Low impact of climate change on subalpine grasslands in the Swiss Northern Alps

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Abstract

While phenological shifts and migration of isolated species under climate change have already been observed on alpine summits, very few studies have focused on community composition changes in subalpine grasslands. Here we use permanent plots monitored since 1954 and precisely located phytosociological censuses from 1970 to study compositional changes of subalpine grasslands in two distinct regions of the Swiss Northern Alps. In both areas, warming trends during the monitoring period were associated with changes in land management (abandonment of goat and sheep pasturing or grazing replaced by mowing). Old and recent inventories were compared with correspondence analyses (CA). Ecological indicator values, community-affinities and biological traits of the species were used to infer the factors responsible for triggering the observed changes. In both regions, subalpine grasslands were stable with smaller changes than have previously been observed in alpine environments. Only a few species appeared or disappeared and changes were generally limited to increasing or decreasing frequency and cover of certain taxa. At one site, grazing abandonment favoured fallow species. Some of these species were located at their upper altitudinal distribution limits and may have spread because of rising temperatures. In both areas, declining species were predominantly alpine and low growing species; their decline was probably due to increased competition (e.g., shade) with more vigorous subalpine taxa no longer limited by grazing. We conclude that vegetation communities can respond rapidly to warming as long as colonisation is facilitated by available

space or structural change. In the subalpine grasslands studied, changes were mainly driven by land management. These communities have a dense vegetation cover and newly arriving herbaceous species preferring warmer conditions may take some time to establish themselves. However, climate disturbances, such as exceptional drought, may accelerate community changes by opening gaps for new species.

Introduction

Climate warming will induce plant migration toward higher altitudes and more northern latitudes. Upward shifts of the treeline ecotone have been documented since the end of the Little Ice Age (e.g., Kullman 2001; Camarero & Gutierrez 2004; Vittoz *et al.* 2008a) and increases in species richness in alpine and subnival vegetation in the Alps have been observed (e.g., Braun-Blanquet 1957; Braun-Blanquet 1975; Hofer 1992; Grabherr *et al.* 1994; Walther *et al.* 2005a; Vittoz *et al.* 2006; Pauli *et al.* 2007; Vittoz *et al.* 2008b). Similar changes have been recorded in arctic ecosystems, with a northward shift of the treeline ecotone (D'Arrigo *et al.* 1987), invasion of shrubs into former tundra vegetation and increasing plant biodiversity in mountain areas (Klanderud & Birks 2003; Tape *et al.* 2006). In warmer conditions, migration has been observed for plant species like mistletoe (*Viscum album*) in the Swiss Central Alps (Dobbertin *et al.* 2005) and *Ilex aquifolium* in the undergrowth of Danish and Swedish forests (Walther *et al.* 2005b).

Numerous studies modeled plant distributions in mountain areas to predict future distribution and potential extinction risk (e.g., Guisan & Theurillat 2000; Dirnböck *et al.* 2003). However, since plant species are expected to shift their ranges individualistically under changing climatic conditions (Huntley 1991), species distribution models (SDM; Guisan & Thuiller 2005) based solely on abiotic correlations of current distributions may fail to predict future species distributions in altered biotic environments (Guisan & Zimmermann 2000; Pearson & Dawson 2003; Randin *et al.* 2006). In fact, only a few studies have incorporated mechanistic rules of biotic interactions such as interspecific competition or facilitation (Silvertown *et al.* 1992; Dullinger *et al.* 2005), although their importance has been proven experimentally (Theodose & Bowman 1997). Choler *et al.* (2001) demonstrated that facilitation in alpine plant communities apparently allows species from lower elevations to move up the slope. Conversely, Dullinger *et al.* (2005) found that pine negatively affects the recruitment of spruce and larch at the edge of the subalpine zone, suggesting that plant-plant interactions may decrease the rate of species migration during climate warming. Callaway *et al.* (2002) showed that competition dominates interactions in the subalpine belt, while positive interactions are more important in the alpine belt.

Rapid increases in biodiversity and species turnover reported in alpine to subnival communities during the last century (e.g., Braun-Blanquet 1957; Grabherr *et al.* 1994; Walther *et al.* 2005a) may be promoted by high levels of invasion susceptibility of communities with ample available space in open vegetation, mainly structured by facilitative interactions. In contrast, subalpine grasslands may be much more resistant to invaders (e.g., Dullinger *et al.* 2003). In these dense plant communities, opportunities for potential immigrants to establish themselves may depend on disturbances (Burke & Grime 1996).

In the European Alps, anthropogenic activities have modified vegetation for 5,000 years (e.g., Tinner & Theurillat 2003). Fire and grazing (cattle, goat, and sheep) in subalpine belts have lowered the treeline ecotone and strongly influenced species distribution. However, cattle activity

has been decreasing since around 1850-1900 (Bätzing 1991). Many pastures are abandoned and trees are recolonising subalpine grasslands (e.g., Motta & Nola 2001; Vittoz *et al.* 2008a). This induces species distribution shifts, which are superimposed on top of the possible climate warming impact. On this basis, Körner (2005) suggested that this grassland abandonment will outweigh climate change impacts on mountain vegetation.

Whereas many studies have measured the phenology or growth of individual species under natural or experimental conditions (e.g., van Wijk *et al.* 2004; Hollister *et al.* 2005a; Sebastia 2007) or monitored plant migration in open alpine and subnival vegetation (e.g., Walther *et al.* 2005a; Pauli *et al.* 2007), only a few have focused on climate change impacts on species composition of subalpine grasslands (Price & Waser 2000). Here we used permanent plots from the Schynige Platte, among the oldest in Switzerland (Hegg 1992), in combination with re-recorded precisely localized censuses in the Vallon de Nant, to analyse changes in plant composition and dominance of subalpine grasslands during the second half of the 20th century. We hypothesized that changes driven by climate warming were less pronounced in these grasslands as compared to open alpine and subnival communities, due to higher plant density and hence lower invasion susceptibility, and that observed changes were mostly linked to land-use management.

Location and methods

Study sites

Both study sites are located in the Northern Alps biogeographical region of Switzerland (Fig. 1). Annual precipitation is around 1,600 mm (Vallon de Nant, 46°14' N, 7°06' E, below designated by Nant, and Schynige Platte, 46°39' N, 7°55' E, below designated by Schynige), regularly distributed throughout the year (Zimmermann & Kienast 1999).
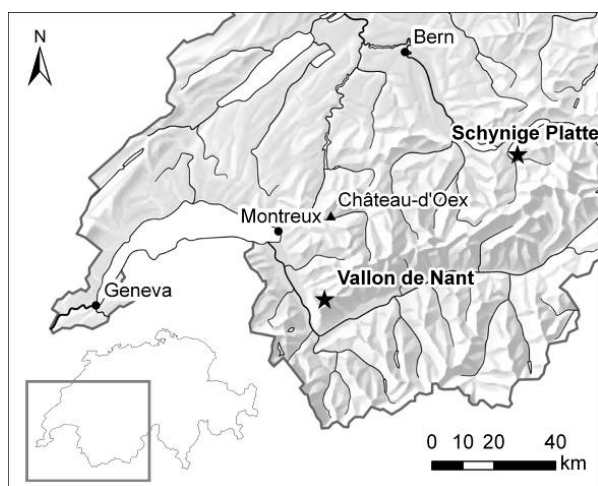
Fig. 1 Location of the study sites in Switzerland (Vallon de Nant and Schynige Platte), the Château-d'Oex meteorological station and some important towns.

The two study sites belong to the subalpine belt and are naturally dominated by *Picea abies* forests, which have been frequently converted into pasture for cattle breeding for hundreds of years. The plots in Nant are situated along a small valley, between 1,370 and 1,815 m a.s.l., covering the overall altitudinal gradient of the subalpine belt. The approximate mean annual temperature ranges between 3.5-5.3°C (Zimmermann & Kienast 1999). In Schynige, all the plots are clustered in a small research area (0.3 ha) at 1,920 m a.s.l., at the upper limit of the subalpine level. The mean annual temperature is 1.8°C (Zimmermann & Kienast 1999).

Nant was previously grazed by cattle, goats and sheep. Goat and sheep breeding was seriously reduced in 1940 and abandoned in 1970 (Dutoit 1983). The slopes, considered in this study, are now only grazed by wild chamois (*Rupicapra rupicapra*) or are slowly colonised by *Alnus viridis* and *Acer pseudoplatanus,* except in avalanche pathways. Cattle are still grazing the flat parts of the valley (not considered here because of the absence of old data). Schynige was also grazed by cattle in the past, but the research area was fenced in 1930 (Lüdi 1936). The fences were given up in 1956 and cattle grazed the area until 1975 when fences were re-erected. Since then, the experimental area has been mowed every other year.

Annual mean temperature, as measured by the meteorological station in Château-d'Oex (MeteoSwiss; 980 m a.s.l., Fig. 1), has shown a strong increase since around 1970 (App. 1 in supplemental archives). In the 20th century, Rebetez & Reinhard (in press) observed a temperature increase of 1.37°C in Switzerland, i.e., twice the increase in the Northern Hemisphere, and a mean temperature increase of 0.57°C per decade since 1975.

Field samplings

The vegetation of Nant was described by Dutoit (1983), based on a set of vegetation censuses following the method of Braun-Blanquet (Braun-Blanquet 1964). The plots were not marked in the field but the geographic coordinates were precisely measured on a 1:10,000-map and accurately drawn irregularities on the map (gullies, very large stones, or groups of trees) helped to locate the plots. Our study used a subset of plots in the two dominant grassland types of the subalpine belt. Both types are confined to calcareous substrates and share many species, but *Seslerion albicantis* occupies the driest slopes (mainly on the south-facing or very steep slopes) whereas *Caricion ferrugineae* prefers more shady sites or moister soils. All but two of the plots were first sampled between July and September of 1970; the two others were sampled in 1969 and 1978 respectively).

In 2006, we re-located the plots by means of a Global Positioning System (GPS, Trimble GeoXT) receiver. The coordinates documented by Dutoit (1983) were defined as the centre of a circle with a radius of 30 m. Within this circle, we selected a site of the same size as the original plot (usually 10 m²) based on the slope, aspect and position relative to the surface morphology as reported by Dutoit (1983). If the plot position could not be unambiguously located in this way or if most of the circle area was overgrown by shrubs, no data were taken.

Re-located plots were recorded following the same methods as Dutoit (1983). In order to account for species recorded in 1970 but now existing outside of the plots because of small location shifts, we completed the censuses with inventories of supplementary species growing on the 100 m²-area around the plots (hereafter called extended plots). The 19 plots retained (6 in *Seslerion albicantis* and 13 in *Caricion ferrugineae*) were distributed on both sides of the valley, with either an eastern (ENE-SE) or a western (WSW-NW) aspect, and slopes ranging between 22-52° (mean 33.7 ± 7.6°).

In 1930, Lüdi started an experiment with permanent plots in Schynige to find ways to improve the quality of pastures dominated by *Nardus stricta* (Lüdi 1936). He set up 340 permanent plots, marked with wooden stakes. Each plot was 1 m^2, and plots were grouped into different fertilisation experiments. Sampling frequency varied through time, but 23 control plots were retained that were never fertilized; these were inventoried around 1935 (1932-1935), 1954 (1953-1954), in 1990 and in 2002. Plant cover was estimated as a percentage, with 0.5% being the smallest value. All plots had a SSE-aspect with a slope of 20°.

Nomenclature of species follows Aeschimann *et al.* (1996).

Data analyses

Three types of problems are frequent in this type of monitoring: mistakes in species identification, overlooked species and inter-observer differences in coverage estimates (e.g., & Hallam 2002; Klimeš 2003; Vittoz & Guisan 2007). We limited identification mistakes by aggregating all easily confusable, closely related species into one taxon in all subsequent analyses. There is no way to check for overlooked species and we had to be conscious of differences in data quality. Dutoit (1983) inventoried the plots in Nant by herself in 1970, while our study involved two to three botanists in 2006. The higher sampling effort may have caused an apparent increase in the number of species (Vittoz & Guisan 2007). In Schynige, Lüdi initially was interested in agronomy and probably did not care much about rare species in the original 1935 inventory. Later on, the plots were re-recorded with more interest in diversity. Plots showed an important, probably artificial, species increase between 1935 and 1954; we thus retained only the 1954, 1990 and 2002 inventories in our analyses. Finally, to be able to compare the data from both regions, estimates by percent in Schynige and in the Braun-Blanquet scale in Nant were converted to the same scale (Table 1).

Table 1 Scales used for plant cover estimates at Vallon de Nant, corresponding values in percentages at Schynige Platte, and the transformations used in the analyses.

Braun-Blanquet scale in Vallon de Nant	Percents in Schynige Platte	Values used in analyses
r		0.1
+	0.5	0.5
1	1-5	1
2	6-25	2
3	26-50	3
4	51-75	4
5	76-100	5

To avoid giving too much weight to rare species, all subsequent analyses were conducted by excluding species with fewer than three occurrences in all plots and for all years at a site. Correspondence analysis (CA; Bénzécri 1973) was performed in R (R Development Core Team 2007) separately for both sites, to identify possible coherent shifts of the plots between the different inventories (Vittoz & Hainard 2002; Köhler *et al.* 2005). The significance of the CA axis was estimated by comparing the observed variance of the axis to a random distribution. One thousand permutations of the species abundance across the plots were performed while keeping prevalence and abundance constant. The significance of temporal shifts in species composition

along the first three axes of CA was tested by MANOVA by differences of axis scores among inventory dates against the intercept.

In order to interpret vegetation change in terms of environmental factors, ecological indices were calculated for each inventory. These indices were based on species-specific ecological indicator values (Landolt 1977). Plot values were derived as cover-weighted averages of the values of all species recorded during a specific inventory. The values vary between 1 and 5, indicating an increasing demand on light (L), temperature (T), soil humidity (F), humus amount (H), nutrient amount (N) and pH (R). The plot values were correlated with their position along the first two axes of the CA (Pearson correlation). In Nant we also correlated the axes with plot altitude, slope and calculated radiation (total amount of energy received in June-August related to the slope and aspect; Zimmerann & Kienast 1999).

Species increasing in abundance were classified into three different groups: (N) new species, absent in the first inventory and present in at least three plots in one of the following inventories; (F) species with an increasing frequency in three or more plots between the first and last inventory; (C) species with an increasing mean cover ≥0.3 between the first and last inventory and present in at least three plots at each inventory. In Schynige, species with strongly fluctuating frequencies between inventories (alternating increase and decrease) were not retained. Similarly, species decreasing in abundance were classified into the following three groups: (d) disappeared species, present in at least three plots in one of the previous inventories and absent in the last one; (f) species with a decreasing frequency in three or more plots between the first and last inventory; (c) species with a decreasing mean cover ≥0.3 between the first and last inventory and present in at least three plots at each inventory. In Nant, the d and f criteria were tested by comparing the original data with the species lists in the extended plots and in Schynige, strongly fluctuating species were discarded. Marginal models for contingency tables (Lang & Agresti 1994; Lang & Eliason 1997) were used to test the significance of shifts in the cover-abundance of each species during the time of inventory.

The sociologic affinity, i.e., the affinity for certain habitat types, of decreasing and increasing species was compared with that of the stable species (no change recorded) in each site following affinity specifications in Ellenberg *et al.* (1991). We then calculated an elevation index for each species following specifications in Binz & Heitz (1990). For each species, these authors gave the optimum and tolerance in terms of altitudinal belts. Here, we assign a value of 1 for the colline belt, 2 for the montane, 3 for the subalpine and 4 for the alpine belt. The elevation index of a species was calculated as the weighted mean of the altitudinal belts occupied (weight of 2 for belts occupied regularly, 1 for belts rarely occupied). These means were compared using a Wilcoxon test.

Species were finally compared for some important biological traits in growth, reproduction and competition. The growth form was simplified from Pignatti (2005) in 7 categories (phanerophytes, chamaephytes, caespitose hemicryptophytes, hemicryptophytes with rosette, other hemicryptophytes, geophytes and therophytes). Plant maximum height and blooming months (first and last months) were used from Aeschimann *et al.* (2004). The CSR-strategy (Grime 1979) and the reproduction type (only sexual, mainly sexual, sexual and clonal, mainly clonal) followed the BIOLFLOR database (Klotz *et al.* 2002). The potential dispersal distance was simplified into three categories (short, medium and long dispersal distance) from the Vittoz & Engler (2007) classification method. Quantitative variables were compared with t-tests (after a log-transformation for plant maximum height) and categorical variables with χ^2-tests.
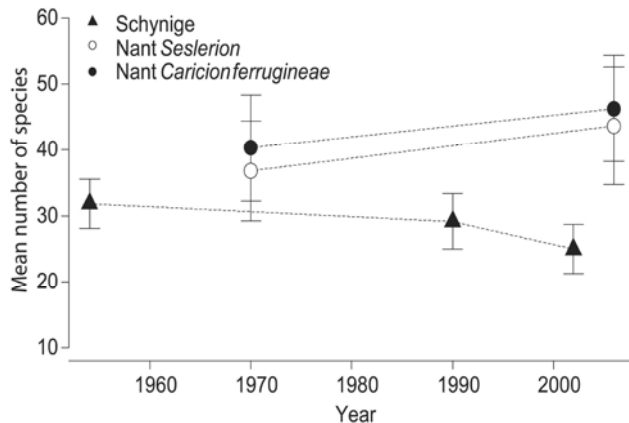
Fig. 2 Mean number of species (with standard deviation) observed in the different surveys at Vallon de Nant (1970 and 2006) and Schynige Platte (1954, 1990 and 2002). The Vallon de Nant data are separated into two vegetation types.

Results

Between 1970 and 2006 the mean number of species increased from 36.8 ± 7.6 to 43.7 ± 8.9 in one grassland type (*Seslerion albicantis*; p=0.035 with a Wilcoxon signed-rank test) and from 40.3 ± 8.1 to 46.3 ± 8.1 in the other one (*Caricion ferrugineae*; p=0.017) in Nant (Fig. 2). 120 species had ≥3 occurrences in all inventories. Conversely, there was a decrease in Schynige (p<0.001) from 31.9 ± 3.8 in 1954 to 25.8 ± 3.8 species in 2002 (Fig. 2). 68 species had ≥3 occurrences in all inventories.

At both sites, CA revealed unidirectional general trends of vegetation change, with low but significant (p<0.001) variance explained by the axes (Figs. 3-4). In Nant, the shift was similar for both vegetation types and significant with a MANOVA (p<0.001; Fig. 3). The first CA axis was correlated with increasing temperature, soil humidity and nutrient availability and with decreasing light and pH (Table 2). The second axis was correlated with increasing temperature and pH and with decreasing light, soil humidity and humus (Table 2). There was a negative correlation of the first axis with altitude (r=-0.472, p=0.003) and slope (r=-0.439, p=0.006) and a negative correlation of the second axis with altitude (r=-0.419, p=0.009). In Schynige, the plot showed a coherent shift between the 1954 and 2002 inventories, parallel to axis 2 (Fig. 4) and was highly significant with a MANOVA (p<0.001 for 1954-1990, 1990-2002 and 1954-2002). The first axis of the CA was correlated with increasing temperature and humus and with decreasing light, humidity, nutrients and pH. The second axis was correlated with decreasing light (Table 2).
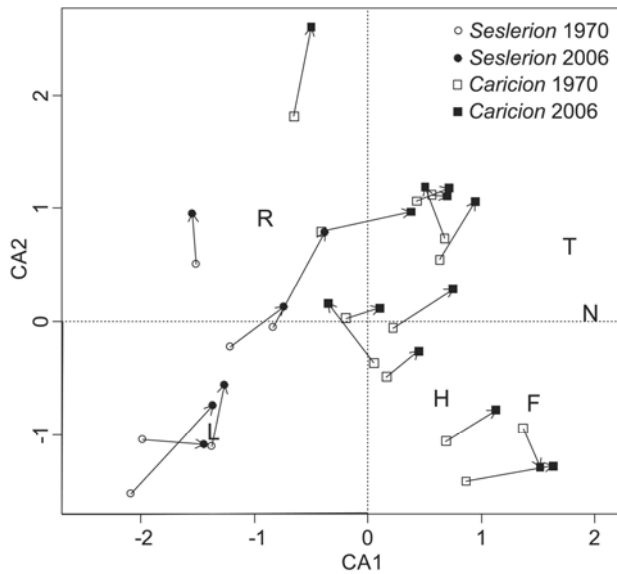
Fig. 3 Correspondence analysis with the relevés of Vallon de Nant. Symbols separate sampling years and vegetation types (*Seslerion albicantis* and *Caricion ferrugineae*). Arrows indicate the shift of each plot. The first axis represents 14.9% of the total variance and the second 8.8%. Both axes are significant (p<0.001). The ecological indicator values (**L** light, **T** temperature, **F** soil humidity, **H** humus amount, **N** nutrient amount, **R** pH; Landolt 1977) are projected by using the Pearson correlation of the weighted average of each inventory with its position along the two axes (correlation is multiplied by 2).
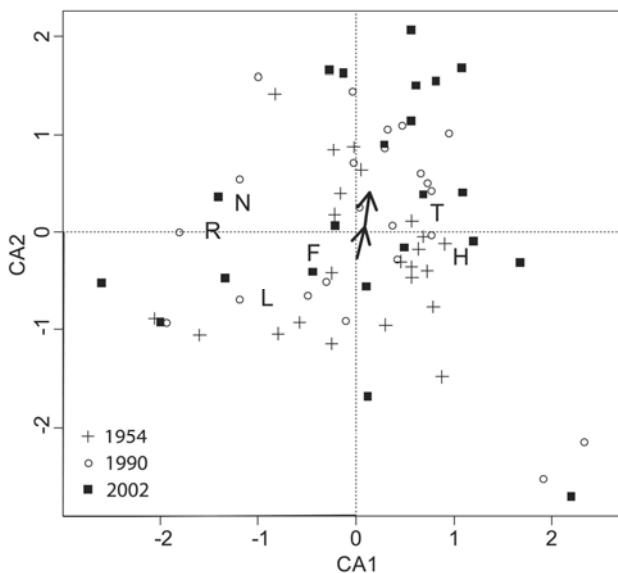

Fig. 4 Correspondence analysis with the relevés of Schynige Platte. Symbols separate sampling years. Arrows indicate the shift of the average position of each year. The first axis represents 9.3% of the total variance and the second 8.0%. Both axes are significant (p<0.001). Ecological indicator values are as in Fig. 3.

Table 2 Pearson correlation of mean ecological values (Landolt 1977), with the first two axes of the CA for Vallon de Nant and Schynige Platte. NS not significant, * p<0.05, ** p<0.01, *** p<0.001.

	Vallon de Nant		Schynige Platte	
	Axis 1	Axis 2	Axis 1	Axis 2
Light (L)	-0.710***	-0.511**	-0.489***	-0.330**
Temperature (T)	0.858***	0.339*	0.378**	0.105[NS]
Soil humidity (F)	0.698***	-0.352*	-0.256*	-0.096[NS]
Humus amount (H)	0.287[NS]	-0.333*	0.492***	-0.119[NS]
Nutrient amount (N)	0.944***	0.041[NS]	-0.619***	0.155[NS]
pH (R)	-0.491**	0.462**	-0.772***	0.019[NS]

Thirty-three species were classified as increasing and 13 as decreasing in Nant (App. 2 and 3). *Centaurea montana* was the only new species in the plots (already present in the valley in 1970), *Heracleum sphondylium, Galium anisophyllon, Rubus saxatilis* and *Carex ornithopoda* had the highest frequency increases and *Trifolium medium, Brachypodium pinnatum* and *Calamagrostis varia* had the highest cover increases, although none were significant with marginal models. Only *Trifolium badium* disappeared from the plots; no species decreased in frequency and *Carex sempervirens, Alchemilla conjuncta* aggr. and *Hedysarum hedysaroides* showed the most pronounced cover decreases (significant with marginal models only for *Carex sempervirens*). Increasing species were mainly associated with fallows, wood edges or were those that had a wide ecological tolerance, while decreasing species were mainly associated with alpine grasslands (Fig. 5). Altogether, increasing species had a lower elevation index than did decreasing species (Fig. 6) and were taller than stable species, while stable species were taller than decreasing species (Table 3, Fig. 7). Apart from ≥40% of species with a CSR-strategy in both increasing and decreasing species groups, the increasing group was dominated by C-species (C or CS) while the decreasing group was dominated by S-species (CS or S; Table 3, Fig. 8). All other compared biological traits were not significant (Table 3).
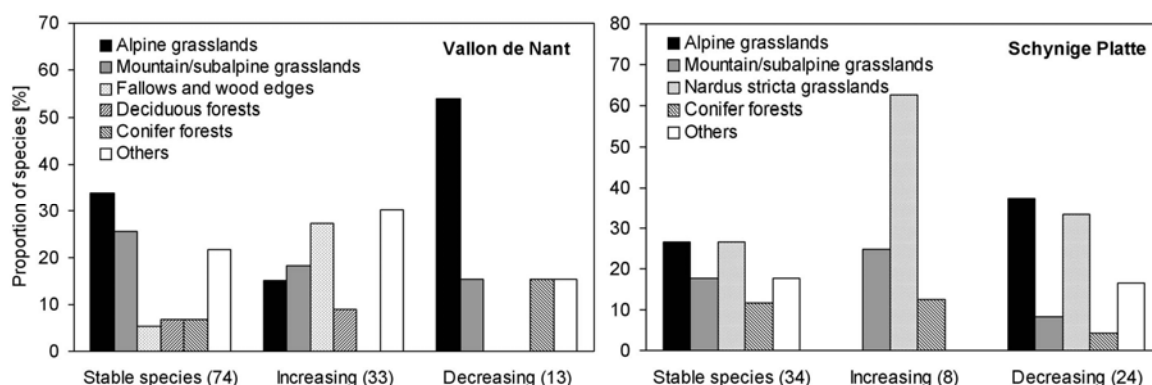
Fig. 5 Sociologic affinity (Ellenberg *et al.* 1991) of the species at Vallon de Nant (left) and Schynige Platte (right) for the complete list of observed species (all species), as well as the increasing and the decreasing species. The number of species considered in each category is between brackets.

Eight species were classified as increasing and 24 as decreasing in Schynige (App. 4 and 5), and only *Rhinanthus alectorolophus* was new in our plots. It was already present in Schynige in one fertilized experimental plot in 1935, but showed a very strong progression in the last decade. The other frequency increases were weaker, but *Nardus stricta* and *Gentiana purpurea* showed a significant cover increase with marginal models (App. 4). Of the species that disappeared, *Vaccinium vitis-idaea* and *Euphrasia minima* had the highest original frequencies and 14 species were half (or less) as frequent (App. 5). *Calluna vulgaris, Arnica montana* and *Potentilla erecta* cover decreased significantly. Alpine grassland species decreased and there was a turnover among species associated with *Nardus stricta* grasslands (Fig. 5). There was no significant difference in the elevation index of increasing or decreasing species (Fig. 6) and no differences in the biological traits that were considered (Table 3).

Table 3 Differences (p-values) in biological trait distributions between stable, decreasing and increasing species at Vallon de Nant and Schynige Platte (see Location and methods for the analyses).

	Vallon de Nant			Schynige Platte		
	Stable vs Decreasing	Stable vs Increasing	Decreasing vs Increasing	Stable vs Decreasing	Stable vs Increasing	Decreasing vs Increasing
Number of species	74 / 13	74 / 33	13 / 33	34 / 24	34 / 8	24 / 8
Growth form	0.370	0.489	0.052	0.690	0.282	0.838
Maximum height	**0.007**	**0.040**	**0.000**	0.298	0.427	0.146
First month of blooming	0.647	0.952	0.697	0.932	0.335	0.391
Last month of blooming	0.758	0.356	0.411	0.381	0.596	0.926
CSR-strategy	0.164	0.379	**0.014**	0.294	0.420	0.597
Sexual vs clonal reproduction	0.948	0.069	0.444	0.599	0.537	0.765
Dispersal distance (3 classes)	0.225	0.430	0.139	0.861	0.360	0.452

**Discussion**

Vegetation changes

Observed changes at both sites were minor, with low variance explained by axes in both CA plots (Figs. 3-4). Structuring and dominant species remained the same at both sites with fluctuations only for the cover values of dominant species and frequency changes of low cover species. Mean species richness increase per plot was 16% in Nant over the 36-year survey. This significant increase is probably partly due to better sampling (2-3 botanists in 2006 instead of one in 1970; Vittoz & Guisan 2007). Conversely, there was a significant (22%) decrease in species richness in Schynige over 48 years (Fig. 2). In both regions, only one new species was recorded in the plots sampled, while one species was lost in Nant and six were lost in Schynige (App. 2-5). In comparison, the mean number of species increased by 26% between 1983 and 2003 on ten alpine-nival summits in the Alps (Walther *et al*. 2005a), by 11.8% between 1994 and 2004 in 362 plots in the Austrian Alps (2,900-3,450 m a.s.l.; Pauli *et al*. 2007) and by 27-42% between 1988 and 2003 in 48 plots in German alpine grasslands (1,800-2,350 m a.s.l.; Kudernatsch *et al*. 2005). Although not directly comparable, these values indicate that the subalpine sites of Schynige and Nant did not show a species richness increase comparable to what was previously observed in the alpine-nival levels in recent decades at other locations.
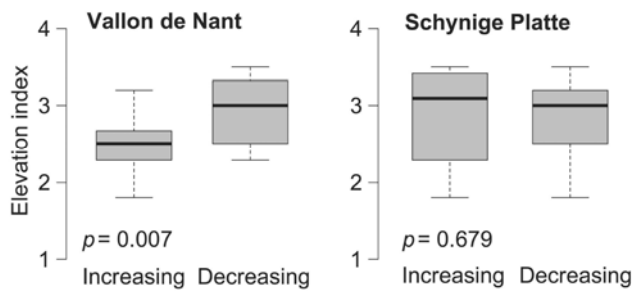
Fig. 6 Elevation index of the increasing and decreasing species at Vallon de Nant (left) and Schynige Platte (right). The central lines are the medians, the boxes represent the second and third quartiles and horizontal lines indicate the outliers. The p-values are from the Wilcoxon test.
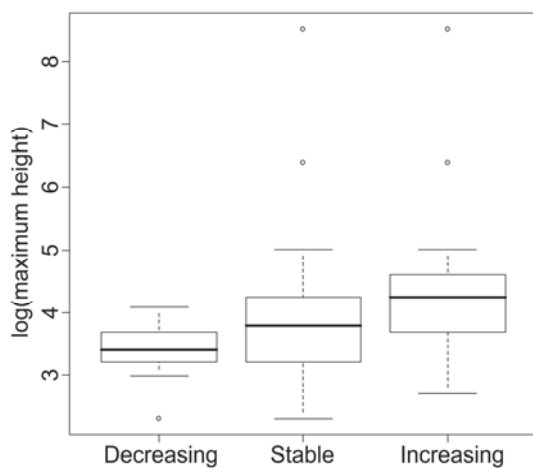
Fig. 7 Maximum height (following Aeschimann *et al.* 2004) of the decreasing, stable and increasing species at Vallon de Nant (logarithm of the height in cm; box-plots as in Fig. 6).
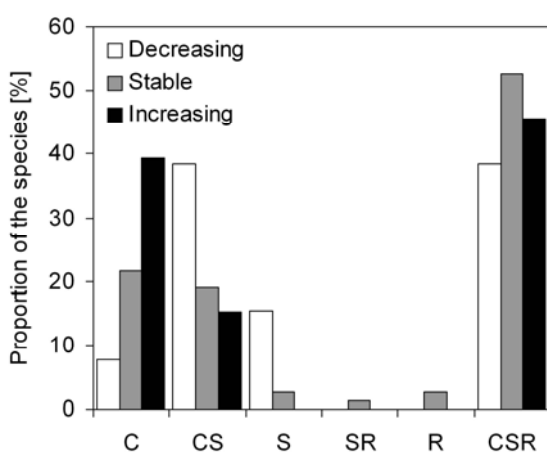
Fig. 8 Distribution of the CSR-strategy (following Klotz *et al.* 2002) among the decreasing, stable and increasing species at Vallon de Nant.

The coherent change observed in the plots in Nant was mainly associated with decreasing light (more shade-preferring species) and increasing temperature according to correlations with ecological indicator values (Table 2, Fig. 3). A large number of increasing species were from fallows and wood edges (e.g., *Centaurea montana*, *Chaerophyllum villarsii* and *Trifolium medium*) or had a wide ecological amplitude. However, among these species, many were also common in abandoned pastures (*Astrantia major*, *Calamagrostis varia*, *Carex flacca*, *Gentiana lutea*, *Rubus saxatilis*; Oberdorfer 1990; Mayer & Grabner 2004). The trends of *Brachypodium pinnatum* and *Trifolium medium* were particularly remarkable in this context as these two species are well known efficient colonisers of abandoned grasslands (Mayer & Grabner 2004; Köhler *et al*. 2005). This indicates that the main driver behind these changes was probably the abandonment of goat and sheep grazing on the slopes. In correspondence, the species that decreased in Nant were mainly associated with short, alpine grasslands (Figs. 5 and 7), like *Trifolium badium*, *Carex sempervirens*, *Alchemilla conjuncta* aggr., *Hedysarum hedysaroides* and *Anthyllis vulneraria* subsp. *alpestris*. Their decline was probably driven largely by the increasing density of taller (Fig. 7) and more competitive (Fig. 8) subalpine plants and fallow species, which were no longer restrained by livestock grazing (Pöyri *et al*. 2006). The higher elevation index of decreasing species compared to the increasing species (Fig. 6) has two possible explanations: (i) The warmer climate of recent decades may have favoured lowland species, as indicated by some of the increasing species which are around their upper altitudinal distribution limit in the region (*Brachypodium pinnatum*, *Trifolium medium*, *Vincetoxicum hirundinaria*; Binz & Heitz 1990 and data from the MODIPLANT project (Guisan 2005; Randin *et al*. 2006), (ii) But species from alpine grasslands are generally able to grow in the subalpine belt (Binz & Heitz 1990) when grazing maintains low grass height, but they are naturally limited by forests or taller plants. Hence, the decrease of elevation index may correspond to a return to a natural situation after pasture abandonment. Management and climate can have similar effect on the elevation index and experiments would be necessary to clarify the observations.

In Schynige, changes were unidirectional and significant as well, but weak along axis 2, which had a low explained variance (Fig. 4). *Rhinanthus alectorolophus* showed the most important increase, especially pronounced after 1990. Future inventories will determine if this is a real trend or only a temporary fluctuation, but this species is at its upper altitudinal distribution limit (Binz & Heitz 1990) at the monitoring plots and the high climate warming rate of the last decades (App. 1; Rebetez & Reinhard in press) may have triggered this recent development. As in Nant, many decreasing species belonged to the alpine grassland group (e.g., *Euphrasia minima*, *Soldanella alpina*) or had low foliage distribution (e.g., *Selaginella selaginoides*, *Plantago alpina*, *Crepis aurea*, *Arnica montana*; App. 5), although no significant change was recorded for plant height (the available data corresponded to the maximum plant height but not to the foliage position). These low plants may have suffered from the change from annual grazing to biannual mowing, corresponding with increasing grass density (Fischer & Wipf 2002) and mean height (at least every two years). This is corroborated by the decreasing light conditions detected with ecological values (Table 2, Fig. 4), although this result should be considered cautiously because of the low variance explained by the axis. However, it is possible that the disappearance of *Euphrasia minima* is linked to the increase of *Rhinanthus alectorolophus*, as both are unspecialized hemi-parasites (Hartl & Wagenitz 1975) and *Euphrasia* was situated at its lower altitudinal limit (Binz & Heitz 1990). Phoenix & Press (2005) hypothesized that the wide host range of hemi-parasites like *Rhinanthus* may facilitate their migration under warmer conditions.

Climate change and community composition

The influence of climate change on vegetation has already been shown with numerous examples (see Walther *et al.* 2002; Parmesan & Yohe 2003 for reviews). Important changes or quick reactions were recorded when the colonising species could occupy sparsely covered areas, other available ecological niches, or when they were taller than the original species. Available space is found on alpine-nival summits in the Alps where a high plant diversity increase was recorded during the 20th century (e.g., Hofer 1992; Grabherr *et al.* 1994; Walther *et al.* 2005a; Vittoz *et al.* 2006). Climate is the major factor limiting their altitudinal distribution; the species are colonising areas with low plant cover. Mistletoe (*Viscum album* subsp. *austriacum*), a parasite of *Pinus sylvestris,* climbed 200 m during the 20th century in the Swiss Central Alps (Dobbertin *et al.* 2005). Pine trees exist at about 500 m above the current mistletoe distribution and no other parasite is present. The ecological niche is thus free to be colonised under the new climatic conditions. Similarly, *Ilex aquifolium,* a forest undergrowth species, spread recently to the north in Scandinavia (Walther *et al.* 2005b). Its quick shift was facilitated by its presence in gardens and probably also by the low density of forest undergrowth. *Ilex aquifolium* is indeed one of the rare very shade tolerant, tall shrubs in Central Europe (Landolt 1977) that can colonise this niche.

Colonisation by taller species was recorded by Braun-Blanquet (1975), who monitored a snowbed community in the Alps for 26 years. Plant diversity and cover increased over time, with a shift from moss-dominated vegetation to flowering plants. A similar structural change was recorded in summer warming experiments in Alaskan arctic tundra, with shrub cover and size increasing at the expense of shade sensitive lichens and bryophytes (Hollister *et al.* 2005b; Wahren *et al.* 2005; Tape *et al.* 2006). The observed upward shift of the altitudinal treeline ecotone in many mountain regions (e.g., Kullman 2001; Camarero & Gutierrez 2004; Vittoz *et al.* 2008a) proceeds identically with the substitution of low alpine grasses by trees.

Plant composition changes inside a community without structural changes are less common. These have been observed in South Switzerland forests, where introduced, evergreen broad-leaved species (*Cinnamomum glanduliferum, Laurus nobilis, Prunus laurocerasus, Trachycarpus fortunei*) are replacing native deciduous species following a lengthening of the growing season and a strong decrease in the number of frost days (Gianoni *et al.* 1988; Walther 2002; Walther *et al*. 2007). Another species replacement was recorded in mountain forests of Northern Spain, where *Quercus ilex* has been invading degraded stands of *Fagus sylvatica* because of warmer temperatures (Peñuelas & Boada 2003).

In contrast to these studies recording major changes, our results show that changes under climate warming have until now been limited in semi-natural subalpine grasslands. A similar low rate of change was found in a four year warming experiment in a subalpine grassland in West-Central Colorado (Price & Waser 2000). The authors explained this result (compared to the pronounced responses recorded in warming experiments in the Arctic tundra) by summer dry conditions cancelling out the effects of earlier snowmelt. But drought is not a problem in the Northern Alps, and the small changes with climate warming are better explained by interactions between plants. Kikvidze *et al.* (2001) and Callaway *et al.* (2002) observed that competition dominates interactions between species in subalpine grasslands, where conditions are less physically stressful than in alpine grasslands, where facilitation is more important. In Nant and Schynige, it is probable that newly arrived species, close to their physiological limit for temperature, have to germinate and grow in the middle of dense plant cover, and that many of them (e.g., Poaceae and Cyperaceae) with high longevity slow down species replacement (Theurillat & Guisan 2001).

This strongly limits their survival and thus the rate of change in subalpine grasslands. However, an insufficient dispersal of low subalpine or montane plants to colonise the studied sites (Malcolm *et al.* 2002), due to ecological (e.g., large forests) or topographical obstacles, may partly explain the grassland stability. By comparison, the quick migration of *Ilex aquifolium* (Walther *et al.* 2005b) and the evergreen broad-leaved species (Walther 2002) were facilitated by human introductions in gardens.

Competition also restricts alpine species growth in subalpine grasslands (Choler *et al.* 2001), although climate is not directly an obstacle. Indeed, alpine and arctic plants respond to warmer temperatures by changing resource allocation toward reproductive organs rather than by increasing growth (Hollister *et al.* 2005a). This interpretation agrees with the proposition that alpine plants will be competitively displaced by taller subalpine plants under climate warming (Theurillat & Guisan 2001).

Future trends in these subalpine grasslands

Both study sites will probably diverge in the future if land use similar to that during recent decades is maintained. After completely abandoning grazing in Nant, future colonisation by shrubs and trees is unavoidable, except in some snow avalanche pathways. Evidence of this evolution is already present (increasing *Salix appendiculata* and *Larix decidua*), and forest shadow will exclude the remaining alpine plants. In Schynige, however, mowing will prevent such colonisation. Either changes will be observed progressively in the future with isolated colonisation of new species and the disappearance of others, or vegetation composition will be more and more decoupled from climatic conditions. Experiments and data are insufficient to determine precisely what will happen, but major quick changes may follow disturbances which open gaps in the grassland. For example, population outbreaks of field voles open such gaps and exceptional climatic droughts may kill large numbers of the dominant species (van der Maarel 1996; Gigon 1997).

Conclusion

Species colonisation induced by climate warming may be rapid on high mountain summits with incomplete plant ground cover or when there is a clear structural change, like trees invading alpine grasslands. However, the invasion of new herbaceous species into the subalpine grasslands that we studied was obviously hampered by the density of resident species; both regions showed only limited changes in vegetation composition. At Vallon de Nant, abandonment of grazing favoured plants from fallow and wood edge communities, whose taller size shadowed low-growing alpine species. However, climate change cannot be excluded as an influence, because some of the increasing species are close to their highest distribution limit. At Schynige Platte, mowing replaced grazing; the weak observed changes appear to be mainly associated with higher plant density and height that caused species with low foliage, e.g., the alpine plants, to decrease or disappear. However, climate change may be responsible for the development of *Rhinanthus alectorolophus,* perhaps to the detriment of *Euphrasia minima* as both are hemi-parasites. In sum, the observed changes in vegetation composition agreed with Körner's hypothesis (2005) that future vegetation changes in mountain areas will be influenced more by anthropogenic management than by climate change. Supplementary data from other subalpine grasslands are necessary to determine whether this stability is a general trend.

Acknowledgments

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Appendices (supplemental archives)

Appendix 1 Temperature in 20th century in Château-d'Oex (980 m, MeteoSwiss data). The thin line gives the mean annual temperature and the broad line a decadal average.
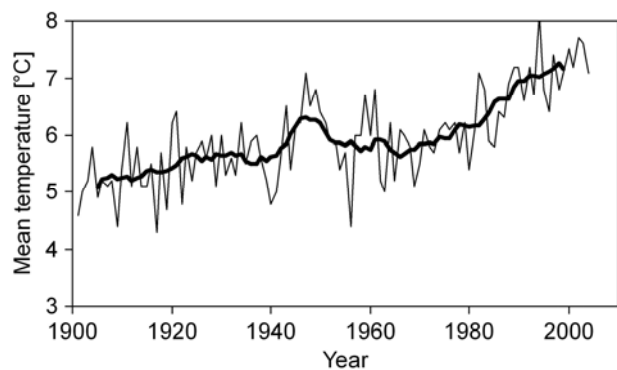
Appendix 2 Increasing species in Vallon de Nant. Change is the type of increase: **N** new species, **F** frequency increase and **C** cover increase.

Species	Frequency			Mean cover			Change
	1970	2006	Difference	1970	2006	Difference	
Centaurea montana	0	3	3		0.10	0.10	N
Aposeris foetida	3	7	4	0.50	1.01	0.51	FC
Festuca rubra aggr.	8	12	4	0.94	1.26	0.32	FC
Brachypodium pinnatum	3	6	3	0.67	1.42	0.75	FC
Chaerophyllum villarsii	3	6	3	0.50	0.95	0.45	FC
Heracleum sphondylium s.l.	3	10	7	0.50	0.43	-0.07	F
Galium anisophyllon	9	15	6	0.50	0.23	-0.27	F
Rubus saxatilis	2	7	5	0.75	0.54	-0.21	F
Carex ornithopoda	2	7	5	0.50	0.27	-0.23	F
Petasites paradoxus	2	6	4	0.30	0.68	0.38	F
Daphne mezereum	1	5	4	0.10	0.34	0.24	F
Hieracium murorum aggr.	10	14	4	0.55	0.44	-0.11	F
Campanula scheuchzeri	2	6	4	0.50	0.37	-0.13	F
Ranunculus montanus	11	15	4	0.64	0.48	-0.16	F
Carduus defloratus s.str.	8	12	4	0.51	0.30	-0.21	F
Viola biflora	1	4	3	0.50	0.90	0.40	F
Salix appendiculata	1	4	3	0.10	0.30	0.20	F
Laserpitium latifolium	10	13	3	0.90	1.06	0.16	F
Vincetoxicum hirundinaria	5	8	3	0.50	0.63	0.13	F
Briza media	5	8	3	0.50	0.58	0.08	F
Crepis pyrenaica	10	13	3	0.66	0.70	0.04	F
Gentiana lutea	4	7	3	0.40	0.40	0.00	F
Astrantia major	12	15	3	0.88	0.87	-0.01	F
Knautia dipsacifolia s.str.	9	12	3	0.78	0.76	-0.02	F
Leucanthemum vulgare aggr.	16	19	3	0.59	0.51	-0.08	F
Alchemilla vulgaris aggr.	1	4	3	1.00	0.80	-0.20	F
Polygonum viviparum	7	10	3	0.50	0.30	-0.20	F
Potentilla erecta	9	12	3	0.83	0.61	-0.23	F
Agrostis stolonifera	4	7	3	1.25	1.01	-0.24	F
Trifolium medium	4	5	1	0.50	1.42	0.92	C
Calamagrostis varia	16	17	1	2.31	2.94	0.63	C
Carex flacca	5	7	2	0.60	1.00	0.40	C
Larix decidua	3	3	0	0.37	0.67	0.30	C

Appendix 3 Decreasing species in Vallon de Nant. The disappearance of species is evaluated between the original census and the extended area of the new census. Change is the type of decrease: **d** disappeared species and **c** cover decrease. ° $p<0.1$, * $p<0.05$, ** $p<0.01$ for marginal models about mean cover changes.

Species	Frequency (extended plot)			Frequency			Mean cover			Change
	1970	2006	Difference	1970	2006	Difference	1970	2006	Difference	
Trifolium badium	3	0	-3	3	0	3	0.50			d
Carex sempervirens	15	18	3	15	16	1	3.67	2.06	-1.60	c**
Alchemilla conjuncta aggr.	13	18	5	13	13	0	1.27	0.46	-0.81	c
Hedysarum hedysaroides	3	4	1	3	4	1	1.33	0.63	-0.71	c
Rhinanthus alectorolophus	9	12	3	9	9	0	1.06	0.42	-0.63	c
Anthyllis vulneraria subsp. alpestris	8	10	2	8	8	0	1.00	0.40	-0.60	c
Erica carnea	6	7	1	6	4	-2	1.58	1.00	-0.58	c
Trifolium pratense s.str.	9	11	2	9	8	-1	0.94	0.40	-0.54	c
Dryas octopetala	4	4	0	4	3	-1	1.50	1.03	-0.47	c
Linum alpinum	6	12	6	6	6	0	0.83	0.47	-0.37	c
Polygala chamaebuxus	10	12	2	10	10	0	0.90	0.57	-0.33	c
Helianthemum nummularium s.l.	16	18	2	16	17	1	1.60	1.29	-0.31	c
Thesium pyrenaicum	5	7	2	5	2	-3	0.80	0.50	-0.30	c

Appendix 4 Increasing species in Schynige Platte. Change is the type of increase: **N** new species, **F** frequency increase and **C** cover increase. P-values as in appendix 3.

Species	Frequency				Mean cover				Change
	1954	1990	2002	Difference	1954	1990	2002	Difference	
Rhinanthus alectorolophus	0	1	15	15		0.50	0.63		N
Galium pumilum	1	5	6	5	0.50	0.50	0.67	0.17	F
Trifolium alpinum	1	0	4	3	0.50		0.88	0.38	F
Nardus stricta	23	23	22	-1	2.30	3.09	2.68	0.38	C*
Homogyne alpina	13	17	15	2	0.58	0.82	0.97	0.39	C
Gentiana purpurea	20	23	21	1	0.88	1.11	1.19	0.32	C°
Agrostis capillaris	19	14	19	0	0.66	0.75	1.00	0.34	C
Solidago virgaurea subsp. minuta	22	23	21	-1	0.75	1.04	1.05	0.30	C

Appendix 5 Decreasing species in Schynige Platte. Change is the type of decrease: **d** disappeared species, **f** frequency decrease and **c** cover decrease. P-values as in appendix 3.

Species	Frequency				Mean cover				Change
	1954	1990	2002	Difference	1954	1990	2002	Difference	
Vaccinium vitis-idaea	7	1	0	-7	0.6	0.5			d
Euphrasia minima	6	16	0	-6	0.6	0.5			d
Selaginella selaginoides	4	0	0	-4	0.5				d
Carex ornithopoda	4	0	0	-4	0.5				d
Gentiana campestris s.l.	3	2	0	-3	0.5	0.5			d
Ligusticum mutellina	3	2	0	-3	0.5	0.8			d
Plantago alpina	23	18	9	-14	1.0	0.8	0.9	-0.1	f
Crocus albiflorus	14	12	1	-13	0.6	0.5	0.5	-0.1	f
Festuca rubra aggr.	20	13	7	-13	1.1	0.8	1.1	0.1	f
Calluna vulgaris	20	7	8	-12	1.2	1.1	1.0	-0.2	f°
Crepis aurea	15	11	3	-12	0.7	0.6	0.7	0.0	f
Viola calcarata	15	8	3	-12	0.5	0.6	0.8	0.3	f
Ranunculus montanus aggr.	15	11	4	-11	0.7	0.5	0.5	-0.2	f
Soldanella alpina	13	12	2	-11	0.5	0.5	0.5	0.0	f
Phleum alpinum	15	14	4	-11	0.7	0.6	0.8	0.1	f
Pseudorchis albida	15	5	4	-11	0.5	0.5	0.6	0.1	f
Avenella flexuosa	14	9	6	-8	1.1	0.9	1.0	-0.1	f
Pulsatilla alpina s.l.	11	13	4	-7	1.2	1.2	1.4	0.1	f
Cerastium fontanum subsp. vulgare	10	4	3	-7	0.5	0.5	0.7	0.2	f
Thesium alpinum	7	2	2	-5	0.6	0.5	0.5	-0.1	f
Leontodon helveticus / hispidus	22	20	17	-5	1.1	1.0	1.1	-0.1	f
Polygala alpestris	12	7	8	-4	0.5	0.5	0.6	0.0	f
Arnica montana	23	23	21	-2	2.5	1.2	1.4	-1.0	c**
Potentilla erecta	23	23	21	-2	1.3	1.2	1.0	-0.3	c*