The role of landuse and natural determinants for grassland vegetation composition in the Swiss Alps

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Abstract

The Alps provide a high habitat diversity for plant species, structured by broad- and fine-scale abiotic site conditions. In man-made grasslands, vegetation composition is additionally affected by the type of landuse. We recorded vegetation composition in 216 parcels of grassland in 12 municipalities representing an area of 170 × 70 km\textsuperscript{2} in the south-eastern part of the Swiss Alps. Each parcel was characterized by a combination of altitudinal level (valley, intermediate, alp), traditional landuse (mown, grazed), current management (mown, grazed, abandoned), and fertilization (unfertilized, fertilized). For each parcel we also assessed the abiotic factors aspect, slope, pH value, and geographic coordinates, and for each municipality annual precipitation and its cultural tradition. We analysed vegetation composition using (i) variation partitioning in RDA, (ii) cover of graminoids, non-legume forbs, and legumes, and (iii) dominance and frequency of species. Species composition was determined by, in decreasing order of variation explained, landuse, broad-scale abiotic factors, fine-scale abiotic factors, and cultural tradition. Current socio-economically motivated landuse changes, such as grazing of unfertilized former meadows or their abandonment, strongly affect vegetation composition. In our study, the frequency of characteristic meadow species was significantly smaller in grazed and even smaller in abandoned parcels than in still mown ones, suggesting less severe consequences of grazing for vegetation composition than of abandonment. Therefore, low-intensity grazing and mowing every few years should be considered valuable conservation alternatives to abandonment. Furthermore, because each landuse type was characterized by different species, a high variety of landuse types should be promoted to preserve plant species diversity in Alpine grasslands.

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Zusammenfassung

Die Alpen bieten vielfältige Lebensräume für Pflanzenarten, die durch gross- und kleinräumige abiotische Standortfaktoren strukturiert werden. In vom Menschen geschaffenem Grasland wird die Vegetationszusammensetzung zusätzlich durch die Art der Landnutzung beeinflusst. Wir untersuchten die Vegetationszusammensetzung von 216 Graslandparzellen in 12 Gemeinden im südöstlichen Teil der Schweizer Alpen, in einem Gebiet von 170 × 70 km\textsuperscript{2}. Jede Parzelle wurde durch eine Kombination von Höhenstufe (Tal, Mittelstufe, Alp), traditioneller Landnutzung (gemäht, beweidet, brach) und Düngung (gedüngt, ungedüngt) beschrieben.

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Introduction

The European Alps provide a high habitat diversity. Environmental conditions and vegetation composition vary due to broad-scale factors such as altitude, precipitation, or geographic location, reflecting different climatic conditions, and fine-scale site factors, like variation in slopes, aspects, and soils (Ellenberg, 1996). Below the timberline, many man-made grasslands replace cleared forests, and for hundreds of years these grasslands have been maintained by mowing or grazing (Bätzing, 2003). The intensity of these landuses and the economic return are largely determined by the fertilization level (van der Hoek, van Mierlo, & van Groenen-dael, 2004). In recent decades, agricultural landuse and its intensity have been changing for socio-economic reasons (Bätzing, 1993). These changes include intensified landuse of easily accessible parcels of land and reduced labour in parcels yielding only small returns (Tasser & Tappeiner, 2002). The latter mostly concerns unfertilized meadows, which frequently are very steep and laborious to mow. Some of these meadows have nowadays been abandoned while others are grazed by cattle or sheep instead of being mown. Previous – more local – studies suggest that these changes have severe impacts on the vegetation composition of Alpine grasslands (Fischer & Wipf, 2002; Stampfli & Zeiter, 2004; Tasser & Tappeiner, 2002; Zoller & Bischof, 1980). However, comprehensive studies covering larger geographic ranges, including abiotic site conditions, several combinations of landuse, and landuse changes at several altitudes as potential determinants of grassland vegetation, are still missing.

We studied vegetation composition of 216 grassland parcels of different landuse and geographic characteristics in the Swiss Alps. The parcels were situated at different altitudes in 12 municipalities representing an area of 170 × 70 km ranging from Central to Eastern Switzerland. We studied grassland parcels that had been used as pastures or meadows (both fertilized and unfertilized) and currently were mown, grazed, or abandoned. To account for potential regional or cultural differences, each of the three main cultural traditions in the Swiss Alps (Romanic, Germanic, and Walser) was represented by four municipalities. The three cultural traditions with their characteristic agricultural practices have contributed to the landscape diversity of the Alps (Bätzing, 2003). Traditionally, self-sufficient mixed farming was practiced in the Romanic cultural tradition. Hereditary partitioning of parcels led to a still visible small-grained parcel structure. In Germanic municipalities scattered single-farm houses were surrounded by fields and meadows mainly used for dairy farming. The Walser, Alemannic people from the Valais in south-eastern Switzerland, migrated eastwards and settled at higher altitudes, as lower parts of the valleys were already occupied. Apart from farming, they lived on trade and maintenance of Alpine passes. Socio-economic differences are still remarkably pronounced among these cultural traditions (Pfister, 2004).

Our main hypothesis was that vegetation composition of grasslands in the Swiss Alps is strongly affected by cultural traditions and broad- and fine-scale abiotic site conditions, but that differences in landuse play an equally important role. Moreover, we expected recent changes in landuse to affect species composition. More specifically, we asked: (1) Do fine-scale abiotic variables and altitude differ among landuse types? (2) How do cultural traditions, landuse, and abiotic variables affect plant species composition of grassland parcels? (3) How do these factors affect cover of the life-forms graminoids, legumes, and non-legume forbs? (4) How do these factors affect the dominance of grassland species? (5) Moreover, because the most common among the
ongoing changes in land use are grazing or abandonment of unfertilized former meadows, we especially addressed the consequences of these specific land use changes for the frequency of characteristic species of unfertilized meadows.

**Methods**

**Study sites**

We studied grasslands in 12 municipalities representing an area of approximately 170 × 70 km in southeastern Switzerland. Each of the three cultural traditions, Romanic, Germanic, and Walser, was represented by four municipalities (see Fig. 1, in Maurer, Weyand, Fischer, & Stöcklin, 2006). We selected the municipalities with the restriction that their agricultural character had only changed moderately during the last 50 years (e.g. no heavy land consolidation), they were not very touristic (no large skiing-areas) and did not have more than about 1500 inhabitants. Due to settlement history, Germanic municipalities were located in the northern parts of the Alps, and Romanic and Walser municipalities in central and southern parts.

In collaboration with local farmers, we selected grassland parcels at the valley bottom (about 1000 m a.s.l.), at intermediate altitudes (about 1500 m a.s.l.), and at the alp (about 2000 m a.s.l.) in each municipality according to the following sampling scheme: each parcel was characterized by the combination of traditional land use (mown or grazed), current management (mown, grazed, or abandoned), and fertilization (fertilized or unfertilized). In principle, 12 land use combinations per municipality and altitudinal level were possible, but not all were actually present (see Fig. 2C; Maurer et al. 2006). The design included grassland parcels without any known land use changes and parcels whose use had been changed at least 5 years ago. When it was impossible to find parcels whose type of land use had changed, we selected two parcels of the concerned type of former land use to increase sample size. The unfertilized meadows were usually cut once a

**Fig. 1**. Venn diagram presenting percentages of unique contribution of (a) land use, (b) broad-scale abiotic factors, (c) cultural traditions, and (d) fine-scale abiotic factors to plant species composition in 216 grassland parcels in the Swiss Alps based on a redundancy analysis (RDA) with $R^2$ adjusted for unequal numbers of variables among groups. Fractions (e) to (o) represent variation shared between the different groups of variables. The sum of fractions (a) to (o) is 0.246 and represents the total explained variation while (p) represents the residual variation that cannot be explained. Fractions (a) to (d) differ significantly from each other ($p = 0.001$).

**Fig. 2**. Cover (± SE) of the life-forms (A) graminoids, (B) forbs, and (C) legumes in 216 grassland parcels in the Swiss Alps relative to total plant cover. Each land use type is characterized by its combination of fertilization (unfertilized, fertilized), traditional land use (mown, grazed), and current management (M = Mown, G = Grazed, A = Abandoned). Numbers in the columns indicate the replicate parcels.
year while the fertilized meadows were cut between two and four times. Grazing intensity varied among years depending on the weather. Altogether, we selected 216 parcels, that is, 12–24 per municipality.

Vegetation records

We visited each grassland parcel once (2002 or 2003) when the vegetation was best developed, shortly before the start of mowing or grazing. In each parcel, we took two vegetation records in plots of 5 m \( \times \) 5 m \( \text{m}^2 \) at a distance of 5 m by estimating the percentage ground cover of all vascular plant species. Plots were situated at least 5 m from the parcel’s edge, were considered representative for the whole parcel’s structure, and were selected randomly concerning their vegetation to prevent a bias in plant species diversity. We calculated mean cover values of the two vegetation records for each species in a parcel and used these averaged species lists comprising a plot area of 50 m \( \text{m}^2 \) for further calculations. For each parcel we calculated the percentage cover of the life-forms graminoids (Poaceae, Cyperaceae, Juncaceae), legumes, and non-legume forbs relative to total plant cover as a measure of species composition, further on for simplicity called ‘cover’. In the analysis of life forms, we did not consider woody species or orchids due to their low frequency. To measure the heterogeneity of the within-parcel species composition, we calculated the Jaccard index of the two vegetation records (described in Magurran, 2004). For the processing of species lists and the calculations of cover of life-forms and Jaccard indices we used the program VEGEDAZ (Küchler, 2004). Nomenclature follows Lauber and Wagner (2001) except for Anthoxanthum, where we aggregated A. odoratum and A. alpinum, and for Pou, where we aggregated P. annua and P. supina. Furthermore, we recorded mean altitude of the parcel, aspect (deviation from South), slope (degrees), soil pH, and geographic coordinates. Additionally, we estimated the mean annual precipitation for 1998–2002 using data of the nearest meteorological station (either in the study-municipalities or in the next municipality).

Statistical analysis

Differences of fine-scale abiotic variables and altitude among landuse factors

We analysed whether fine-scale abiotic variables (pH, slope, aspect) and mean altitude of parcels differed among landuse types (fertilization, traditional landuse, current management including abandonment, mowing, and grazing). We calculated one-way analyses of variance (ANOVA) with abiotic factors and altitude as dependent variables and landuse factors as explaining factors. In case of a significant ANOVA result we also calculated Tukey’s HSD.

Gradients in species composition

We assessed the impact of the landuse factors traditional landuse, current management, and fertilization, the broad-scale abiotic factors mean yearly precipitation, east–west and north–south coordinates, and altitude, the fine-scale abiotic factors, pH value, slope, and aspect, and cultural tradition on plant species composition by partitioning variation with a redundancy analysis (RDA). For RDA we followed Peres-Neto, Legendre, Dray, and Borcard (2006) and used a Hellinger-transformed species matrix and \( R^2 \) adjusted for different numbers of variables among the four groups of factors.

Cover of life-forms and Jaccard index

To analyse the impact of the variables aspect, slope, pH, cultural tradition, municipality, altitude, fertilization, traditional landuse (mowing vs. grazing), abandonment, and current landuse (mowing vs. grazing) on the cover of the life-forms graminoids, legumes, and non-legume forbs as well as on the Jaccard index of two vegetation records per parcel, we used an analysis of covariance (ANCOVA) model with sequential sums of squares introducing the variables in the model in the above listed order and all pairwise interactions. We tested effects of cultural tradition against remaining variation among municipalities and of all other factors against variation due to remaining differences among parcels.

Species dominance

To assess species dominance within parcels, we calculated mean cover per parcel relative to total cover for each species within each landuse combination and ranked species in decreasing order of their relative cover values. We considered the 10 species with the highest cover values within a landuse combination as dominant. We did not consider abandoned meadows that had been fertilized for this analysis, as they were represented by only two parcels.

Species pools per landuse type

Because not all landuse types were present for each combination of municipality and altitudinal level, we studied different numbers of parcels for each landuse type (Fig. 2C). Therefore, we used a permutation procedure to compare the total number of species that occur in fertilized and unfertilized meadows (37 parcels in both groups) and fertilized and unfertilized pastures (42 and 68 parcels, respectively), independent of traditional landuse. For each landuse type, we calculated species accumulation data with 1000 random permutations of parcels. We used least-squares fits to
the non-linear species–area curve \( S \approx cA^z \) (where \( S \) is the number of species, \( A \) the area in m\(^2\), and \( c \) and \( z \) are constants; Krebs, 1994) to these data to estimate the values of \( c \) and \( z \) for fertilized and unfertilized meadows and pastures. Based on these values, we calculated the total number of species expected in vegetation records of 70 parcels (\( = 3500 \) m\(^2\)) of each type. Using a \( \chi^2 \)-test, we analysed whether total species numbers differed between fertilized and unfertilized meadows and pastures.

**Effects of landuse changes of former unfertilized meadows**

We were especially interested in the consequences of landuse changes on the vegetation of unfertilized meadows. Our study design did not include repeated vegetation records in parcels undergoing landuse changes; instead we used a space-for-time approach to assess these consequences. We prepared a list of characteristic species of unfertilized meadows that had always been mown (93 species), which we defined as species occurring in more than 20\%, but less than 80\% of all unfertilized meadows and assessed their frequency as the percentage of unfertilized meadows in which the species occurred. This excluded both very rare species and species which were common regardless of the type of landuse. Then we assessed the percentage of unfertilized traditionally mown parcels that nowadays were used as pastures and of those that had been abandoned in which these characteristic meadow species occurred. We compared the relative frequency of the 93 species in each pair of the three types of landuse using paired \( t \)-tests. Thereafter, we calculated the relative difference in frequency of these species between unfertilized meadows that were still mown and the grazed and abandoned parcels.

We did all statistical analyses with the program R (R Development Core Team, 2006) except for the RDA for which we used VarCan (Peres-Neto et al., 2006). To calculate the species accumulation curves we used the R package vegan (Oksanen, Kindt, Legendre, & O’Hara, 2006).

**Results**

In the 216 parcels, we recorded 561 plant species of which 317 species occurred in more than four parcels, 75 species occurred in \( \geq 20\% \) of the parcels, and 33 species occurred in \( \geq 40\% \) of the parcels. Only 72 of the 561 species occurred in all landuse types. Per municipality we recorded between 176 and 284 (mean 229) plant species.

The expected accumulated number of species in 70 parcels of unfertilized meadows was 431, in unfertilized pastures 477, in fertilized meadows 281, and in fertilized pastures 398, i.e. the negative effect of fertilization on species richness was more pronounced in mown grasslands than in grazed ones (\( df = 1, \chi^2 = 5.5673, p < 0.05 \)).

**Abiotic variables and landuse factors**

Except for the differences in slope between fertilized and unfertilized parcels, the differences of abiotic variables among landuse factors were small, leading to low coefficients of determination (Table 1).

Mean altitude of parcels differed among all landuse factors. Abandoned and currently grazed parcels were situated at higher altitudes than current meadows (Tukey’s HSD, \( p < 0.05 \) each). Unfertilized parcels were situated at higher altitudes than fertilized ones (\( p < 0.001 \), Table 1), and traditionally grazed parcels tended to be situated at higher altitudes than traditionally mown ones (\( p = 0.072 \), Table 1). Current meadows tended to be more south-oriented than current pastures (Tukey’s HSD, \( p = 0.055 \)) and traditionally mown parcels were more south-oriented than traditionally grazed ones (\( p < 0.001 \); Table 1). Abandoned parcels were steeper than current meadows and pastures (Tukey’s HSD, \( p < 0.01 \) each), and unfertilized parcels were steeper than fertilized ones (\( p < 0.001 \); Table 1). Parcels formerly used as meadows were steeper than former pastures (\( p < 0.01 \); Table 1). The mean soil pH values of the parcels did not differ between any of the landuse factors (Table 1).

**Species composition in parcels of different landuse**

Altogether, the analysed variables explained 24.6\% of all observed variation in plant species composition in the RDA. The detailed results of the variation partitioning including all interactions among the four groups of variables are shown in a Venn-diagram (Fig. 1). Among the four groups of variables, landuse had the strongest impact explaining 32.9\% of the total explained variation, followed by broad-scale abiotic factors explaining 27.6\% of the total explained variation, fine-scale abiotic

| Table 1. Overview of one-way ANOVAs analyzing differences in fine-scale abiotic variables and altitude among landuse factors (coefficient of determination \( r^2 \) and their significances) of 216 grassland parcels in the Swiss Alps |
|-------------------|-----------------|-----------------|
|                   | Current management | Traditional landuse | Fertilization |
| Altitude          | 0.044***         | 0.015*           | 0.093***      |
| Aspect            | 0.034*           | 0.086***         | 0.003         |
| Slope             | 0.064***         | 0.033**          | 0.230**       |
| pH                | 0.001            | 0.002            | 0.001         |

Current management includes abandoned, mown, and grazed parcels; traditional landuse includes mown and grazed parcels; fertilization includes fertilized and unfertilized parcels. *\( p < 0.05 \), **\( p < 0.01 \), ***\( p < 0.001 \), †\( p < 0.1 \)
factors explaining 8.1% of the total explained variation, and cultural tradition explaining 2.4% of the total explained variation. The interactions between landuse and broad-scale abiotic factors (9.5%), landuse and fine-scale abiotic factors (8.7%), and broad-scale abiotic factors and cultural tradition (5.0%) also explained a considerable amount of the total explained variation.

Species composition of the two vegetation records per parcel was more similar to each other, i.e. they had higher Jaccard indices, in fertilized than in unfertilized parcels \((p < 0.05)\), in traditionally mown than in traditionally grazed parcels \((p < 0.01)\), and in used compared with abandoned parcels \((p < 0.001)\).

**Landuse and dominant species**

Each landuse combination harboured a characteristic set of dominant species, although *Anthoxanthum odoratum* agg. and *Festuca rubra* agg. were among the 10 most dominant species in all landuse combinations (Table 2). In unfertilized parcels, the 10 most dominant species covered about 30% of the plot-area relative to total cover, while in fertilized parcels it was more than 40%. *Ranunculus acris*, *Taraxacum officinale* agg., and *Trifolium repens* were only among the dominant species in fertilized parcels, while *Carex sempervirens* and *Leontodon hispidus* s.l. were only among the dominant species in unfertilized parcels. *Alchemilla xanthochlora* agg. and *Poa alpina* were only dominant in pastures. *Briza media*, *Laserpitium latifolium*, and *Rhinanthus alectorolophus* were only dominant in unfertilized meadows that had always been mown, and *Geranium sylvaticum* and *Heracleum sphondylium* s.l. were only dominant in fertilized meadows that had also traditionally been mown. These results demonstrate that differences in species composition between parcels of different landuse were not just limited to relatively rare species.

**Table 2.** Mean proportion of relative cover (%) in all types of landuse combination for each of 28 species dominant in at least one landuse combination

<table>
<thead>
<tr>
<th>Fertilization</th>
<th>Unfertilized</th>
<th>Fertilized</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Traditional landuse</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Current landuse</td>
<td>Mown</td>
</tr>
<tr>
<td><strong>Festuca rubra</strong> agg.</td>
<td>7.5</td>
<td>6.5</td>
</tr>
<tr>
<td><strong>Anthoxanthum odoratum</strong> agg.</td>
<td>3.9</td>
<td>4.0</td>
</tr>
<tr>
<td><em>Agrostis capillaris</em></td>
<td>2.7</td>
<td>3.4</td>
</tr>
<tr>
<td><em>Nardus stricta</em></td>
<td>1.7</td>
<td>5.9</td>
</tr>
<tr>
<td><em>Trifolium pratense</em> ssp. <em>pratense</em></td>
<td>2.4</td>
<td>1.9</td>
</tr>
<tr>
<td><em>Dactylis glomerata</em></td>
<td>1.5</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Alchemilla xanthochlora</em> agg.</td>
<td>1.3</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Trifolium repens</em> ssp. <em>repens</em></td>
<td>0.9</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Chaerophyllum villarsii</em></td>
<td>2.3</td>
<td>1.5</td>
</tr>
<tr>
<td><em>Phleum ruhaceticum</em></td>
<td>0.7</td>
<td>1.5</td>
</tr>
<tr>
<td><em>Poa alpina</em></td>
<td>0.2</td>
<td>1.8</td>
</tr>
<tr>
<td><em>Taraxacum officinale</em> agg.</td>
<td>0.1</td>
<td>0.5</td>
</tr>
<tr>
<td><em>Carex sempervirens</em></td>
<td>2.1</td>
<td>2.4</td>
</tr>
<tr>
<td><em>Potentilla erecta</em></td>
<td>2.0</td>
<td>1.7</td>
</tr>
<tr>
<td><em>Rumex alpestris</em></td>
<td>0.7</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Leontodon hispidus</em> s.l.</td>
<td>2.7</td>
<td>1.7</td>
</tr>
<tr>
<td><em>Ranunculus acris</em></td>
<td>0.5</td>
<td>0.9</td>
</tr>
<tr>
<td><em>Geranium sylvaticum</em></td>
<td>0.9</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Trisetum flavescens</em></td>
<td>1.1</td>
<td>0.1</td>
</tr>
<tr>
<td><em>Brachypodium pinnatum</em></td>
<td>0.7</td>
<td>0.6</td>
</tr>
<tr>
<td><em>Potentilla aurea</em></td>
<td>1.1</td>
<td>1.7</td>
</tr>
<tr>
<td><em>Vaccinium myrtillus</em></td>
<td>0.9</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Briza media</em></td>
<td>1.9</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Calamagrostis villosa</em></td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Molinia caerulea</em></td>
<td>0.3</td>
<td>0.5</td>
</tr>
<tr>
<td><em>Poa trivialis</em> ssp. <em>trivialis</em></td>
<td>0.2</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Laserpitium latifolium</em></td>
<td>1.9</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Phleum hirsutum</em></td>
<td>0.4</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Species are listed in declining order of their overall frequency. The 10 most dominant species within each landuse combination are marked in bold. Nomenclature is according to Lauber and Wagner (2001) except for *Anthoxanthum* agg.
Cover by plant species of different life-forms

Cover of the different life-forms was mainly affected by differences in landuse. In fertilized parcels, legume cover was higher ($p < 0.001$) and graminoid cover was lower ($p < 0.05$) than in unfertilized parcels. In abandoned parcels, graminoid cover was higher than in agriculturally used parcels, and especially so in formerly grazed parcels (Fig. 2A; interaction traditional landuse by abandonment: $p < 0.05$). Accordingly, forb and legume cover were lower in abandoned than in agriculturally used parcels ($p < 0.001$ for both; Fig. 2B and C).

In current pastures, graminoid cover was insignificantly higher and forb cover insignificantly lower than in current meadows (Fig. 2A and B). Legume cover was higher in traditional meadows than in traditional pastures, and especially so in fertilized parcels (interaction fertilization by traditional landuse, $p = 0.08$). Among the unfertilized traditional meadows, legume cover was lower in current pastures than in still mown ones, whereas among fertilized traditional meadows, it was higher in current pastures than in still mown ones (Fig. 2C).

Apart from landuse effects, we detected lower graminoid cover in parcels with steeper slopes ($p < 0.001$) and a higher one in parcels with higher pH-values ($p < 0.001$).

In summary, results indicate that among the landuse factors, fertilization and abandonment caused stronger shifts in proportions of life-forms than the difference between mowing and grazing did, while abiotic factors were of minor importance.

Effects of landuse change of unfertilized former meadows

Mean frequency of the 93 characteristic meadow species (see Methods) was significantly lower in traditional meadows that had been converted to pastures ($-13.1\%$, $p < 0.05$; Fig. 3) or were abandoned ($-24.8\%$, $p < 0.001$; Fig. 3) than in still mown grasslands.

In pastures, 58 of the 93 species occurred less frequently (mean decrease 36.7%), while 35 occurred more frequently (mean increase 25.3%) than in former meadows. Species generally considered to be rather common (Achillea millefolium, Ajuga reptans, Dactylis glomerata, Veronica chamaedrys), or indicating high nutrient levels (e.g., Rumex alpestris, Taraxacum officinale agg.) were more frequent in current pastures than in continuous meadows. In contrast, the orchid Gymnadenia conopsea was 74% less frequent, and Listera ovata was missing completely.

In abandoned unfertilized meadows, 67 of the 93 species were less frequent (mean decrease 46.0%), while 26 of the 93 species were more frequent (mean increase 29.8%) than in meadows that were still mown. Even some typical meadow-species such as Paradiesa liliastrum and Pulsatilla alpina s.l. were 61.9% and 115.8% more frequent, respectively, in abandoned parcels. However, this was an exception, as many of the species with higher frequency in abandoned unfertilized former meadows were common species of light forests and also included the dwarf shrub Vaccinium vitis-idaea.

In summary, grazing and abandonment of unfertilized former meadows induce strong shifts in species composition and a generally reduced frequency of characteristic species of unfertilized meadows.

Discussion

Effects of landuse

Landuse types were not distributed randomly in the landscape. The analyses of differences in abiotic variables among landuse types confirmed the assumption that farmers in the Swiss Alps try to optimize their workload. Abandoned parcels were situated at higher altitudes or had steeper slopes, which implies a low accessibility, while only parcels at lower altitudes and with lower slopes were fertilized. However, the low values of the coefficients of determination in the ANOVAs (Table 1) show that the relatively large effects of landuse factors on plant species composition can only to a small proportion be related to associated abiotic factors.
Effects of agricultural landuse on plant species composition accounted for more than 30% of the total explained variation. Fertilization of grasslands is of course agriculturally important as it increases productivity. But it also alters interspecific competition, which causes changes in species composition and reduces species diversity in favour of dominant species that are limited in growth at lower nutrient levels (Tilman, 1997). Compared with the vegetation of unfertilized parcels, we found the vegetation of fertilized parcels to be more homogeneous. This was probably caused by the occurrence of fewer but more abundant species as shown in an accompanying analysis of species richness and evenness (Maurer et al., 2006). The increase in legume cover and a reduced graminoid cover in fertilized parcels suggest that not nitrogen, but rather phosphorus was the most limiting factor in unfertilized parcels. As nodule development, and therefore legume growth, requires adequate amounts of phosphorus (Bordeleau & Prévost, 1994) these findings suggest phosphorus limitation of the grassland soils (Bobbink, 1991; Stöcklin & Körner, 1999).

Changes in vegetation composition and cover values are particularly strong after abandonment of grassland in the Alps (e.g., Bischof, 1984; Tasser & Tappeiner, 2002; Zoller, Bischof, Erhardt, & Kienzle, 1984). The higher graminoid cover and lower legume and forb cover in abandoned compared with still used parcels in our study reflect that graminoids effectively spread at the expense of other species (Stammel, Kiehl, & Pfadenhauer, 2003), especially after landuse changes (Fischer & Wipf, 2002). This is most likely due to their ability of pronounced clonal growth (Stöcklin, 1992). The larger difference in graminoid cover in abandoned pastures than in abandoned meadows compared with still grazed and mown parcels, respectively, is likely to be due to the more frequent occurrence of vegetation gaps, such as hoof prints, which promote clonally colonizing graminoids.

Effects of abiotic variables

Effects of broad-scale abiotic factors, reflecting climatic differences, accounted for almost 30% of the total explained variation in plant species composition of our Alpine grasslands. This is an amount of explained variation comparable to that explained by agricultural landuse, while the fine-scale abiotic variables were less important but nevertheless explained a significant proportion of the variation. Such a pattern of comparable effects of landuse and abiotic factors has also been observed in a study in Norway (Vandvik & Birks, 2002). Parcels situated in the northern part of the Swiss Alps experience a much wetter and probably also cooler climate than those situated in the southern and southeastern parts.

The independence of cover of the different life-forms from altitude implies that the observed altitudinal effects result from a replacement of montane by subalpine species, and of subalpine by alpine species within life-forms with increasing altitude.

Effects of cultural traditions

Possibly, differences in plant species composition among grasslands in municipalities of different cultural traditions were mainly related to geographic and climatic differences as indicated by the large effect of broad-scale abiotic variables and the small effect of cultural traditions. Germanic municipalities are located in the wetter northern part of the Swiss Alps because Alemannic people immigrated into the Alps from the North, while Walser and Romanic municipalities are located in southern parts with a drier climate (Bätzing, 2003). Accordingly, the vegetation of grasslands in Germanic municipalities indicated moister conditions than in Romanic and Walser municipalities (data not shown). Even if the remaining variation in species composition explained by cultural traditions was small, this is remarkable because cultural differences consist of socio-economic factors that are only indirectly related to landuse.

Consequences of grazing or abandonment of unfertilized meadows

Unfertilized meadows in general, and the ones addressed in our study in particular, harbour a very species-rich vegetation (Ellenberg, 1996; Maurer et al., 2006). Because mowing is very labour-intensive, many of these unfertilized grasslands have either been converted to pastures or abandoned completely. Unfertilized parcels converted to pastures had only slightly and non-significantly fewer plant species than parcels that are still mown (Maurer et al., 2006). However, conversion to pastures had considerable impacts on species composition. In many parcels, characteristic meadow-species were replaced by generalist plant species, supporting similar findings after landuse changes in South Tyrol (Tasser & Tappeiner, 2002). Moreover, although they were not additionally fertilized, parcels converted to pastures were colonized by some species indicating higher nutrient levels. This supports the idea that grazing animals create nutrient-rich patches and thereby open new niches in otherwise nutrient-poor grasslands (Vandenbos & Bakker, 1990; WällisDeVries, Bakker, & van Wieren, 1998).

Many plant species characteristic of unfertilized meadows were less frequent in abandoned meadows.
However, our results suggest that abandoned parcels can also serve as a refuge for certain species, at least for some time. Nowadays, unfertilized meadows have to be mown yearly to be fully subsidized, while traditionally some of them were only mown every two or three years. Therefore, reproduction of sensitive and late-flowering species may be reduced by earlier and more frequent mowing. In calcareous grasslands, some long-lived forbs of high conservation value tend to be favoured when grasslands are either cut late in autumn or abandoned because this enables storing of nutrients (Köhler et al., 2005). We expect the refuge function of abandoned unfertilized meadows to be limited to species whose requirements are not satisfied by present conditions in meadows. Furthermore, species have to be tall enough not to be impaired by reduced light in abandoned parcels as it has also been observed in abandoned calcareous grasslands (Köhler et al., 2005). To preserve plant species diversity of unfertilized meadows, parcels should be mown regularly, but not necessarily every year.

Conclusions

Along with broad-scale abiotic factors, landuse plays an important role in shaping the plant species composition of grasslands in the Swiss Alps. Therefore, the current socio-economically motivated landuse changes in the Alps have strong impacts on the grassland species composition. These impacts strongly depend on the type of landuse change. The change from unfertilized meadows to pastures suggests less severe consequences for vegetation composition than abandonment, and therefore low-intensity grazing should be considered a valuable alternative to abandonment. Abandoned grasslands may serve as a refuge for only a few characteristic grassland species. Most plants typical of unfertilized meadows are reduced in frequency, when unfertilized meadows are converted to pastures or abandoned. Therefore, to preserve sensitive species in the long run, mowing unfertilized meadows every few years should be promoted as a highly valuable conservation practice, as it can provide the seeds and niches to maintain a high plant species richness and a vegetation composition typical of unfertilized meadows.

Because of the strong differences in plant species composition between differently used parcels of grassland, we conclude that effective financial incentives to farmers should also take the actual plant species composition into account. Moreover, because all landuse combinations are associated with their own characteristic set of species, maintaining a high diversity of plant species in the landscape requires a high diversity of landuse types. Therefore, at the scale of farms, municipalities, and valleys, subsidies should not favour only one particular type of grassland use but a combination ultimately maintaining a high plant species diversity both within and among grasslands.

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