperature seems to be the main driver on windy ridges, the snow cover duration is probably decisive for the dynamics of snowbed communities.

On windy ridges, warmer temperatures probably induce an earlier growth in spring (Vitasse et al. 2017), allowing colonisation by grassland species, which were previously rare because of their high sensitivity to frost compared with specialist species of windy ridges. Moreover, the deposition of nutrients by aeolian dust might also improve the growing conditions for vascular plants. On the other hand, we do not have data indicating that snow cover has decreased on windy ridges, and up to now, there is no visible impact of the shorter snow cover duration on plant species composition. But, in this habitat, snow cover is by definition irregular and the typical species are adapted to deep frosts in winter. Hence, the vegetation of windy ridges seems to have been mainly influenced by temperature increases, either directly or indirectly by dust deposition following the growing areas of glacial moraines.

In snowbeds, the shorter snow cover duration is probably the main driver of vegetation change, by extending the growing season and so enabling taller species from surrounding grasslands to colonise snowbeds or to increase their cover. This might also be caused by reduced water availability in the middle of summer, which might be compounded by projected reductions in summer precipitation in the Alps (CH2018 2018). Although not rich in species, snowbeds shelter many species that are restricted to this habitat, most of them needing humic soils to grow. Therefore, the loss of snowbeds at lower elevations might not be compensated by areas made newly available by warmer conditions or glacier retreat.

This study was restricted to one valley, with particular climatic and geologic conditions. Similar comparisons in other alpine areas would be helpful to obtain a broader view of the present changes in high mountain vegetation under climate change, and the respective influences of other local factors, such as nitrogen deposition and grazing, on vegetation dynamics. Indeed, a good understanding of variation at fine scales and confounding factors are important to improve predictive models of climate change impacts on mountain vegetation. It would be particularly interesting to address the question of aeolian dust deposition, contrasting areas that are poor or rich in recent glacial moraines. Quantification of these deposits are also necessary, since these data are rare in the Alps, although aeolian deposition may play a major role in the soil formation of high alpine areas now available for plant colonisation. Finally, data on climate change impacts on lichens in the Alps are still lacking, with all available studies in Europe until now coming from Scandinavia.

Compliance with ethical standards

Ethical Statement The authors declare that they respected ethical standards.

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent The investigation in the field was conducted with authorisation of the *Burgergemeinde Zermatt*.

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Additional supporting information in the online version of this article (see „Supplementary Material") contains the following appendices:
Table S1 List of the retained associations with the typical species, the ecological conditions and the number of historical relevés.

Table S2 List of the plots retained in this study, with the classification, the year, authors and number of species, the coordinates, the elevation, the aspect and the slope.

Table S3 Species of the acidophilic windy ridges with a relative frequency change > 15% and/or a relative cover change > 5%.

Table S4 Species of the basophilic windy ridges with a relative frequency change > 15% and/or a relative cover change > 5%.

Table S5 Species of the typical snowbeds with a relative frequency change > 15% and/or a relative cover change > 5%.

Table S6 Species of the wet snowbeds with a relative frequency change > 15% and/or a relative cover change > 5%.

Fig. S1 Clustering of windy ridge and snowbeds.

Supplementary material

Contrasting impacts of climate change on the vegetation of windy ridges and snowbeds in the Swiss Alps

Loïc Liberati, Swanee Messerli, Magalì Matteodo & Pascal Vittoz

Table S1 List of the retained associations with the generic wording used in the article, the period when the historical inventories were realised (with the median between brackets), the typical species, the ecological conditions, the name of the corresponding associations in Prunier et al. (2017) and the number of historical relevés included in the study.

Name used in the article	Period of the historical relevés	Main species	Association (Prunier et al. 2017)	Ecological characteristics	Number of relevés
Basophilic windy ridges	1982-1995 (1993)	Dominated by *Elyna myosuroides, Silene exscapa, Carex curvula subsp. rosae, Agrostis alpina* and *Sesleria caerulea;* characterized by *Minuartia sedoides, Festuca quadriflora, Carex parviflora, Carex rupestris* and *Anthyllis vulneraria subsp. valesiaca*	*Elyno-Caricetum rosae*	Windy ridges with surficial soil, neutral to slightly acidic	21
			Caricetum fimbriatae	Same, on serpentine	1
Acidophilic windy ridges	1980-1995 (1995)	Dominated by *Elyna myosuroides, Silene exscapa, Agrostis alpina, Festuca halleri, Helictotrichon versicolor, Loiseleuria procumbens, Lloydia serotina* and *Carex curvula s.str.* ; characterized by *Minuartia recurva, Luzula lutea, Pulsatilla vernalis* and *Veronica bellidioides*	*Elynetum myosuroidis*	Windy ridges with acidic soil, often rich in humus	17
			Caricetum curvluae elynetosum myosuroidis	Transition between windy ridges and high-alpine, acidic grasslands	4
Typical snowbeds	1971-1995 (1993)	Dominated by *Alchemilla pentaphyllea, Salix herbacea, Gnaphalium supinum, Agrostis rupestris* and/or *Carex foetida;* characterized by *Sibbaldia procumbens, Geum montanum* and *Sedum alpestre*	*Salicetum herbaceae*	Hollows or north-facing slopes with long snow cover, with acidic soil	9
			Caricetum foetidae	Same, momentary wet in spring	5
			Polytrichetum sexangularis	Same, with very long snow cover	1
Wet snowbeds	1989-1995 (1995)	Dominated by *Carex bicolor* and *Salix herbacea;* characterized by *Polygonum viviparum, Saxifraga oppositifolia, Carex parviflora, Sagina saginoides, Ranunculus glacialis, Sagina saginoides* and/or *Carex maritima*	*Salici herbaceae-Caricetum lachenalii*	Terraces or slopes with long snow cover, along small streams or alpine lakes, with humic soil	12
			Junco triglumis-Caricetum bicoloris	Same, with little humic soil, e.g. on glacial moraine	4

Table S2 List of the plots retained in this study, with the classification in this study (habitat), the code (according to Steiner 2002), the year, authors and number of species for the historical and recent inventories, the coordinates measured in 2016 (GPS Trimble GeoXH, ±1 m; coordinate projection CH1903), the elevation, the aspect, the slope and the original classification (association).
All the floristic data (exhaustive historical and recent relevés) are deposited at Info Flora (www.infoflora.ch).

Habitat	Code	Historial inventory			Recent inventory			Coordinates		Elevation	Aspect	Slope	Association
		Year	Author	# spec.	Year	Author(s)	# spec.	W-E	S-N	[m asl]	[°]	[°]	
Basophilic windy ridges	5	1995	F. Meyer	26	2016	L. Liberati, S. Messerli, P. Vittoz	35	620808	93589	2547	345	20	*Elyno-Caricetum rosae*
	23	1995	F. Meyer	36	2016	L. Liberati, S. Messerli	51	619841	93924	2465	360	36	*Elyno-Caricetum rosae*
	46	1995	F. Meyer	42	2016	L. Liberati, S. Messerli, P. Vittoz	54	620980	93900	2410	360	29	*Elyno-Caricetum rosae*
	64	1995	F. Meyer	32	2016	L. Liberati, S. Messerli, M. Vust	29	620171	93877	2482	338	30	*Elyno-Caricetum rosae*
	68	1995	F. Meyer	23	2016	L. Liberati	27	620446	92935	2670	358	5	*Elyno-Caricetum rosae*
	114	1995	F. Meyer	16	2016	L. Liberati, S. Messerli	20	621044	92631	2546	360	0	*Elyno-Caricetum rosae*
	178	1995	F. Meyer	11	2016	L. Liberati	16	621602	92417	2645	325	10	*Elyno-Caricetum rosae*
	189	1995	F. Meyer	20	2016	L. Liberati	21	620262	93382	2684	308	8	*Elyno-Caricetum rosae*
	222	1995	F. Meyer	27	2016	L. Liberati	27	622390	91385	2811	340	8	*Elyno-Caricetum rosae*
	234	1995	F. Meyer	21	2016	L. Liberati	23	622264	91532	2765	360	0	*Elyno-Caricetum rosae*
	238	1995	F. Meyer	20	2016	L. Liberati	28	622498	91502	2758	5	5	*Elyno-Caricetum rosae*
	1134	1993	S. Reist	37	2016	L. Liberati, S. Messerli	32	626742	98187	2556	5	30	*Elyno-Caricetum rosae*
	1172	1993	S. Reist	49	2016	L. Liberati	67	626389	96424	2421	335	15	*Elyno-Caricetum rosae*
	1189	1993	S. Reist	45	2016	L. Liberati	41	626999	96965	2638	290	25	*Elyno-Caricetum rosae*
	3210	1993	C. Käsermann	30	2016	L. Liberati	50	621944	98029	2539	250	42	*Elyno-Caricetum rosae*
	3414	1993	C. Käsermann	16	2016	L. Liberati	20	621301	96446	2776	310	18	*Elyno-Caricetum rosae*
	4368	1982	J.-L. Richard	23	2016	L. Liberati	24	624296	92500	2697	270	17	*Caricetum fimbriatae*
	4754	1985	J.-L. Richard	29	2016	L. Liberati	40	620186	93648	2569	345	30	*Elyno-Caricetum rosae*
	4755	1985	J.-L. Richard	28	2016	L. Liberati	37	620189	93485	2630	338	28	*Elyno-Caricetum rosae*
	4835	1986	J.-L. Richard	31	2016	L. Liberati	36	626183	93451	2791	360	17	*Elyno-Caricetum rosae*
	4839	1986	J.-L. Richard	14	2016	L. Liberati	19	626455	93065	2943	270	8	*Elyno-Caricetum rosae*
	4930	1987	J.-L. Richard	17	2016	L. Liberati	16	626218	93439	2809	340	32	*Elyno-Caricetum rosae*
	5215	1992	J.-L. Richard	47	2016	L. Liberati, S. Messerli	65	621880	97179	2488	360	38	*Elyno-Caricetum rosae*
Acidophilic windy ridges	13	1995	F. Meyer	23	2016	L. Liberati, S. Messerli, P. Vittoz	26	621002	93819	2455	34	8	*Elynetum myosuroidis*
	14	1995	F. Meyer	25	2016	L. Liberati, S. Messerli	28	620873	93822	2450	330	20	*Elynetum myosuroidis*
	29	1995	F. Meyer	35	2016	L. Liberati	42	621305	92582	2556	360	5	*Elynetum myosuroidis*
	62	1995	F. Meyer	26	2016	L. Liberati	29	620307	93695	2556	10	8	*Elynetum myosuroidis*
	67	1995	F. Meyer	21	2016	L. Liberati	28	620434	92880	2673	160	8	*Elynetum myosuroidis*
	75	1995	F. Meyer	21	2016	L. Liberati	30	622027	92423	2610	340	25	*Elynetum myosuroidis*
	76	1995	F. Meyer	33	2016	L. Liberati, S. Messerli	34	622021	92586	2560	56	30	*Caricetum curvulae elynetosum*
	119	1995	F. Meyer	15	2016	L. Liberati	23	621010	92308	2682	60	8	*Caricetum curvulae elynetosum*
	135	1995	F. Meyer	24	2016	L. Liberati, S. Messerli	37	619966	94060	2434	320	20	*Elynetum myosuroidis*
	184	1995	F. Meyer	23	2016	L. Liberati, S. Messerli	29	621832	92933	2480	12	18	*Elynetum myosuroidis*
	185	1995	F. Meyer	16	2016	L. Liberati	26	620508	93107	2650	390	5	*Caricetum curvulae elynetosum*
	186	1995	F. Meyer	27	2016	L. Liberati	39	620371	93318	2673	50	18	*Elynetum myosuroidis*
	200	1995	F. Meyer	21	2016	L. Liberati	23	621155	93625	2486	35	17	*Elynetum myosuroidis*
	230	1995	F. Meyer	17	2016	L. Liberati, S. Messerli	24	620660	93717	2514	50	5	*Elynetum myosuroidis*
	1076	1993	S. Reist	42	2016	L. Liberati, S. Messerli, P. Vittoz	48	626415	96224	2484	310	10	*Elynetum myosuroidis*
	2001	1993	S. Krähenmann	37	2016	L. Liberati, S. Messerli, P. Vittoz	46	629128	95656	2643	320	30	*Elynetum myosuroidis*
	2075	1993	S. Krähenmann	39	2016	L. Liberati	46	628449	95489	2524	340	35	*Elynetum myosuroidis*
	2077	1993	S. Krähenmann	40	2016	L. Liberati	48	628387	95439	2539	345	40	*Elynetum myosuroidis*
	2078	1993	S. Krähenmann	31	2016	L. Liberati, S. Messerli, P. Vittoz	45	628767	95544	2560	335	30	*Elynetum myosuroidis*
	2080	1993	S. Krähenmann	45	2016	L. Liberati	45	628681	95488	2565	350	40	*Elynetum myosuroidis*

Habitat	Code	Historical inventory			Recent inventory			Coordinates		Elevation	Aspect	Slope	Association
		Year	Author	# spec.	Year	Author(s)	# spec.	W-E	S-N	[m asl]	[°]	[°]	
Typical snowbeds	19	1995	F. Meyer	27	2016	S. Messerli	23	620899	93609	2526	25	20	*Caricetum foetidae*
	59	1995	F. Meyer	11	2016	S. Messerli	14	620348	93648	2554	0	0	*Salicetum herbaceae*
	210	1995	F. Meyer	9	2016	S. Messerli	13	622989	91141	2821	0	0	*Caricetum foetidae*
	2040	1993	S. Krähenmann	14	2016	S. Messerli	23	630389	96009	2816	240	5	*Caricetum foetidae*
	2149	1993	S. Krähenmann	13	2016	S. Messerli	25	628687	96431	2883	0	0	*Salicetum herbaceae*
	2176	1993	S. Krähenmann	16	2016	S. Messerli	31	628590	96479	2884	0	0	*Salicetum herbaceae*
	2733	1971	J.-L. Richard	11	2016	S. Messerli, L. Liberati, M. Matteodo	18	620720	93410	2542	0	0	*Caricetum foetidae*
	3027	1993	C. Käsermann	19	2016	S. Messerli, L. Liberati	25	621486	97462	2461	15	25	*Salicetum herbaceae*
	3034	1993	C. Käsermann	11	2016	S. Messerli	16	622359	98459	2721	310	25	*Salicetum herbaceae*
	3060	1993	C. Käsermann	13	2016	S. Messerli, L. Liberati	20	621642	97028	2605	340	15	*Salicetum herbaceae*
	3061	1993	C. Käsermann	9	2016	S. Messerli	17	621757	96879	2625	30	2	*Salicetum herbaceae*
	3076	1993	C. Käsermann	16	2016	S. Messerli	28	621100	99040	2608	0	0	*Salicetum herbaceae*
	3336	1993	C. Käsermann	9	2016	S. Messerli	13	622017	98813	2755	0	0	*Caricetum foetidae*
	3671	1993	C. Käsermann	12	2016	S. Messerli	25	622392	99075	2756	190	8	*Salicetum herbaceae*
	4924	1992	J.-L. Richard	8	2016	S. Messerli	12	627149	92830	3002	190	8	*Polytrichetum sexangularis*
Wet snowbeds	104	1995	F. Meyer	8	2016	S. Messerli	8	619533	93691	2554	0	0	*Junco triglumis-Caricetum bicoloris*
	116	1995	F. Meyer	18	2016	S. Messerli	24	621025	92450	2619	30	38	*Salici herbaceae-Caricetum lachenalii*
	118	1995	F. Meyer	20	2016	S. Messerli	21	621063	92335	2660	70	25	*Salici herbaceae-Caricetum lachenalii*
	183	1995	F. Meyer	16	2016	S. Messerli	21	621572	92488	2591	360	20	*Salici herbaceae-Caricetum lachenalii*
	187	1995	F. Meyer	13	2016	S. Messerli	19	620333	93347	2680	25	5	*Junco triglumis-Caricetum bicoloris*
	224	1995	F. Meyer	16	2016	S. Messerli	17	622504	91393	2786	45	7	*Salici herbaceae-Caricetum lachenalii*
	233	1995	F. Meyer	14	2016	S. Messerli	30	622246	91484	2775	340	8	*Salici herbaceae-Caricetum lachenalii*
	236	1995	F. Meyer	14	2016	S. Messerli	12	622194	91654	2727	0	0	*Salici herbaceae-Caricetum lachenalii*
	262	1995	F. Meyer	12	2016	S. Messerli	18	622166	91698	2720	35	4	*Junco triglumis-Caricetum bicoloris*
	264	1995	F. Meyer	16	2016	S. Messerli	22	621995	91964	2686			*Salici herbaceae-Caricetum lachenalii*
	1119	1993	S. Reist	10	2016	S. Messerli	17	627449	97212	2928	305	3	*Salici herbaceae-Caricetum lachenalii*
	3178	1993	C. Käsermann	23	2016	S. Messerli	30	621601	98187	2457	0	0	*Salici herbaceae-Caricetum lachenalii*
	4535	1992	J.-L. Richard	14	2016	S. Messerli	24	624886	92413	2747	5	360	*Salici herbaceae-Caricetum lachenalii*
	4541	1992	J.-L. Richard	15	2016	S. Messerli	31	622325	91975	2614	0	0	*Salici herbaceae-Caricetum lachenalii*
	4645	1992	J.-L. Richard	22	2016	S. Messerli	25	622356	98977	2752	180	2	*Salici herbaceae-Caricetum lachenalii*
	8380	1989	B. Bressoud	7	2016	S. Messerli	18	624840	92435	2740	0	0	*Junco triglumis-Caricetum bicoloris*

Table S3 Species of the acidophilic windy ridges with a relative frequency change > 15% (upper part of the table) and/or a relative cover change > 5% (lower part of the table). Species with less important changes are not retained in the table. Significant changes, according to a permutation test, are in bold.

Species	**Habitat (Landolt et al. 2010)**	**Relative historical frequency [%]**	**Relative recent frequency [%]**	**Difference of frequency [%]**	**Frequency p-value**	**Mean historical relative cover [%]**	**Mean recent relative cover [%]**	**Difference of cover [%]**	**Cover p-value**
Euphrasia minima	Acidophilic alpine grasslands	**26.3**	**73.7**	**47.4**	**0.002**	1.4	0.5	-0.9	0.762
Leontodon helveticus	Acidophilic alpine grasslands	26.3	52.6	26.3	0.099	3.5	0.5	-2.9	0.329
Selaginella selaginoides	Basophilic alpine grasslands	31.6	57.9	26.3	0.087	0.9	0.5	-0.5	0.869
Erigeron uniflorus	Acidophilic alpine grasslands	5.3	31.6	26.3	0.111	0.1	0.4	0.4	-
Poa alpina	Eutrophic grasslands	26.3	52.6	26.3	0.113	1.0	1.7	0.8	0.812
Androsace obtusifolia	Acidophilic alpine grasslands	36.8	63.2	26.3	0.100	1.4	0.5	-0.9	0.740
Antennaria carpatica	Windy ridges	63.2	84.2	21.1	0.092	1.2	1.1	-0.2	0.957
Phyteuma hemisphaericum	Windy ridges	21.1	42.1	21.1	0.155	1.3	0.3	-1.0	-
Veronica fruticans	Rocks and screes	0.0	21.1	21.1	0.195	0.0	0.5	0.5	-
Minuartia verna	Dry grasslands	0.0	21.1	21.1	0.157	0.0	0.6	0.6	-
Homogyne alpina	Acidophilic alpine grasslands	31.6	52.6	21.1	0.210	3.1	2.1	-1.0	0.719
Potentilla crantzii	Basophilic alpine grasslands	10.5	31.6	21.1	0.207	1.4	0.9	-0.5	-
Veronica aphylla	Windy ridges	5.3	26.3	21.1	0.201	0.5	0.7	0.2	-
Gentiana brachyphylla	Windy ridges	42.1	63.2	21.1	0.232	0.9	0.5	-0.4	0.900
Agrostis alpina	Windy ridges	68.4	84.2	15.8	0.217	8.1	7.5	-0.7	0.821
Loiseleuria procumbens	Heathlands	57.9	73.7	15.8	0.200	24.0	18.1	-5.9	0.090
Hieracium piliferum aggr.	Acidophilic alpine grasslands	52.6	68.4	15.8	0.295	1.0	1.7	0.7	0.796
Galium anisophyllon	Basophilic alpine grasslands	0.0	15.8	15.8	0.318	0.0	0.6	0.6	-
Pyrola minor	Heathlands	0.0	15.8	15.8	0.319	0.0	0.3	0.3	-
Potentilla aurea	Acidophilic alpine grasslands	10.5	26.3	15.8	0.358	1.4	0.6	-0.8	-
Achillea nana	Rocks and screes	42.1	57.9	15.8	0.368	0.7	0.6	-0.1	0.984
Salix serpillifolia	Windy ridges	47.4	63.2	15.8	0.381	6.1	2.6	-3.6	0.258
…									
Polygala alpestris	Basophilic alpine grasslands	15.8	0.0	-15.8	0.345	0.6	0.0	-0.6	-
Salix breviserrata	Shrublands	10.5	10.5	0.0	1.000	11.9	24.0	12.2	-
Elyna myosuroides	Windy ridges	89.5	100.0	10.5	0.452	13.9	19.4	5.5	0.099
Lotus corniculatus aggr.	Basophilic alpine grasslands	15.8	26.3	10.5	0.565	3.2	8.7	5.5	-
Carex curvula s.str.	Acidophilic alpine grasslands	42.1	36.8	-5.3	0.781	10.6	15.6	5.1	0.101
…									
Lloydia serotina	Windy ridges	89.5	89.5	0.0	1.000	6.8	1.7	-5.1	0.108
Carex curvula subsp. rosae	Windy ridges	10.5	5.3	-5.3	0.728	12.5	4.1	-8.4	-
Carex sempervirens	Basophilic alpine grasslands	10.5	15.8	5.3	0.789	16.7	8.0	-8.6	-
Astragalus alpinus	Basophilic alpine grasslands	5.3	0.0	-5.3	0.768	14.7	0.0	-14.7	-

Table S4 Species of the basophilic windy ridges with a relative frequency change > 15% (upper part of the table) and/or a relative cover change > 5% (lower part of the table). Species with less important changes are not retained in the table. Significant changes, according to a permutation test, are in bold.

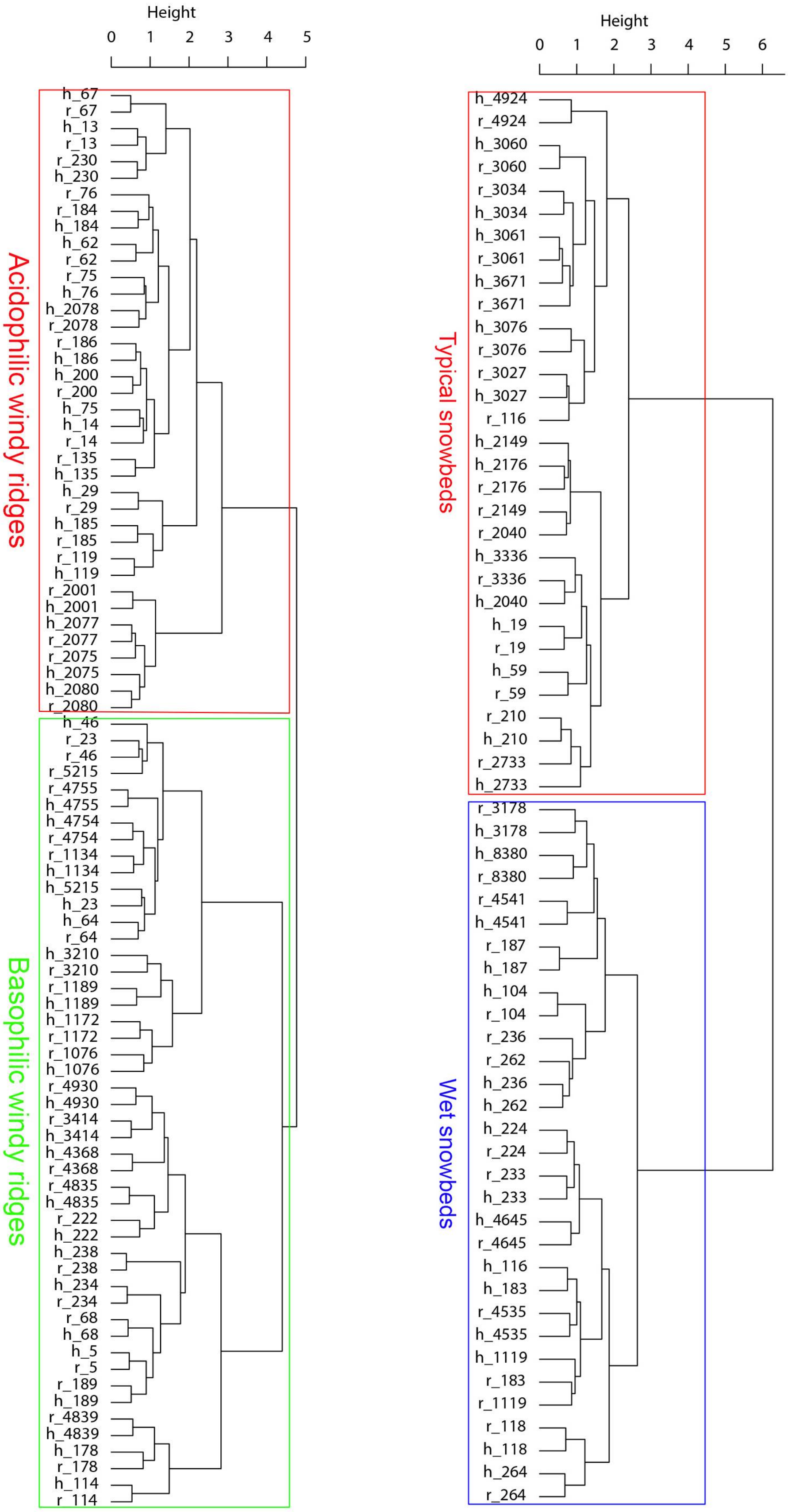
Species	**Habitat (Landolt et al. 2010)**	**Relative historical frequency [%]**	**Relative recent frequency [%]**	**Difference of frequency [%]**	**Frequency p-value**	**Mean historical relative cover [%]**	**Mean recent relative cover [%]**	**Difference of cover [%]**	**Cover p-value**
Euphrasia minima	Acidophilic alpine grasslands	**29.2**	**66.7**	**37.5**	**0.004**	3.7	0.6	-3.0	0.281
Campanula scheuchzeri	Basophilic alpine grasslands	**37.5**	**66.7**	**29.2**	**0.009**	0.7	0.5	-0.2	0.947
Agrostis alpina	Windy ridges	**54.2**	**83.3**	**29.2**	**0.023**	4.8	5.6	0.8	0.771
Festuca violacea aggr.	Basophilic alpine grasslands	29.2	50.0	20.8	0.109	2.1	6.8	4.7	0.101
Phyteuma hemisphaericum	Windy ridges	0.0	20.8	20.8	0.102	0.0	0.3	0.3	-
Gentiana campestris s.str.	Acidophilic alpine grasslands	4.2	25.0	20.8	0.115	0.5	0.5	0.0	-
Salix herbacea	Snowbeds	12.5	29.2	16.7	0.165	0.9	1.0	0.0	-
Oxytropis helvetica	Basophilic alpine grasslands	16.7	33.3	16.7	0.172	11.0	9.2	-1.8	-
Juncus jacquinii	Acidophilic alpine grasslands	12.5	29.2	16.7	0.149	4.4	0.5	-3.9	-
Anthoxanthum alpinum	Acidophilic alpine grasslands	4.2	20.8	16.7	0.204	0.5	0.8	0.3	-
Poa alpina	Eutrophic grasslands	54.2	70.8	16.7	0.223	1.2	1.5	0.3	0.919
Salix serpillifolia	Windy ridges	45.8	62.5	16.7	0.203	3.7	3.9	0.2	0.926
Veronica aphylla	Windy ridges	4.2	20.8	16.7	0.220	3.3	0.4	-2.8	-
Festuca halleri aggr.	Acidophilic alpine grasslands	25.0	41.7	16.7	0.203	6.3	3.0	-3.3	0.215
…									
Carex ericetorum	Windy ridges	50.0	29.2	-20.8	0.099	5.7	1.7	-4.0	0.153
Carex fimbriata	Basophilic alpine grasslands	4.2	4.2	0.0	1.000	41.9	49.9	8.1	-
Sesleria caerulea	Basophilic alpine grasslands	45.8	45.8	0.0	1.000	**8.7**	**15.4**	**6.7**	**0.030**
Erigeron uniflorus	Acidophilic alpine grasslands	20.8	20.8	0.0	1.000	1.0	6.5	5.5	-
…									
Silene exscapa	Rocks and screes	91.7	91.7	0.0	1.000	9.5	4.0	-5.5	0.074
Festuca laevigata	Basophilic alpine grasslands	4.2	4.2	0.0	1.000	13.4	0.4	-13.0	-

Table S5 Species of the typical snowbeds with a relative frequency change > 15% (upper part of the table) and/or a relative cover change > 5% (lower part of the table). Species with less important changes are not retained in the table. Significant changes, according to a permutation test, are in bold.

Species	Habitat (Landolt et al. 2010)	Relative historical frequency [%]	Relative recent frequency [%]	Difference of frequency [%]	Frequency p-value	Mean historical relative cover [%]	Mean recent relative cover [%]	Difference of cover [%]	Cover p-value
Leontodon helveticus	Acidophilic alpine grasslands	**20.0**	**60.0**	**40.0**	**0.020**	2.4	1.3	-1.1	-
Festuca halleri aggr.	Acidophilic alpine grasslands	**26.7**	**66.7**	**40.0**	**0.027**	5.1	1.4	-3.7	0.601
Sagina saginoides	Snowbeds	**0.0**	**40.0**	**40.0**	**0.030**	0.0	0.6	0.6	-
Gnaphalium supinum	Snowbeds	53.3	86.7	33.3	0.059	9.2	4.6	-4.6	0.477
Veronica alpina	Snowbeds	60.0	93.3	33.3	0.060	3.2	2.2	-1.0	0.89
Agrostis schraderiana	Acidophilic alpine grasslands	13.3	40.0	26.7	0.139	1.9	11.5	9.6	-
Festuca violacea aggr.	Basophilic alpine grasslands	13.3	40.0	26.7	0.144	2.5	1.5	-1.0	-
Cirsium spinosissimum	Ruderal areas	13.3	40.0	26.7	0.155	0.6	1.7	1.1	-
Phleum alpinum aggr.	Eutrophic grasslands	6.7	26.7	20.0	0.298	0.4	10.0	9.6	-
Anthoxatum odoratum	Acidophilic alpine grasslands	0.0	20.0	20.0	0.299	0.0	2.1	2.1	-
Minuartia sedoides	Acidophilic alpine grasslands	20.0	40.0	20.0	0.301	21.6	7.1	-14.6	-
Geum montanum	Acidophilic alpine grasslands	33.3	53.3	20.0	0.301	1.1	3.1	2.0	0.787
Carex curvula s.str.	Acidophilic alpine grasslands	33.3	53.3	20.0	0.303	4.8	3.1	-1.7	0.777
Cerastium cerastoides	Snowbeds	40.0	60.0	20.0	0.304	1.1	0.7	-0.4	0.955
Phyteuma hemisphaericum	Windy ridges	6.7	26.7	20.0	0.305	0.0	0.4	0.4	-
Senecio incanus s.str.	Acidophilic alpine grasslands	0.0	20.0	20.0	0.305	0.0	0.5	0.5	-
Deschampsia cespitosa	Eutrophic grasslands	0.0	6.7	6.7	0.730	0.0	18.2	18.2	-
Nardus stricta	Acidophilic alpine grasslands	40.0	53.3	13.3	0.363	1.3	7.9	6.6	0.347
…									
Alchemilla pentaphyllea	Snowbeds	86.7	93.3	6.7	0.868	25.0	19.4	-5.6	0.384
Salix herbacea	Snowbeds	73.3	86.7	13.3	0.321	29.2	23.3	-6.0	0.383
Cerastium pedunculatum	Rocks and screes	6.7	0.0	-6.7	0.729	6.4	0.0	-6.4	-
Carex foetida	Snowbeds	66.7	66.7	0.0	1.000	26.2	18.9	-7.3	0.282
Carex lachenalii	Snowbeds	13.3	6.7	-6.7	0.722	11.6	0.6	-11.0	-
Luzula alpinopilosa	Snowbeds	6.7	6.7	0.0	1.000	13.3	0.8	-12.5	-
Minuartia sedoides	Acidophilic alpine grasslands	20.0	40.0	20.0	0.301	21.6	7.1	-14.6	-

Table S6 Species of the wet snowbeds with a relative frequency change > 15% (upper part of the table) and/or a relative cover change > 5% (lower part of the table). Species with less important changes are not retained in the table. Significant changes, according to a permutation test, are in bold.

Species	Habitat (Landolt et al. 2010)	Relative historical frequency [%]	Relative recent frequency [%]	Difference of frequency [%]	Frequency p-value	Mean historical relative cover [%]	Mean recent relative cover [%]	Difference of cover [%]	Cover p-value
Veronica alpina	Snowbeds	**25.0**	**62.5**	**37.5**	**0.020**	2.3	0.8	-1.5	0.813
Leontodon helveticus	Acidophilic alpine grasslands	**18.8**	**56.3**	**37.5**	**0.022**	2.0	0.7	-1.3	-
Campanula scheuchzeri	Basophilic alpine grasslands	6.3	37.5	31.3	0.066	1.1	0.4	-0.7	-
Pedicularis kerneri	Acidophilic alpine grasslands	6.3	31.3	25.0	0.132	1.1	0.5	-0.6	-
Carex sempervirens	Basophilic alpine grasslands	0.0	25.0	25.0	0.134	0.0	8.0	8.0	-
Euphrasia minima	Acidophilic alpine grasslands	25.0	50.0	25.0	0.144	0.3	1.1	0.8	0.92
Sagina saginoides	Snowbeds	37.5	56.3	18.8	0.261	2.5	0.9	-1.6	0.808
Salix serpillifolia	Windy ridges	0.0	18.8	18.8	0.264	0.0	1.6	1.6	-
Carex bicolor	Wetlands	50.0	68.8	18.8	0.272	20.3	9.0	-11.4	0.117
Festuca quadriflora	Basophilic alpine grasslands	6.3	25.0	18.8	0.279	4.4	1.2	-3.2	-
Lotus corniculatus aggr.	Basophilic alpine grasslands	6.3	25.0	18.8	0.285	0.5	0.5	0.0	-
Gnaphalium supinum	Snowbeds	18.8	37.5	18.8	0.288	2.5	3.1	0.5	-
Agrostis rupestris	Acidophilic alpine grasslands	6.3	25.0	18.8	0.291	3.3	3.9	0.6	-
Leucanthemopsis alpina	Acidophilic alpine grasslands	25.0	43.8	18.8	0.291	0.3	0.6	0.3	0.965
Trifolium badium	Basophilic alpine grasslands	0.0	18.8	18.8	0.295	0.0	1.4	1.4	-
Soldanella alpina	Eutrophic grasslands	0.0	18.8	18.8	0.297	0.0	1.7	1.7	-
…									
Carex lachenalii	Snowbeds	56.3	37.5	-18.8	0.285	10.9	10.5	-0.4	0.951
Androsace alpina	Rocks and screes	18.8	0.0	-18.8	0.302	0.7	0.0	-0.7	-
Carex capillaris	Basophilic alpine grasslands	12.5	12.5	0.0	1.000	8.6	28.0	19.4	-
Festuca rubra aggr.	Alpine/eutrophic grasslands	0.0	6.3	6.3	0.819	0.0	12.9	12.9	-
Nardus stricta	Acidophilic alpine grasslands	6.3	6.3	0.0	1.000	3.3	12.9	9.7	-
Homogyne alpina	Acidophilic alpine grasslands	0.0	12.5	12.5	0.490	0.0	8.5	8.5	-
Carex nigra	Wetlands	0.0	6.3	6.3	0.821	0.0	8.3	8.3	-
Juncus triglumis	Wetlands	25.0	18.8	-6.3	0.819	6.5	13.4	7.0	-
Anthoxatum odoratum	Acidophilic alpine grasslands	0.0	12.5	12.5	0.512	0.0	6.9	6.9	-
Trifolium pallescens	Rocks and screes	0.0	6.3	6.3	0.821	0.0	5.3	5.3	-
…									
Saxifraga aizoides	Wetlands	12.5	25.0	12.5	0.539	8.6	1.6	-7.0	-
Luzula alpinopilosa	Snowbeds	18.8	31.3	12.5	0.552	11.9	3.7	-8.2	-
Deschampsia cespitosa	Eutrophic grasslands	12.5	12.5	0.0	1.000	21.3	7.2	-14.2	-
Carex frigida	Wetlands	6.3	6.3	0.0	1.000	16.4	0.9	-15.5	-
Salix hastata	Shrublands	6.3	6.3	0.0	1.000	31.8	5.3	-26.5	-



All the plots of windy ridges stay in the same group between historical and recent inventories.

Among the snowbeds, the plot 116 shifted from wet to typical snowbeds.

Fig. S1 Clustering of windy ridge (left) and snowbed (right) plots based on Hellinger distance and Ward aggregation. Historical (Steiner 2002) inventories are preceded by *h* and recent ones by *r*.