

## Accepted Manuscript

Title: Long-term effects of grazing on subalpine and alpine grasslands in the Central Alps, Austria

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PII: S1439-1791(16)30200-6

DOI: <http://dx.doi.org/doi:10.1016/j.baae.2017.07.005>

Reference: BAAE 51045

To appear in:

Received date: 28-10-2016

Accepted date: 31-7-2017

Please cite this article as: {<http://dx.doi.org/>

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<AT>Long-term effects of grazing on subalpine and alpine grasslands in the Central Alps, Austria

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<ABS-HEAD>**Abstract**

<ABS-P>The effects of grazing exclusion on species diversity and functional diversity were analyzed along an elevation gradient from the subalpine (1960 m a.s.l.) to the lower and upper alpine zone (2275 m - 2650 m a.s.l.) in the Austrian Central Alps for 15 years. Nine sites were chosen, including grasslands at different elevations, a bog and a glacier foreland site at the lower alpine zone and a snowbed at the upper alpine zone. Data were acquired by frequency counts in 1 m<sup>2</sup> permanent plots inside each fenced area (three plots per site) and outside in grazed areas (three plots). Diversity indices and functional diversity were analyzed by means of generalized linear mixed models (GLMMs). Exclosure, duration of exclusion and exclosure\*years (interaction effect) were defined as predictor variables. Multivariate ordination techniques were used to (i) determine species responses to grazing exclusion (pRDA, partial redundancy analysis) and (ii) to create a distance matrix representing the changes between exclosures and control plots per year (NMDS, non-metric multidimensional scaling). At the subalpine grassland, first differences between exclosure and control plots occurred already only after three years, at the upper alpine zone after four and five years. Contrary to our expectation, dwarf shrubs did not increase within the exclosures of the subalpine grassland. Instead, mainly the tall forb *Geranium sylvaticum* increased. Species richness significantly decreased at the exclosures of the subalpine zone, the snowbed and at one upper alpine grassland sites. The communities of the glacier foreland and the bog were hardly affected by grazing exclusion.

<ABS-P>We conclude that plant species and communities react individually depending on elevation and grazing animals. Grazing exclusion studies at high elevations should definitely to be carried out in the long-term.

<KWD>Keywords: elevation gradient; exclusion; frequency; ordinations; permanent plots;

## Introduction

Worldwide, terrestrial ecosystems are subjected to fundamental changes due to exogenous perturbations (Parmesan & Yohe 2003; Müller, Gnauck, Wenkel, Schubert & Bredemaier 2010). Besides climate change, land-use changes belong to the most significant drivers of ecosystem modifications (Sala, Chapin, Armesto, Berlow, Bloomfield et al. 2000). In the Central Austrian Alps, grazing regimes at the treeline date back more than 6000 years (Vorren, Mørkved & Bortenschlager 1993, Bortenschlager 1999). Thus, plant communities and species adapted to grazing for thousands of years. From the 1950s onwards, many of the upper montane and subalpine meadows and pastures of the Alps were abandoned. As a consequence, secondary succession led to dwarf shrub encroachment and reforestation or to

the growth of tall forbs (Mayer & Erschbamer 2014) followed by a considerable loss in species diversity (Schütz, Wohlgemuth, Achermann, Krüsi & Grämiger 2000; Tasser & Tappeiner 2002; Niedrist, Tasser, Lüth, Della Via & Tappeiner 2009). As to the alpine zone, i.e. at grasslands above the potential treeline, we have no clear idea of how grazing cessation will affect species richness and community composition (Mayer & Erschbamer 2014). Generally, the importance of low-intensity land use for the maintenance of plant species richness in the Alps was emphasized manifold (review in Virtanen 2000; see also Camenisch & Schütz 2000; Schütz et al. 2000; Tasser & Tappeiner 2002; Dullinger, Dirnböck, Greimler & Grabherr 2003; Spiegelberger, Matthies, Müller-Schärer & Schaffner 2006; Virtanen, Salminen & Strömmer 2008; Niedrist et al. 2009; Speed, Austrheim, Hester & Myrsterud 2013; Strebel & Bühler 2015). However, only few studies considered grazing effects at highest elevations (Loison, Toigo & Gaillard 2003; Mayer, Kaufmann, Vorhauser & Erschbamer 2009; Mayer & Erschbamer 2014; Pardo, Doak, García-González, Gómez & García 2015). Alpine species might respond with a considerable delay to grazing cessation due to their slow growth and their extended age which enable them to persist for a long time. So far, investigations at the alpine zone suggested a delayed reaction of the plant communities to grazing exclusion (Mayer et al. 2009; Mayer & Erschbamer 2014; Pardo et al. 2015). Regarding changes in species richness at the plot scale, divergent results were obtained in the alpine zone. Mayer and Erschbamer (2014) recorded a decreasing diversity after 11 years, whereas Pardo et al. (2015) found no effects on species richness even after 19 years of grazing exclusion in the Pyrenees. Low numbers or the absence of grazers favor fast-growing, tall species which prevent the occurrence of inferior, slow growing, small/prostrate species; thus diversity will decline. To evaluate these changes, the C-S-R plant strategy concept of Grime (1979) is an appropriate tool (Moog, Kahmen & Poschlod 2005). Grazing was found to reduce the competitively dominant species through gap creation, promoting weaker species in gaps (Kohler, Gillet, Gobat & Buttler 2006; Mariotte, Buttler, Kohler, Gilgen & Spiegelberger 2012). Thus, C-strategists (competitive, tall-growing species) should increase (Lavorel, de Bello, Grigulis, Lepš, Garnier et al. 2011), whereas S-strategists (stress tolerant, small/prostrate species) should decrease with grazing exclusion. R-strategists (ruderal species) might be favored by grazing (Grime 1979; Hodgson, Wilson, Hunt, Grime & Thompson 1999), however, in subalpine and alpine environments this group hardly occurs. Community response varies along elevation and environmental gradients (Oesterheld & Semmartin 2011). In lowlands, the largest grazing exclusion effects were found on sub-humid and/or highly productive sites (Milchunas, Sala & Lauenroth 1988, Milchunas & Lauenroth 1993), provoking a higher diversity on these sites (Proulx & Mazumder 1998). Vegetation changes due to cattle grazing in lowlands were faster at moist compared to dry conditions (Persoon 1984).

In this paper, we present the results of a long-term monitoring study started in 2000 in the Austrian Central Alps with the main objective to observe the effects of grazing exclusion along an elevation gradient from the subalpine to the upper alpine zone (Mayer et al. 2009, Mayer & Erschbamer 2014). After 7 years, grazing effects were found to be significant only at the subalpine zone (Mayer et al. 2009, Mayer & Erschbamer 2014). After 15 years of grazing exclusion, however, we expected significant community and functional changes also at the lower and upper alpine zone. The following hypotheses were tested:

- 1) <1>\*1\*>After 15 years, grazing exclusion affects species diversity and species composition along the whole elevation gradient;
- 2) <2>\*1\*>At the alpine zone, grazing exclusion effects are considerably delayed compared to the subalpine zone;

- 3) <3><sup>1</sup>At the subalpine zone, an increase of dwarf shrubs occurs on the enclosure plots;
- 4) <4><sup>1</sup>Moist conditions favor species richness in the absence of grazing;
- 5) <5><sup>1</sup>Functional diversity changes significantly with grazing exclusion, i.e. competitive/tall species increase; stress tolerant/small/ prostrate species decrease.</LIST>

## Materials and methods

### Study sites

The nine study sites (Table 1, Fig. 1) are located at Obergurgl in the inner Oetz valley (Tyrol, Austria). All sites belong to the Long Term Ecosystem Research (LTER) site Obergurgl within the platform LTSER Tyrolean Alps (<http://www.lter-austria.at/ta-tyrolean-alps/>) and are located from the subalpine zone (1960 m a.s.l., actual treeline at 2100-2300 m a.s.l.) to the upper alpine zone (2650 m a.s.l.). At the subalpine grassland (S1), livestock type and stocking rate (6 cattle per 1 ha, from the beginning of July to the beginning or end of August each year) as well as grazing system (rotational) were by far too high (8.00 animal unit months ha<sup>-1</sup> while optimal stocking rates would be 2.33; calculations according to Guggenberger, De Ros and Venerus 2007 in Mayer et al. (2009)). The other research sites were characterized by a traditional grazing regime, the animals strolling around on relatively large areas. At the lower alpine sites (S2-S4; Schoenwieskopf), sheep, goats and Haflinger horses grazed the area from mid June to mid September. Sheep and horses grazed occasionally at the Rotmoos bog (S5) and the glacier foreland of the Rotmoosferner (S6). At the upper alpine sites (S7-S9; Mt Hohe Mut) only sheep were present. Cattle did not occur at the lower and upper alpine sites. Mayer et al. (2009) calculated stocking rates between 2.22 and 0.40 animal unit months ha<sup>-1</sup> for the sites S2-S4 and S7-S9, respectively, the rates being lower than the suggested optimal ones (Guggenberger et al. 2007). However, animals frequently concentrated at these sites, especially around the fences. Thus, grazing pressure probably was essentially higher than determined by Mayer et al. (2009), however, exact numbers were not available for these sites. In Table 1 estimations of the grazing pressure according to personal observations are given. Grazing exclusion fences were established in summer 2000 at S1, S2-S4, and S7-S9 (for plot sizes see Table 1). S6 was established in summer 2001 and S5 in summer 2005. Due to logistic and permission problems, the fences were not equal in size (Table 1). From 2000 till 2011-2012, wooden fences of 1.5 m height were used the whole year round, from then on electric fences of 1.5 m height were established after each winter. At S5, an electric fence was used from the beginning. At each exclusion site, three permanent plots of 1 m<sup>2</sup> were marked within the fenced area (EX) and three outside as grazed controls (CO).

### Data collection

Frequency was counted in the course of 15 years during the main growing season (mid July to the end of August) within the 1 m<sup>2</sup> plots by means of a frequency frame, divided into 100 subplots. Within the subplots, presence-absence of the species was recorded. All vascular plant species and lichens were determined on species level (nomenclature follows Fischer, Oswald & Adler 2008; Wirth 1995); the mosses were classified as *Polytrichum* spp., *Sphagnum* spp. or other Bryophyta. The monitoring was carried out in 1 to 3-years intervals. The C-S-R strategy types followed Landolt et al. (2010). The following strategies were distinguished: CCS = competitors with stress-tolerant components, CSS = stress-tolerators with competitive components, SSS = stress-tolerators, RSS = stress-tolerators with ruderal components, CRS = intermediate strategists. RRS = ruderals with stress-tolerant components were omitted due to scarce presence (only *Euphrasia minima* was present in some plots). Potential growth height of the species was identified according to Fischer et al. (2008) and three classes were defined: tall (> 20 cm), small (5-20 cm) and prostrate (< 5 cm).

### Statistical analyses

Species richness, Shannon diversity (natural log-based) and Evenness (based on Shannon diversity) were calculated in TURBOVEG for WINDOWS 2.118 (Hennekens 1998-2015). The frequency sum of each functional group member (i.e. five C-S-R strategy classes, three classes of potential plant height) was related to the total frequency sum per sample, values ranging between 100% and 0%. For the statistical analyses of diversity indices and functional diversity, generalized linear mixed models (GLMMs) were used. GLMMs are ideal for data with prevailing non-normal distribution and, in our case, because temporal (repeated measure) autocorrelations had to be accounted for as random effects (Bolker et al. 2009). To calculate overall trends, 'Study site' was used as grouping factor (= block variable). As predictor variables, exclosure, duration of exclusion (years) and the interaction term exclosure\*years were defined. Exclosure effects were coded as 'EX', temporal effects (number of years of exclusion) as 'Yrs' and the interaction effects as 'EX\*Yrs' for repeated measure in GLMMs. For all calculations, the Gaussian probability distribution model was used. All GLMMs were performed in IBM SPSS Statistics Version 23. IBM SPSS Statistics Version 24 was used to calculate significant differences in species numbers.

As multivariate ordination technique, pRDA (partial redundancy analysis) was selected to represent linear combinations of the explanatory variables (EX, Yrs, EX\*Yrs). Axis 1 of the pRDA represented the interaction effect EX\*Yrs. Using the results of axis 1, trends of each species were deduced from polynomial and linear regressions in SigmaPlot 11.0 (Systat Software Inc. 2008) and R<sup>2</sup> for each species is given in Appendix A.

Mean Euclidian distance was calculated in CANOCO 5, using the first step of NMDS (non-metric multidimensional scaling) to create a distance matrix. Frequency means of exclosures and controls were compared to identify deviations per year.

### Results

Mean species numbers per 1 m<sup>2</sup> in 2014 were highest in the controls of the subalpine site S1 (31 species, Fig. 2), followed by the glacier foreland site S6 (ca. 27 species in the exclosure plots and 24 in the controls). Comparing the first and the last year, species richness changed in the exclosure plots, however, significant decreases were only found at S9 (p=0.047) and at S4 (weakly significant, p=0.055). With exception of the lower alpine site S3, all control plots

had an increase in species numbers, though being significant only at the subalpine site S1 ( $p=0.03$ ), at the upper alpine site S8 ( $p=0.016$ , Fig. 2) and weakly significant at the upper alpine site S9 ( $p=0.07$ ). The size of the exclusion areas (small vs. larger fenced areas; see Table 1) had no significant effect on the changes of species numbers ( $p=0.106$ ). According to GLMMs, highest significant overall effects of grazing exclusion and duration of exclusion ( $p<0.001$ ) on species richness and functional diversity occurred. Grazing exclusion (EX, Table 2) led to significant effects on species richness at S1, S5, S8 and S9. Shannon diversity significantly changed at S2, Evenness at S4 (Table 2). The interaction effect EX\*Yrs was significant at the sites S1, S5, S7 and S9 (Table 2).

At the subalpine grassland S1, winners of grazing exclusion were the forbs *Geranium sylvaticum* and *Viola biflora* (Appendix A). Several species decreased in frequency at S1, among them some graminoids such as *Phleum rhaeticum*, *Nardus stricta* and *Poa alpina*, legumes such as *Lotus corniculatus* and *Trifolium pratense* ssp. *nivale*, and the dwarf shrub *Vaccinium vitis-idaea* (Appendix A). At the lower alpine grasslands, winners were the Bryophyta at S2 and S4. Also several herbs increased, whereas cryptogams decreased. At the upper alpine grasslands, winners were different from one site to the other (for instance, *Phyteuma hemisphaericum* increased at S8, whereas it decreased at S9 under grazing exclusion, Appendix A). Grasses increased at S9 (*Anthoxanthum alpinum*, *Poa alpina*). Some snowbed species decreased at S7 and S9 (*Arenaria biflora*, *Mutellina adonidifolia*, *Sibbaldia procumbens*, Appendix A). At S5 and S6, only two to three species reacted to grazing exclusion, though in opposite directions (Appendix A).

Community changes, measured by the Euclidean distance between exclosure and control plots, were highest at S1, followed by S7 and S9 (Fig. 3). Considerable distances between exclosure and control plots were recognized at S1 from the third year, at S7 from the fourth year, at S9 from the fifth year onwards. All other sites showed fluctuations but lacked a pronounced deviation (Fig. 3).

The frequency of competitors (CCS) was significantly affected by grazing exclusion at S8 and S9 (Table 3). At S1, S2, S6, S7 and S9, the interaction EX\*Yrs gave significant results (Table 3). CSS's frequency was affected by exclusion at S2, S4, S5 and S8 (Table 3). SSS were hardly present and not affected; RSS changed significantly at the exclosures of S6; intermediate strategists (CSR) were influenced at the exclosures of S8 and S9 (Table 3). Considering potential plant height, tall species were significantly affected at the exclosures of S1, S2 and S8 (Table 3), their frequency increasing at the first two sites and decreasing at the latter one. Small plants' frequency increased at the exclosures of S4. At S1, S2 and S5, only the interaction EX\*Yrs resulted in significantly negative effects for small plants, whereas at S4, S7 and S9 an increase of this class occurred. Prostrate species' frequency was not affected by grazing exclusion, but the interaction EX\*Yrs revealed significant effects at S1, S2, S7, S8 and S9 (Table 3).

## Discussion

All in all, our first hypothesis could not be confirmed: there was no overall decrease of species diversity at the exclosure sites; only three out of nine sites showed a significant decrease; at one site (S5), diversity even increased significantly with time. At the subalpine zone (S1), grazing exclusion effects were detected earlier than at the upper alpine zone, i.e., already after three years of grazing exclusion in contrast to four and five years at S7 and S9, respectively. The continuously increasing canopy height at the subalpine site promoted shade-tolerant tall herbs such as *Geranium sylvaticum* whereas the frequencies of Bryophyta, two legumes, as well as of some Cyperaceae and Poaceae decreased. Among others, already Dupré and Diekmann (2001) revealed that in particular legumes benefitted from grazing,

probably due to the reduction of competitive tall species. Eskelinen and Oksanen (2006) also mentioned a decrease of graminoid species under grazing reduction. However, generalisations for all elevation zones of our study area regarding taxonomic or ecological groups are hardly possible. For instance, the Poaceae *Nardus stricta*, *Phleum rhaeticum* and *Poa alpina* decreased at the subalpine exclosures whereas *Poa alpina* and *Anthoxanthum alpinum* increased at some of the upper alpine exclosures. Thus, species-specific reactions occurred, depending on elevation and probably also caused by differences in grazing animals (cattle on S1, sheep on S7-S9) or varying local environmental conditions.

Contrary to our second hypothesis, no increase of dwarf shrub frequency was recorded at the subalpine exclosure S1; species such as *Vaccinium vitis-idaea* even decreased due to grazing exclusion. This result was surprising. We may speculate that soil moisture conditions and/or nutrient supply might have changed, promoting the tall forb *Geranium sylvaticum* instead of dwarf shrubs. The unexpected reaction may also be attributed to the fact that the competitive *Rhododendron ferrugineum* was not present at all at the permanent plots at the beginning of the research. Dwarf shrubs such as *Rhododendron* and *Vaccinium* spp. actually dominate in the study area on abandoned meadows but not at the exclosure plots. Generally, in the Eastern Central Alps a succession towards woody species and a reforestation occurred during the past decades on abandoned pastures (Tasser, Walde, Tappeiner, Teutsch & Nogler 2007). However, reforestation takes a long time in the study area (i.e., more than 50 years after abandonment), as was highlighted by Mayer, Nagl and Erschbamer (2012). In the exclosure plots no tree seedlings appeared so far.

Generally, under low temperatures or low soil fertility, grazing is expected to have less effects on functional diversity (Diaz, Cabido, Zak, Martínez Carretero & Aranibar 1999). At our study sites, some functional reactions to grazing exclusion were observed. Competitive species showed increasing trends in five of nine exclusion sites. As a consequence, small and/or prostrate species have decreasing trends on these sites. Competition for light is one of the decisive factors in grasslands (Jacquemyn, van Mechelen, Brys & Honnay 2011), driving seedling recruitment and survival of prostrate and/or small species. Our results are in line with the 'Competitive Exclusion Hypothesis' (Grime 1973), explaining that dominant competitors increase due to grazing exclusion, out-competing weaker strategists and provoking a decrease in species richness. In contrast, Pardo et al. (2015) did not find any modification of the strategy types in grassland exclusions of the Pyrenees. Similarly, effects were missing at our sites S3, S5 and S8.

At the upper alpine grassland S8, exclosure and control plots were particularly different at the beginning of the monitoring, although similar plots were chosen. This might be the explanation for the significant exclosure effect (Table 2) as species numbers did hardly change neither in grazed nor in exclosure plots. Here, *Carex curvula* dominates and creates a rather stable community (Grabherr 1987, 1989). Constant diversity was also modelled by Weiss and Jeltsch (2015) for moderately grazed, nutrient-poor communities of low altitudes. According to this model, time spans of 20 to 60 years of grazing cessation are necessary to provoke significant diversity changes. S9, with a rather similar plant community of *Carex curvula*, reacted strongly to grazing exclusion. We hypothesized that this could be an effect of the smaller exclosure area at this site, however, this was not confirmed statistically. Similarly to S7, S9 showed a reduction of some snowbed species. Several long term studies noticed that snowbed communities are transforming into alpine grasslands due to climate change (Matteodo, Ammann, Verrecchia & Vittoz 2016 and citations therein). It seems that grazing and climate change effects interact, impeding a proper interpretation of our results.

The increase in species numbers in most of the control plots along the whole elevation gradient can probably be explained by the overall increase in species richness found in the Alps during the last decades due to climate warming (Erschbamer, Unterluggauer, Winkler & Mallaun 2011; Gottfried, Pauli, Futschik, Akhaltkatsi, Barancok, Benito Alonso et al. 2012;

Pauli, Gottfried, Dullinger, Abdaladze, Akhaltkatsi et al. 2012; Wipf, Stöckli, Herz & Rixen. 2013; Unterluggauer, Mallaun & Erschbamer 2016). Exceptions of this trend were found at the lower alpine grassland sites S3. Here, grazer diversity was most diverse, probably levelling the effects due to warming. Similarly, also Matteodo et al. (2016) found hardly any climate change effects in subalpine-alpine grasslands.

At the bog S5 and the glacier foreland S6, hardly any trends of grazing exclusion effects on species richness were detectable. Species numbers increased within the fenced areas and outside. On these sites, grazing pressure was classified as low, grazers mainly passing here and then. The relatively sparse vegetation cover at the glacier foreland (ca. 67%, Raffl & Erschbamer 2004) and the nutrient-poor soil conditions might be responsible for the missing grazing effects. In the Southern Alps, Dainese, Scotton, Clementel, Pecile and Lepš (2012) found that soil and climate were even more important explanatory variables than grazing pressure in alpine communities. In addition, at the glacier foreland, primary succession (Raffl, Mallaun, Mayer & Erschbamer 2006) may overrule the grazing effect.

At the bog S5, species numbers increased at the exclosures and at the control plots (23% and 15% increase, respectively). Already Socher, Prate, Boch, Müller, Baumbach et al. (2013) mentioned that grazing abandonment on wetter soils does not lead to a decline in diversity. At S5, moist conditions and unpalatable Cyperaceae probably prevent any effects in the short term (9 years exclusion).

## **Conclusions**

From our study we infer that grazing exclusion effects along the investigated elevation gradient are not easy to interpret because plant communities, environmental conditions and grazers varied.

Our essential message is that (i) comparisons should be made within one plant community, for which an adequate quantity of plots have to be established; (ii) environmental conditions such as soil moisture, soil nutrients and microclimate should be measured at each site within and outside the exclosures; (iii) due to the slow species responses, exclosures in high elevations must be monitored for a long time; (iv) repeated monitoring (possibly each year or at least every three years) is essential, as Austrheim, Speed, Evju, Hester, Holand et al. (2016) pointed out recently.

## **<ACK>Acknowledgements**

The initial phase of the study was financially supported by the Environment Dept. of the Tyrolean Federal State Government. We highly acknowledge the funding by the Austrian Academy of Science (ÖAW, MAB Programme) and the Mountain Agriculture Research Unit/University of Innsbruck. We thank Ao.Univ.-Prof. Dr. Rüdiger Kaufmann who was one of the initiators of the monitoring project and we acknowledge the support by the Alpine Research Centre Obergurgl. We are grateful to two anonymous reviewer and Dr. Hövemeyer for their highly valuable comments.

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</BIBL>

# Captions of the figures:

<Figure>**Fig. 1.** Research area in Obergurgl (Ötztal, Tyrol, Austria) showing the nine study sites. Map

Source: © Orthofoto: Land Tirol – data.tirol.gv.at.

<Figure>Fig. 2. Mean species richness and standard errors (SE) for the exclusion plots (EX) and grazed controls (CO) of the nine sites in 2014.

<Figure>Fig. 3. Mean Euclidean distance ( $\pm$  standard error, SE) between exclusion (EX) and control plots (CO) at each of the nine study sites (S1-S9) in the course of the exclusion experiment. Note that some sites were sampled less often than others.

<Figure>Fig. 4: Ordinations of the sites S1 (1960 m a.s.l.), S9 (2650 m a.s.l.), S7 (2600 m a.s.l.) and S4 (2325 m a.s.l.) from 2000 to 2014. NMDS ordinations were rotated on PCA space (see methods).

<Figure>**Figure 5**

### Captions of the tables:

<Table>Table 1. Abbreviations of the investigated sites, elevation zones, plant community and dominant species, altitude, exclosure plot size and estimated grazing pressure (for further informations on grazer numbers and species see Materials and methods).

Sit e	Elevatio n zone	Plant community and dominant species	Altitud e m a.s.l.	Plot size m <sup>2</sup>	Grazing pressur e
S1	Subalpin e	Grassland - <i>Agrostis capillaris</i> , <i>Festuca rubra</i>	1960	140	very high
S2	Lower alpine	Grassland - <i>Nardus stricta</i> , <i>Anthoxanthum odoratum</i> , <i>Potentilla aurea</i>	2275	38	low-high
S3	Lower alpine	Grassland - <i>Nardus stricta</i> , <i>Anthoxanthum odoratum</i> , <i>Scorzoneroides helvetica</i>	2300	146	low-high
S4	Lower alpine	Grassland - <i>Nardus stricta</i> , <i>Poa alpina</i> , <i>Geum montanum</i>	2325	26	low-high
S5	Lower alpine	Bog - <i>Carex nigra</i> , <i>Eriophorum angustifolium</i>	2300	140	low
S6	Lower alpine	Glacier foreland - <i>Kobresia myosuroides</i> , <i>Poa alpina</i>	2300	140	low
S7	Upper alpine	Snowbed - <i>Carex curvula</i> , <i>Gnaphalium supinum</i> , <i>Mutellina adonidifolia</i>	2600	34	low-high
S8	Upper alpine	Grassland - <i>Carex curvula</i> , <i>Avenula versicolor</i>	2650	144	low-high
S9	Upper alpine	Grassland - <i>Carex curvula</i> , <i>Geum montanum</i>	2650	31	low-high

<Table>Table 2. Results of the GLMMs (p-values) at the sites for the effects of EX (exclosure), Yrs (years), and EX\*Yrs (interaction exclosure\*years) on species richness, Shannon diversity and Evenness. Numbers in bold show significant effects.

Attributes	Effects	S1	S2	S3	S4	S5	S6	S7	S8	S9
Species richness	EX	<b>0.002</b>	0.068	0.769	0.295	<b>0.011</b>	0.116	0.509	<b>0.037</b>	<b>&lt;0.001</b>
	Yrs	0.455	<b>0.002</b>	<b>0.029</b>	0.603	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	EX*Yrs	<b>0.006</b>	0.074	0.855	0.187	<b>0.004</b>	0.356	<b>0.043</b>	0.685	<b>0.004</b>
Shannon diversity	EX	0.135	<b>&lt;0.001</b>	0.931	0.146	0.225	0.103	0.821	0.009	0.415
	Yrs	0.896	<b>&lt;0.001</b>	<b>0.031</b>	0.914	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	EX*Yrs	<b>&lt;0.001</b>	0.163	0.078	<b>0.038</b>	0.278	0.289	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Evenness	EX	0.765	0.055	0.505	<b>0.047</b>	0.986	0.287	0.223	0.230	0.813
	Yrs	0.526	<b>0.018</b>	0.695	0.516	<b>0.003</b>	<b>0.002</b>	0.259	<b>&lt;0.001</b>	0.247
	EX*Yrs	<b>0.038</b>	0.108	<b>0.011</b>	0.541	0.418	0.576	<b>0.018</b>	<b>&lt;0.001</b>	<b>0.036</b>

<Table>Table 3. Results of the GLMMs (p-values) at the nine sites for the effects of EX (exclosure), Yrs (years), and EX\*Yrs (interaction exclosure\*years) on the frequency of C-S-R-strategies (CCS = competitors, CSS = stress-tolerant competitors, SSS = stress-tolerators, RSS = ruderal stress-tolerators, CRS = intermediate strategists) and plant height classes (tall, small, prostrate plants). Significant effects in bold.

Functional types	Effects	S1	S2	S3	S4	S5	S6	S7	S8	S9
CCS	EX	0.425	0.422	0.875	0.061	0.225	0.275	0.266	<b>0.006</b>	<b>&lt;0.001</b>
	Yrs	<b>&lt;0.001</b>	0.159	<b>0.013</b>	0.751	0.150	0.184	0.054	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	EX*Yrs	<b>&lt;0.001</b>	<b>0.013</b>	0.448	0.665	0.529	<b>0.003</b>	<b>0.001</b>	0.655	<b>&lt;0.001</b>
CSS	EX	0.211	<b>0.001</b>	0.177	<b>0.021</b>	<b>0.032</b>	0.948	0.771	<b>0.005</b>	0.249
	Yrs	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.001</b>	<b>0.001</b>	<b>0.010</b>	<b>&lt;0.001</b>	0.201	<b>0.029</b>	<b>&lt;0.001</b>
	EX*Yrs	0.421	<b>&lt;0.001</b>	0.331	<b>0.005</b>	0.095	0.145	<b>0.002</b>	0.644	<b>0.033</b>
SSS	EX	-	-	-	-	0.560	-	-	-	-
	Yrs	-	-	-	-	0.341	-	-	-	-
	EX*Yrs	-	-	-	-	0.819	-	-	-	-
RSS	EX	-	-	-	-	-	<b>0.032</b>	0.245	-	-
	Yrs	-	-	-	-	-	<b>0.003</b>	<b>0.039</b>	-	-

	EX*Yrs	-	-	-	-	-	0.374	<b>0.020</b>	-	-
CRS	EX	0.266	0.514	0.238	0.725	0.245	0.881	0.297	<b>0.002</b>	<b>0.020</b>
	Yrs	0.295	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.067	0.161	<b>0.002</b>	<b>0.002</b>	<b>&lt;0.001</b>	<b>0.004</b>
	EX*Yrs	<b>0.014</b>	<b>0.001</b>	0.858	0.218	0.105	0.717	0.461	0.547	0.228
Tall plants	EX	<b>0.028</b>	<b>0.015</b>	0.347	0.576	0.252	-	0.283	<b>&lt;0.001</b>	-
	Yrs	<b>&lt;0.001</b>	0.977	<b>0.001</b>	0.945	<b>&lt;0.001</b>	-	<b>0.038</b>	<b>&lt;0.001</b>	-
	EX*Yrs	<b>&lt;0.001</b>	0.894	0.268	0.679	<b>0.009</b>	-	0.815	<b>&lt;0.001</b>	-
Small plants	EX	0.324	0.500	0.765	<b>0.001</b>	0.684	0.494	0.623	0.101	0.850
	Yrs	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.003</b>	<b>0.004</b>	0.162	<b>&lt;0.001</b>	0.706	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	EX*Yrs	<b>0.033</b>	<b>0.021</b>	0.308	<b>0.005</b>	<b>0.041</b>	0.943	<b>&lt;0.001</b>	0.775	<b>&lt;0.001</b>
Prostrate plants	EX	0.539	0.925	0.681	0.547	0.914	0.495	0.348	0.349	0.850
	Yrs	0.248	<b>&lt;0.001</b>	<b>0.043</b>	<b>0.024</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.079	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	EX*Yrs	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.488	0.993	0.162	0.944	<b>&lt;0.001</b>	<b>0.013</b>	<b>&lt;0.001</b>

<Table>Table 5: Results of the pRDA and Monte Carlo Permutation tests at the sites and subsites, respectively, for plant height. Trends were deduced from regressions:  $R^2 > 0.200$  are given by arrows ( $\uparrow$  = linearly increasing,  $\downarrow$  = linearly decreasing), all other  $R^2$  are given as x; n = not abundant. Given are Eigenvalues of pRDA axis 1, adjusted explanation in % (Expl. % F-value and adjusted p-value. T = tall plants, S = small plants, P = prostrate plants.

Site	Subsite	N	Eigenvalue axis 1	Expl % (adj.)	F	p-value (adj.)	T	S	P
S1		6	0.0821	28.5	15.9	<b>0.0125</b>	$\uparrow$	x	$\downarrow$
S5		18	0.0016	0.6	0.9	0.2395	x	x	x
	S5-1	6	0.0104	2.9	1.6	0.1455	x	x	x
	S5-2	6	0.0097	1.6	0.8	0.3125	x	x	x
	S5-3	6	0.0034	0.4	0.2	0.6990	x	x	x
S7		18	0.0036	5.2	8.7	<b>0.0035</b>	x	x	x
	S7-1	6	0.0185	5.4	2.9	0.0775	x	x	x
	S7-2	6	0.0639	15.7	9.7	<b>0.0095</b>	n	$\uparrow$	$\downarrow$
	S7-3	6	0.0615	16.6	10.3	<b>0.0005</b>	x	$\uparrow$	$\downarrow$

S4b		6	0.0026	1.3	0.5	0.3615	n	x	x
RC		6	0.0239	22.6	6.4	0.1160	x	↓	x

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