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Source: Mountain Research and Development, 28(2) : 148-155

Published By: International Mountain Society

URL: https://doi.org/10.1659/mrd.0964

Mountain Research and Development Vol 28 No 2 May 2008: 148–155 doi:10.1659/mrd.0964

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How Cultural Tradition and Socioeconomically Motivated Changes Are Shaping Grassland Biodiversity in the Swiss Alps

Alpine grasslands are ecosystems with a great diversity of plant species. However, little is known about other levels of biodiversity, such as landscape diversity, diversity of biological interactions of plants with herbivores or fungal pathogens, and genetic diversity. We therefore explored natural and anthropogenic determinants of grassland biodiversity at several levels of biological integration, from the genetic to the landscape level in the Swiss Alps. Differences between cultural traditions (Romanic, Germanic, and Walser) turned out to still affect land use diversity and thus landscape diversity. Increasing land use diversity, in turn, increased plant species diversity per village. However, recent land use changes have reduced this diversity. Within grassland parcels, plant species diversity was higher on unfertilized mown grasslands than on fertilized or grazed ones. Most individual plants were affected by herbivores and fungal leaf pathogens, reflecting that parcels harbored a great diversity of herbivores and pathogens. However, as plant damage by herbivores and pathogens was not severe, conserving these biological interactions among plants is hardly compromising agricultural goals. A common-garden experiment revealed genetic differentiation of the important fodder grass Poa alpina *between mown and grazed sites, suggesting adaptation. Per-village genetic diversity of* Poa alpina *was greater in villages with higher land use diversity, analogous to the higher plant species diversity there. Overall, landscape diversity and biodiversity within grassland parcels are currently declining. As this contradicts the intention of Swiss law and international agreements, financial incentives need to be re-allocated and should focus on promoting high biodiversity at the local and the landscape level. At the same time, this will benefit landscape attractiveness for tourists and help preserve a precious cultural heritage in the Swiss Alps.*

Keywords: *Agricultural policy; agro-environmental subsidies; Alps; biodiversity; cultural traditions; Switzerland.*

Peer-reviewed: *January 2008* ***Accepted:*** *January 2008*

Introduction

Biodiversity comprises several levels of biological integration, including the levels of landscapes, communities, species within communities, biological interactions, and individuals and genes within species (Primack 2002). High biodiversity is thought to be important because it increases the stability of most types of ecosystems (Balvanera et al 2006) and enhances the sustainability of resource exploitation (Klaus et al 2001). Moreover, a great diversity of species and genotypes generally increases stress tolerance of communities, and increasing redundancy of functional relationships in more diverse communities has been reported to protect ecosystems against disturbances (Hooper et al 2005). These ecological reasons to protect biodiversity go hand in hand with other motivations, as many direct economic values and indirect ecosystem services have been derived from biodiversity (Ehrlich and Ehrlich 1992; Daily et al 1997). Moreover, ethical considerations affirm every individual's right to existence and therefore also that of biodiversity as a whole (Aus der Au 2003). And in Europe, as in many other regions of the world, current biodiversity constitutes not only a natural heritage but also a cultural heritage. For this reason too, it should be conserved for future generations. Finally, communities of great plant species diversity are considered aesthetically more valuable by the public than those with low diversity (Junge 2004). This comprehensive importance of biodiversity has been acknowledged in national nature conservation laws and international agreements such as the Convention on Biological Diversity of the United Nations (United Nations 1992).

The European Alpine landscape is characterized by strong natural gradients and large spatial and temporal heterogeneity, which give rise to a great diversity of habitats and species (Theurillat et al 2003). Furthermore, human land use has shaped biodiversity, especially below the treeline where most grasslands are manmade. The plant species diversity of these grasslands is up to 3 times greater than in the forests they replace (Zoller and Bischof 1980). These grasslands contribute to the diverse mosaic of pastures, meadows and forests, making the cultural landscape of the Swiss Alps one of the most plant-species rich in Europe (Väre et al 2003).

In the Swiss Alps 3 main cultural traditions can be distinguished (Bätzing 2003; Figures 1A–1C). Roman culture developed with the increase of the human population in Europe after 1800 BC, when settlements and land use were extended into Alpine valleys. Germanic culture developed after 600 AD, when Alemannic peoples from the North migrated to the wetter northern and northeastern parts of the Alps. After 1200 AD, the Walser, ie Alemannic people from the area that is the modern Canton of Valais, migrated eastwards and settled at relatively high altitudes, because lower parts of the valleys were already occupied. Owing to the highly diverse topography and geology of the Alps and to historical idiosyncrasies, villages with different cultural traditions are not distributed simply in different biogeographic regions of Switzerland, implying that differences between these villages reflect cultural rather than biogeographic differences (Pfister 2004). Prior to the present study, it was unknown whether these cultural traditions still affect biodiversity in the different areas.

Since the Second World War, changing socioeconomic conditions have led to major changes in land use (Stöcklin et al 2007). In the Alps subsistence farming has been largely replaced, mainly by dairy farming (Bätzing 2003). In the grasslands, two opposite developments took place. On the one hand, areas that easily lent themselves to agricultural use were cultivated ever more intensively. The cutting frequency and the amount of fertilizers used have increased, liquid manure has increasingly replaced the traditional use of dung, and more areas are now irrigated. On the other hand, steep or poorly accessible areas, which did not or not easily lend themselves to mechanical cultivation, have increasingly been abandoned (Baur et al 2007) or—to save working time—changed into pastures (Fischer and Wipf 2002). Although there have been many local studies in the Alps, mostly on plants, that strongly suggest that these changes reduce biodiversity, there have been very few larger-scale and comprehensive studies investigating these effects.

This deficiency motivated the present study, aimed at assessing drivers of grassland biodiversity in the Swiss Alps at several levels of biological organization. The present study was carried out as part of Swiss National Research Program 48 (Landscapes and Habitats of the Alps). A particularly important aspect of our research was that in addition to regional, geological, and topographical differences in land use, cultural traditions and modern socioeconomically motivated changes in land use were included as potential determinants of grassland biodiversity. This survey of the most important findings of our project is based on previously published (Maurer et al 2006; Rudmann-Maurer et al 2007a, 2007b) as well as unpublished results of our project.

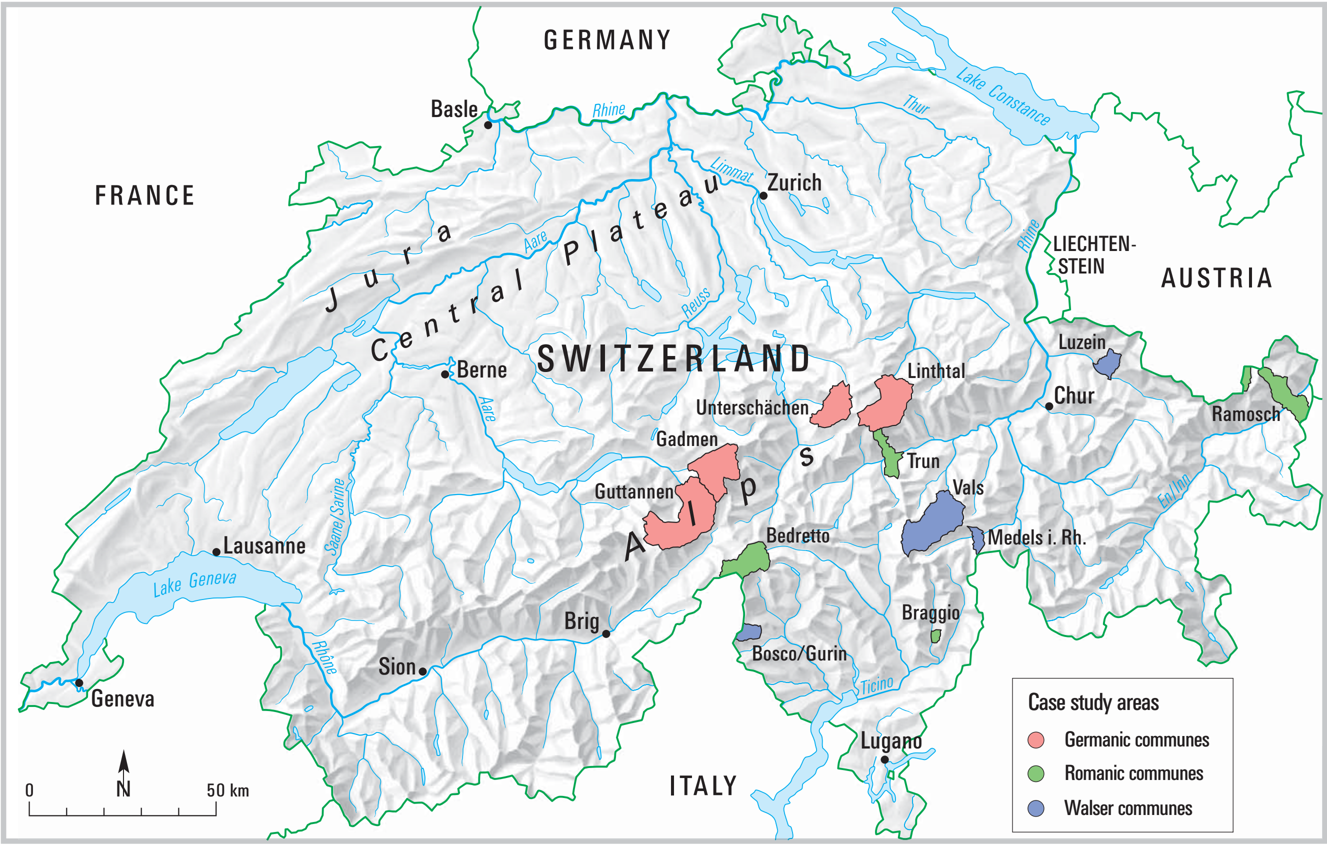
The combination of these results allows us to identify the most important determinants of biodiversity, thus forming the basis for formulating and implementing measures for its conservation. To identify possible conflicts between conservation and agriculture, it is important to analyze whether potential drivers of biodiversity have opposing effects at different levels of biodiversity, and whether factors favoring biodiversity contrast with agricultural goals.

Methods

Previously published results on plant molecular and plant species diversity (Maurer et al 2006; Rudmann-Maurer et al 2007a, b) and the new results combined in this survey are all based on a common study design. Between 2002 and 2004 we studied grassland biodiversity at the levels of 1) landscape diversity, 2) plant species richness, 3) biological interactions of plants, and 4) genetic plant diversity. In 12 villages in the Swiss Alps

FIGURES 1A–1C Views of A) the Romanic village of Ramosch (GR) with clustered houses and different grassland types; B) the Germanic village of Unterschächen (UR) with its scattered farms; and C) the Walser village of Vals (GR), where the space between originally scattered houses has filled up in recent decades. (Photo A by Jürg Stöcklin, Photos B and C by Katrin Rudmann-Maurer)

FIGURE 2 Map of Switzerland with the 12 study villages and their cultural traditions (Romanic, Germanic, and Walser). (Map by Andreas Brodbeck)



(Figure 2) we selected grassland parcels at 3 altitudinal levels—the valley floor (1000–1500 m), intermediate altitudes (1500–2000 m), and the alp level (above 2000 m). Each of the 3 cultural traditions—Romanic, Germanic, and Walser—was represented by 4 villages. We searched for grassland parcels defined by the combination of 3 altitudinal levels, 2 traditional land uses (mown or grazed), 3 current land uses (mown, grazed, or abandoned), and 2 levels of fertilization (fertilized or unfertilized). Thus, for each village and altitudinal level we looked for parcels with 12 different combinations of land use, ie for 432 different types of parcels. The presence or absence of such types of parcels among the 215 parcels finally studied allowed us to draw conclusions on land use, its recent changes, and its diversity.

Landscape diversity

Landscape diversity was measured as the number of different land use types in villages (Maurer et al 2006). We used logistic regression to explore whether cultural traditions, altitude, or type of land use affect the likelihood of occurrence of a certain type of grassland parcel. We also tested whether land use diversity was linked with plant species diversity within a village.

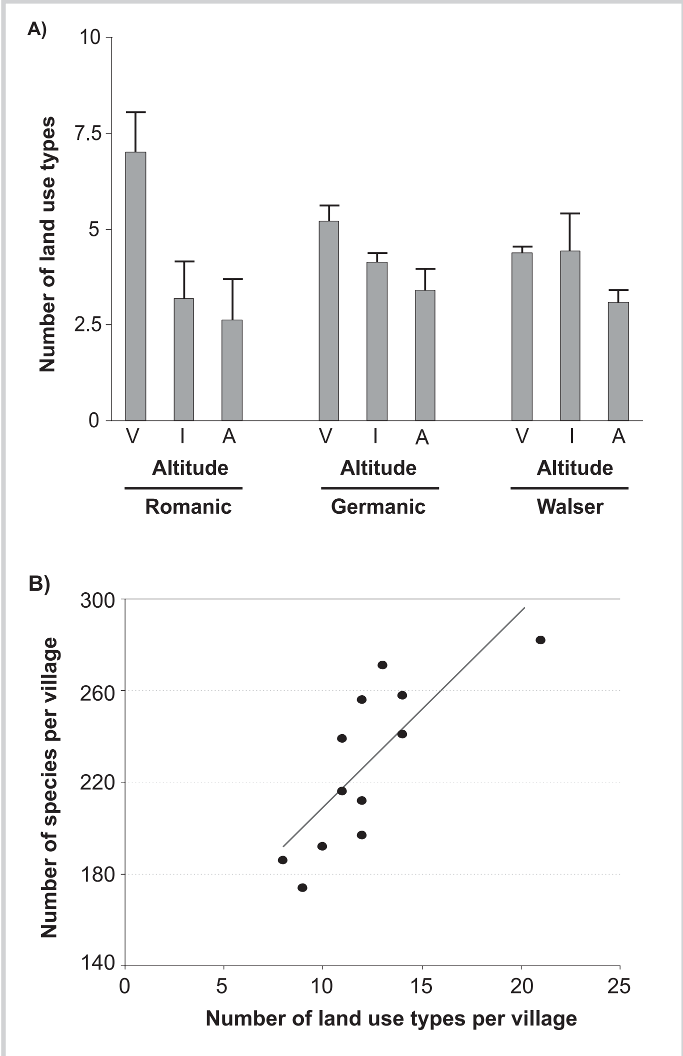
Plant species diversity and vegetation composition

To measure plant species richness we took vegetation records for two randomly selected 5-m x 5-m plots per parcel, estimating ground cover for each species and counting the number of species per record (Maurer et al 2006). Additionally, for each parcel we calculated mean ecological indicator values after Landolt (1977) and percentage of ground cover by functional plant groups—graminoids, forbs, and legumes—per parcel (Rudmann-Maurer et al 2007b). On each plot biomass samples were taken to assess production.

Biological interactions

For analysis of biological interactions of plants with herbivores and fungal leaf pathogens, we sampled leaves of 20 randomly selected plants for each of the functional groups—graminoids, forbs, and legumes—on each of 215 parcels (>12,000 leaves) and analyzed the damaged leaf area and the diversity of types of herbivory and fungal pathogens. We assessed the diversity of herbivory as the number of different types of leaf damage after Crawley (1983) and the diversity of fungal pathogens as the number of larger taxonomic units, including rusts, smuts, mildew, powdery mildew, and fungi causing leaf spots. This procedure allowed us

FIGURES 3A AND 3B Land use diversity. A) Mean number of land use types per cultural tradition and altitudinal level ± SE. V denotes the valley level, I denotes intermediate altitudes, and A denotes the alpine meadow level. B) Relationship between the number of plant species recorded per village and the number of land use types. (Figure reprinted from: Maurer K, Weyand A, Fischer M, Stöcklin J. 2006. Old cultural traditions, in addition to land use and topography, are shaping plant diversity of grasslands in the Alps. *Biological Conservation* 130:438–446, with permission from Elsevier)



to study levels and diversity of herbivory and fungal infestation on all study plots.

Genetic diversity

We studied within-species diversity in the Alpine meadow grass *Poa alpina* L. (Poaceae). This species is widespread in the Swiss Alps and occurs over a large altitudinal range. Due to its frequent occurrence in pastures and nutrient-rich meadows and its high content of fats and proteins, it is among the agriculturally most important fodder grasses (Bachmann 1980; Conert 1998).

We studied molecular genetic diversity of 569 *P. alpina* plants originating from 54 agriculturally used grassland parcels and 20 natural sites. Using 5 microsatellite DNA markers, we analyzed the presence of microsatellite bands and asked whether populations of *P. alpina* from used grassland were differentiated from natural populations, and whether genetic differentiation among villages and among parcels was related to geographic distances and to differences in land use (Rudmann-Maurer et al 2007a). We also explored whether genetic diversity, measured as numbers of bands per plant and per parcel, was related to altitude and land use.

Moreover, in a quantitative-genetic experiment with 1380 plants (2 plants of each of 690 genotypes) from 65 parcels, we tested whether plant performance and reproduction in a common garden in Davos (Canton of Grisons, Switzerland) suggested local adaptation of *P. alpina* to land use and altitude.

Results

Landscape diversity

In Romanic villages, more different parcel types tended to occur on the valley floors than on those in Germanic and Walser villages (Figure 3A; Maurer et al 2006), suggesting that socioeconomic differences among cultural traditions still play a role in shaping landscape diversity. An accompanying socioeconomic analysis showed that the villages of these different cultures are still remarkably different (Pfister 2004). Nevertheless, in all 3 types of village many formerly mown parcels were grazed and many formerly managed grasslands had been abandoned (Maurer et al 2006). Obviously, these changes in land use reduced farmers' workloads.

Plant species diversity

At the village level, greater land use diversity was closely correlated with greater species richness (Figure 3B; Maurer et al 2006). Moreover, the type of land use heavily influenced species diversity within grasslands. Fertilization and abandonment (Table 1; Maurer et al 2006) both reduced plant species richness. On unfertilized parcels grazing slightly reduced species richness compared with mowing, while on fertilized parcels it had a positive influence. Mown unfertilized grasslands harbored the greatest species richness. Moreover, species richness was higher on parcels with low standing crops, revealing a conflict between production and biodiversity. Independent of land use and fertilization, plant species richness was highest at intermediate altitudes (Table 1).

Plant species composition changed with increasing altitude as montane species were replaced by subalpine, and subalpine species were replaced by alpine species (Rudmann-Maurer et al 2007b). In Germanic villages, species composition of parcels indicated more moist conditions than in Romanic and Walser villages. Each land use combination was characterized by a different set of dominant species. Among the land use variables, fertilization and abandonment had the strongest effects on

TABLE 1 Plant species richness per 5 m × 5 m (mean ± standard error) of 216 grassland parcels of different land use at 3 altitudinal levels.

	Currently mown		Currently grazed		
Altitude	**Unfertilized**	**Fertilized**	**Unfertilized**	**Fertilized**	**Abandoned**
Valley	44.38 ± 2.06	28.57 ± 1.51	44.13 ± 1.93	34.21 ± 1.56	31.63 ± 1.92
Intermediate	55.43 ± 3.26	31.23 ± 2.12	50.23 ± 2.72	36.62 ± 2.17	40.27 ± 3.80
Alpine	47.14 ± 4.15	37.0[a)]	47.26 ± 2.75	34.7 ± 1.83	44.91 ± 4.37

[a)] only one parcel

species composition and affected abundances of different functional plant groups and the mean ecological indicator values. The frequency of plant species characteristic of mown grasslands was reduced by grazing of formerly unfertilized meadows, and even more so by abandonment. However, to some degree abandoned parcels also served as refuges for certain meadow species.

Diversity of biological interactions

Herbivory by small animals and fungal pathogen infection were ubiquitous and present on 83% of all leaves. However, the damaged leaf area was <4%, indicating that plant–herbivore and plant–pathogen interactions contribute to community diversity without causing substantial yield reduction for farmers. More leaf damage by herbivory occurred on traditionally mown sites, fertilized sites, and at lower altitudes, while damage by fungal pathogen infection was independent of land use and altitude. Damage by herbivores and fungal leaf pathogens and their diversity increased with greater productivity of the grasslands, but not with greater plant species richness.

Genetic diversity of the important fodder grass *Poa alpina* L.

Poa alpina most frequently occurred on fertilized and grazed parcels and at higher altitudes, in accordance with its preferences described in the literature (Conert 1998). Per-village molecular genetic diversity of *P. alpina* was higher in villages with greater land use diversity (Figure 4A; Rudmann-Maurer et al 2007a), as reported above for plant species richness. In villages of Walser tradition, microsatellite band richness was significantly higher than in Germanic villages (Figure 4B).

Molecular-genetic differentiation between grassland parcels with *P. alpina* was pronounced (>20%) and increased with increasing geographic distance (Rudmann-Maurer et al 2007a). This indicates gene flow was limited and decreased with distance. Moreover, mown and grazed grassland parcels were slightly (>1%) differentiated from each other genetically. Molecular diversity was higher within grazed than within mown parcels.

In the common garden, the proportion of plants with vegetative reproduction—which in the case of *P. alpina* is realized as so-called pseudoviviparous production of bulbils instead of seeds—increased with their altitudinal origin, in line with the hypothesis of an adaptive advantage of vegetative reproduction with increasing altitude. Moreover, plants of *P. alpina* from fertilized parcels had a higher common garden yield than plants from unfertilized parcels, suggesting at least weak adaptation of *P. alpina* to fertilization. Furthermore, plants on grazed parcels allocated more biomass to reproduction than those on natural sites, whereas plants from mown parcels allocated less (Figure 5). This indicates disruptive selection due to land use and is in line with the hypothesis that recruitment is of greater adaptive value on pastures than on meadows. The latter is expected because grazing animals create open sites for seedling establishment.

Discussion

Despite interest in biodiversity research, little is known about the relationship between different levels of biodiversity. Our combined results—for molecular, quantitative genetic and plant species diversity, and for biological interactions of plants with herbivores and pathogens—suggest that plant species richness per study site does not adequately measure biodiversity for all levels of biological integration of plants, despite its wide use for this purpose. It remains to be seen to what extent plant diversity indicates the diversity of other taxa such as birds, bats, other mammals, lichens, or microorganisms. Furthermore, requirements for maintaining one level of biodiversity are not necessarily the same as for others. Finally, if biodiversity is to be understood at all levels, it should not only be considered locally, but also at the landscape scale, taking into account differences in the genetic and species diversity and composition of different natural and differently used anthropogenic habitats.

Cultural traditions affected the level of landscape diversity via the different occurrence of land use types. More different types of parcels occurred on the valley floor belonging to Romanic villages. These differences in land use diversity are likely to be caused by differences in the distribution of an estate to heirs between the Germanic and Romanic cultures (Bätzing 2003). Whereas one son and heir inherited the land in Germanic villages, all children of a family were considered in Romanic villages. In Walser villages, which are situated at higher altitudes, greater pressure to use all available land suited for agricultural production probably reduced the proportion of abandoned land compared with the other villages. Clearly, the old cultural traditions are still affecting land use diversity and thus biodiversity.

The agro-environmental subsidy system implemented in current Swiss agricultural policy applies uniform measures throughout the country. Most subsidies—so-called direct payments—are granted on a per-area and per-animal basis. They consist of a base amount and additional amounts for difficult farming conditions or for particular ecologically-minded efforts. However, except for altitudinal levels, they are not differentiated between biogeographically or culturally different regions (Stöcklin et al 2007). Therefore, the current subsidy system promotes agricultural uniformity, suggesting that the remaining differences in land use diversity and biodiversity brought about by different cultural traditions are likely to disappear within the next decades.

Fertilization strongly reduced plant species richness and changed species composition (Maurer et al 2006; Rudmann-Maurer et al 2007b). It promoted the diversity of different types of herbivory while it decreased the diversity of fungal leaf pathogens and had no effect on diversity within *Poa alpina*. Thus, from the point of view of conservation, fertilization is mainly negative because of its effect on plant species diversity. Of course, fertilized meadows are important in agriculture due to their higher yield compared with unfertilized parcels and therefore undoubtedly will be maintained. Nevertheless, the area of fertilized pastures with low species richness should be kept as small as possible.

Also, abandonment reduced plant species richness severely and changed species composition in favour of more common species (Rudmann-Maurer et al 2007b). Overall, observed effects of abandonment were rather negative for biodiversity at the different studied levels. Nevertheless, abandoned parcels hosted plants from unfertilized meadows which otherwise were endangered, and also contributed to great landscape diversity.

Both mowing and grazing contributed to high plant species richness when parcels were unfertilized (Maurer et al 2006). Grazing of formerly unfertilized meadows reduced plant species richness and the frequency of characteristic species on unfertilized meadows (Rudmann-Maurer et al 2007b). Nevertheless, as vegetation composition differed between mown and grazed parcels, the occurrence of both types of land use enhanced landscape diversity. Traditional mowing promoted plant–herbivore interactions, while grazing enhanced genetic diversity of *P. alpina*. *Poa alpina* has

FIGURES 4A AND 4B Relationship between per-village microsatellite band richness of *Poa alpina* and A) number of land use types investigated per village and B) cultural tradition of 12 villages in the Swiss Alps. Allelic richness is based on a standardized sample size of 16 plants. G denotes the Germanic tradition, R the Romanic tradition, and W the Walser tradition. In Figure 4A, three data points are hidden by others. In Figure 4B error bars denote 1 SE. (Figure reprinted from: Rudmann-Maurer K, Weyand A, Fischer M, Stöcklin J. 2007. Microsatellite diversity of the agriculturally important alpine grass *Poa alpina* in relation to land use and natural environment. *Annals of Botany* 100:1249–1258, with permission from Oxford University Press)

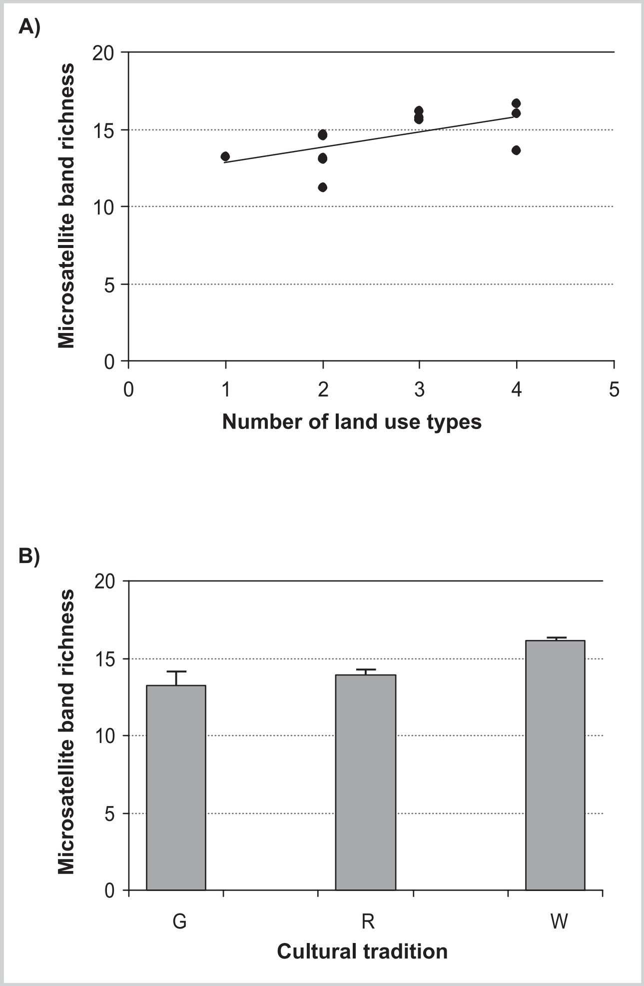
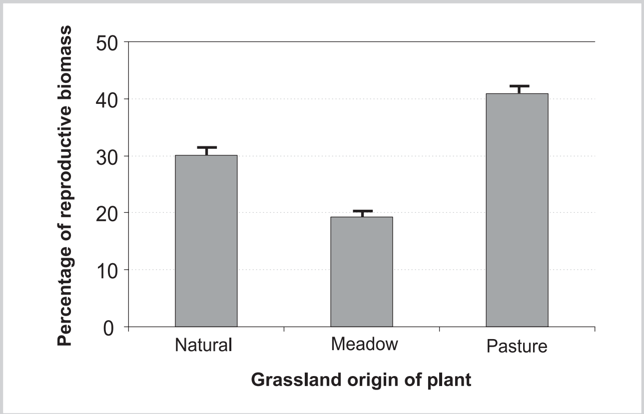


FIGURE 5 Percentage (mean ± SE) of reproductive biomass in *Poa alpina* plants originating from natural, mown, or grazed parcels, and grown in the common garden.



undergone divergent selection in response to mowing and grazing, resulting in genetically different plants on mown and grazed parcels. Because low-intensity grazing has some positive effects at all levels of biodiversity, grazing is clearly preferable to abandonment of grasslands, at least from the perspective of biodiversity.

As each land use combination was characterized by a different set of dominant species, each of them contributed to landscape diversity. The observed plant species composition results from the combination of abiotic factors and land use with different sets of species for each land use type. Unfortunately, continuing changes in land use driven by socioeconomic circumstances have strong and mostly negative impacts on the species diversity and composition of grasslands in the Swiss Alps.

From the combined results of our project, the conclusion emerges that promoting high biodiversity requires a high diversity of land use types within a landscape, which implies a more even distribution of land use types across all altitudinal levels. Unfortunately, current Swiss agricultural policy is concerned mostly with the parcel level. To promote land use diversity, a portion of the financial incentives should be targeted at the farm or even village level. Furthermore, financial incentives should be reallocated to prevent both the ongoing abandonment of grasslands at higher altitudes and intensified use at lower altitudes, with the related severe consequences for biodiversity. However, some abandoned parcels do have a place in a diverse landscape, though abandoned grasslands may occasionally need to be cleared of bushes and trees to prevent reforestation. Considering the ongoing changes in land use, moderate grazing or mowing every few years should be considered as a valuable alternative to abandonment. The most effective way to protect anthropogenic biodiversity, and thereby also economic and aesthetical ecosystem services for society, is to use financial incentives to maintain a high land use diversity of farms and villages.

Conclusion

The combined results of our project demonstrate that human land use affects grassland biodiversity at all levels from the genetic to the landscape level, and that the hundreds of years of agricultural activity have largely shaped current biodiversity. Unfertilized meadows are most likely to be fertilized or grazed, or, if steep and at high altitudes and therefore not easily accessible, to be abandoned (Baur et al 2007). Due to such land use changes, landscape diversity and the number of grassland parcels of great biological value are declining. This contradicts the intentions of Swiss national laws and international agreements such as the Convention on Biodiversity (CBD). Clearly, financial incentives need to be reallocated to focus on promoting and maintaining high biodiversity at the local and at the landscape level (Stöcklin et al 2007). At the same time, this will enhance the attractiveness of the landscape for tourists and help preserve precious cultural heritage in the Swiss Alps.

ACKNOWLEDGMENTS

We thank all involved municipalities, local contact persons, and all farmers who allowed us to work and collect plants on their land. We thank Gregor Klaus for efficient editing help. We acknowledge support by the Swiss National Research Program NRP 48, "Landscapes and Habitats of the Alps" (Grant 4048-064494/1).

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