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Development of the vegetation after abandonment of a sheep summer pasture in subalpine and alpine meadows in Amden (St. Gallen, Switzerland) **over 23 years**

CAS-Arbeit

von
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Abstract

In Amden, canton of St. Gallen in Switzerland, a summer pasture was abandoned in the year 2000. Those subalpine and alpine meadows were before intensively grazed by sheep. Permanently marked plots were installed in 1995 and expanded in 2000 in different vegetation types and altitudes across the pasture area. Relevés were done from 1995 until 2018 on a regular basis. This data was used to investigate how fast the vegetation was changing after summer pasture abandonment, how the different vegetation types react and if the abundance of the species changes over time. For one vegetation type (*Crepido-Festucetum rubrae* vegetation) a significant decline in species richness was detected between 2000 and 2018. Less significant changes were detected for further three vegetation types and no change in species richness was found in *Rumicetum alpinae* vegetation. The analysis of vegetation parameters showed an increase in litter cover and a decrease in in uncovered soil for all plots. The vegetation got over all denser and grew taller in the observed plots. Again, strong changes were observed in *Crepido-Festucetum rubrae* vegetation with a significant increase of herb cover between 1999 and 2018. The analysis of the overall species list revealed a significant decrease of the frequency of 10 species and a significant increase of the frequency of two species between 2000 and 2018 whereas *Rhinanthus alectorolophus* (increase in frequency) and *Poa annua* (decrease in frequency) showed the most significant changes. These results suggest that the studied vegetation types in subalpine and alpine grasslands react very slowly to a change of grazing regime in terms of composition and biodiversity. This underlines the importance of an adjusted grazing management of subalpine and alpine grasslands. Different vegetation types are differently sensible to grazing and overgrazed sites might take decades to recover. However, an extensive summer pasture might be beneficial for the biodiversity of subalpine and alpine regions.

1. Introduction

During the last decades, more and more grazing sites of supalpine and alpine meadows are abandoned in Switzerland since the importance of agricultural use of those grasslands is decreasing (Koch, et al., 2013). Grazing has a main influence on a vegetation and its composition (Landolt, et al., 2003; Wiesmair, et al., 2017). The effect of grazing on the plant biodiversity is in general expected to depend on its intensity – an intermediate grazing level should result in the highest plant diversity (Dullinger, et al., 2003; Pulungan, et al., 2019). However, the plant diversity of a meadow is also influenced by other factors as grazing frequency, abiotic factors, vegetation type and productivity of the site (Koerner, et al., 2018; Rodríguez, et al., 2018). How fast and how drastically a vegetation is changing after alternation or abandonment of grazing depends therefore on various factors. Understanding the effect of agricultural grazing at alpine and supalpine meadows on biodiversity is essential for a conservation management of a region (Fragnière, et al., 2022). The importance of this understanding is increasing since more abandoned grazing sites can be expected in remote alpine areas (Dengler & Tischew, 2018).

Semi-natural grasslands in alpine regions are a hotspot of biodiversity (Dengler, et al., 2014). Small and patchy habitats are formed by differences in geology, climate, and exposition creating a wide range of different niches with specialized plant species. In the Alps, these habitats are often altered by human land use such as logging and grazing. Those human activities have a long tradition in these regions and influence the grassland biodiversity (Fischer, et al., 2008). Although the agricultural dependence on summer pastures is decreasing, it is still an important factor for alpine regions. In Switzerland, this traditional grazing is federally subsidised and the number of livestock on those summer pastures was stable during the past few years (BLW, 2022).

The effect of grazing on a plant community and on the biodiversity in high elevation depends on various factors and is therefore not easy to study. This explains that no unequivocal evidence on the impact of grazing can be found in literature. A study on alpine grassland suggests a clear influence of sheep grazing on vegetation composition, but no major negative effect on biodiversity along a 19-year chronosequence of grazing (Widmer, et al., 2020). They assumed a very slow respond of alpine grasslands to changes of the grazing regime. The effect of grazing on a plant community strongly depends on the affected vegetation type (Kurtogullari, et al., 2020). As a result, plant habitats react differently on pasture abandonment. On large scale, a long-term decline of species diversity is suggested due to a homogenization of the vegetation cover (Dullinger, et al., 2003). In semi-natural meadows, this loss in biodiversity can be restored by reinducing an extensive grazing management (Hellström, et al., 2003). In summer pastures, a moderate intensity management can maintain a high plant diversity (Strebel & Bühler, 2015). On the contrary, overgrazing seems to be a main thread to high elevation grasslands (Fragnière, et al., 2022; Wang, et al., 2019). The slow regeneration rate of alpine plants results in a high sensitivity to depletion and can lead to a reduced vegetation cover, soil erosion and a loss in biodiversity.

For the following work, vegetation surveys of the Amden region in Switzerland were used. This area was formerly intensely grazed by sheep during summertime. Up to 600 animals were grazing each season on the summer pastures Schafberg Leist and Alp Vorderleist (Gilgen, et al., 2003). In the 1990ies, game animals caused heavy damage on young trees in the downhill located protective forest. This situation let to the decision to change the sheep grazing regime. Grazing was reduced in 1994 and finally abandoned in 1999 to promote the migration of chamois and deer out of the forest to their natural foraging environment. Since 1996, the vegetation at permanently marked plots were regularly observed at 26 different sites representing different vegetation types (Schafberg Leist). Another eight permanently marked plots were added in 2000 (Alp Vorderleist). An extensive report on these vegetation surveys was made in 2003 (Gilgen, et al., 2003). Since then, no statistical analysis of the data set was done. This unique data allows to assess the following questions: How fast does the vegetation change after sheep grazing abandonment? Do the different vegetation types change in a different manner? Does the abundance of the present species change over time?

2. Methods

2.1. Study site

The plots 1 to 26 are located at the former summer pasture area of Schafberg underneath Leistchamm in the community of Amden (St. Gallen, Switzerland). The area is a natural terrain unit that spreads over 0.63 km^2 and is mainly orientated in direction of northwest to northeast. The lowest plot is at 1330 m.a.s.l. and the highest is located 2101 m.a.s.l. Geologically, the study area is characterized by limestone (Funk, et al., 2020) and partly quite cliffy. The annually precipitation in this region is between 2000 and 2500 mm per year (Meteoschweiz, 2022).
An additional set of eight plots (27 to 34) were added in the year 2000 at the neighbouring site Vorderleist in the community of Alt St. Johann (St. Gallen, Switzerland). This area is 0.45 km^2 in size and comparable with the first one in terms of steepness, exposition, climatic condition, and altitude of the plots with a range from 1420 to 2100 m.a.s.l. Besides the limestone, this additional area is shaped by a historical landslide (Funk, et al., 2020). In contrast, this side was never as intensely grazed as the Schafberg. Additionally, Schafberg is a hunting ban area whereas hunting is allowed at the site Vorderleist (see figure 1).

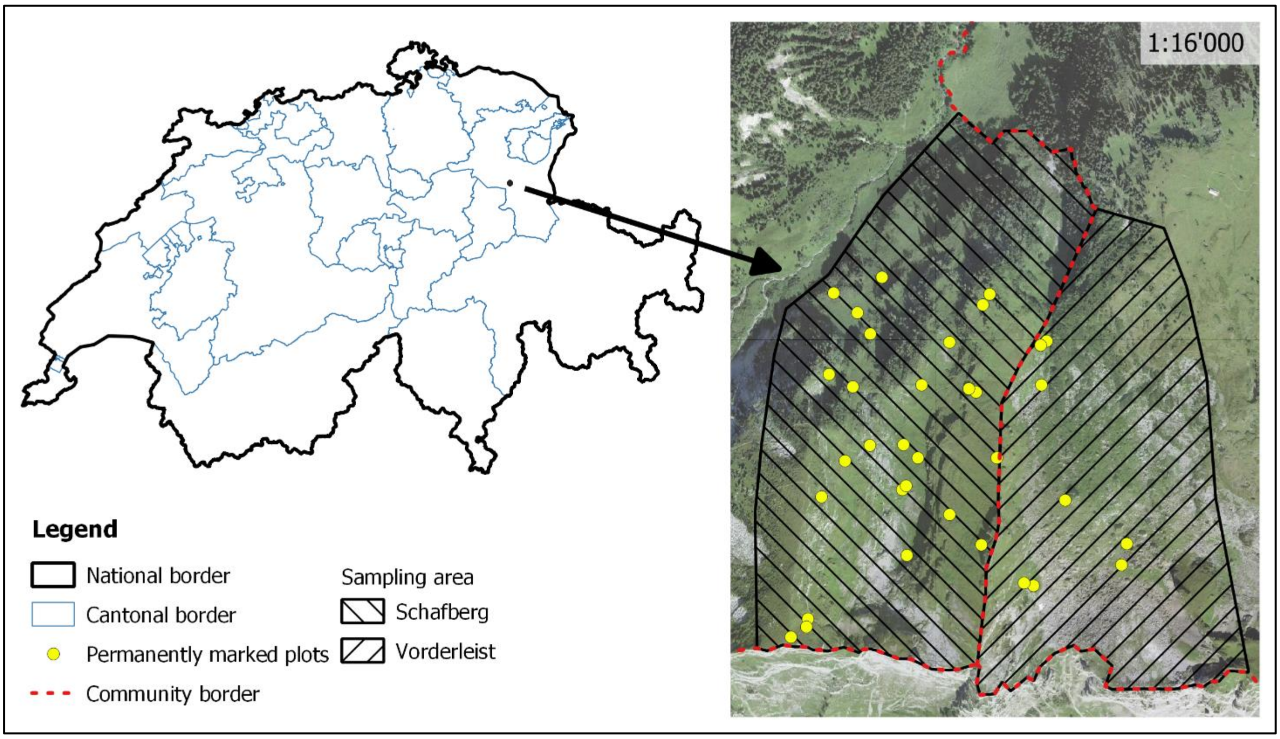

Figure 1: Sampling area Schafberg (plots 1 to 26) and Vorderleist (plots 27 to 34) in canton of St. Gallen, Switzerland. Background: Swissimage 2019, Geodaten © swisstopo (DV084370)

2.2. Field sampling

For each plot a square of 2 x 2 m was permanently marked with large metal nails in each corner to relocate the plots with the aid of a metal detector. Detailed drawings of the surrounding area were done and precise distances to landmarks were taken. A modified version of the cover-abundances scale of Braun-Blanquet (Braun-Blanquet, 1964) was used to estimate the abundance of each vascular plant species found in each plot (see appendix 1). Starting in 1995, relevés were done regularly (see table 1).

Table 1: Sampling frequency of the permanently marked plots at Schafberg (plot 1 - 26) and at Vorderleist (plot 27 - 34)

	1995 [1)]	1996	1997	1998	1999	2000	2001	2002	2004 [1)]	2006	2010/11 [2)]	2018
Plot 1 - 26	x	x	x	x	x	x	x	x	x	x	x	x
Plot 27 - 34						x	x	x	x	x	x	x

[1)] incomplete data set, was excluded in the data analysis.
[2)] data set had to be completed in the following year.

For each plot exposition, altitude and inclination was recorded. The cover of different vegetation layers (herbs, mosses, litter as well as uncovered soil) was also estimated in percent. The total cover of the vegetation at four different height levels was also estimated in percent: the upper layer (above 50 cm), the middle layer (between 25 and 50 cm), the lower layer (between 5 and 25 cm) and the ground layer (between 0 and 5 cm).

Each plot was mapped to a plant sociological association or sub association according to Oberdorfer (Oberdorfer, 1983; Oberdorfer, 1992a; Oberdorfer, 1992b; Oberdorfer, 1993). Additionally, plant sociological mapping was done according to an adjusted mapping key for the entire Schafberg region (data not shown see Gilgen, et al., 2003).

2.3. Data analysis and statistics

The taxonomy of all plant names in the vegetation relevés were checked and if necessary, adjusted to the actual reference for Swiss vascular plant taxa ‘Checklist 2017’ (Juillerat, et al., 2017). The Braun-Blanquet-scale was transformed into percentages using where applicable the arithmetic means of the borders of the Braun-Blanquet classes (see appendix 1). The Software VEGEDAZ (Küchler, 2022) was used to calculate mean cover-weighted indicator values for temperature, continentality, light, humidity, reaction value, nutrients and humus (Landolt, et al., 2010) for each plot. The supervised classification implemented in VEGEDAZ (Küchler, 2022) was used to compare the matching between the different types of Swiss habitat typology (Delarze, et al., 2015; Dengler, et al., 2019), the Jaccard coefficient and the mapped plant sociological association in the field for each plot in the year 2000. The plots were grouped into five different vegetation types (see table 2) based on the superior plant association (associations of *Crepido-Festucetum rubrae*, *Rumicetum alpinae* and *Seslerio-Caricetum sempervirentis),* on vegetation structure (shrub dominated vegetation with *Rhododendron*) or high nutrition conditions (Nutritious lawn and meadow vegetation).

All the following statistical analysis were performed in R (R CORE TEAM, 2021) within the RStudio environment (RStudio Team, 2021). The function ‘specnumber’ and ‘diversity’ of the package ‘vegan’ (Oksanen, et al., 2018) were used to calculate species richness and the diversity indices of Shannon and evenness for all plots in each recoded year.
DCA ordination of plots for the year 2000 and 2018 were conducted with the function ‘decorana’ of the package ‘vegan’ to visualize the vegetation communities (Oksanen, et al., 2018). This ordination method was chosen since the gradient length of the primary axis of the DCA was more than four standard deviations (Leyer & Wesche, 2007). The mean indicator values for humidity,

nutrients, and light, as well as altitude and exposition were correlated with axis of the ordination graph. The ordination was also used to validate the grouping into five vegetation types.

For all the following ANOVA analysis, normal distribution and variance homogeneity of the residuals was examined visually by model diagnostics and boxplots beforehand.
The differences in diversity (richness, Shannon, and evenness) between the distinguished vegetation types and the recorded years were tested with two-factor ANOVAs (year and vegetation type as factor, plot ID as error term). The groups with plots 1 to 26 and plots 1 to 34 were analysed separately since vegetation relevés from 1996 to 1999 were only available in the first group (see table 1). Following, each vegetation type and each year was analysed separately with one-factor ANOVAs (year and vegetation type separately). The significant results were further analysed by Tukey's post hoc test with the function 'HSD.test' of the package 'agricolae' (de Mendiburu, 2019).

The vegetation parameters (vegetation layers of herbs, mosses, litter, and uncovered soil) as well as the total cover of the vegetation at four different height levels were also tested for significant differences between the vegetation groups and years. An arcsine square root transformation ($\sin^{-1}\sqrt{x}$) was used to improve the model diagnostic of these percentual data (Quinn & Keough, 2002). Two-factor ANOVAs were run for the mentioned dependent variables and the sampled years and the five distinguished vegetation type (ANOVA with year and vegetation type as factor, plot ID as error term). All significant results were further analysed by a one-factor ANOVA of the significant factor followed by Tukey's post hoc test with the function 'HSD.test' of the package 'agricolae' (de Mendiburu, 2019).

Finally, the change of frequency of the species in all plots were tested by a sign test (binomial test). For this test, an adjusted species list was used (without insecure species determination, aggregation to higher taxonomic level) and the abundance was converted in presence and absence. The relevés of the year 2000 were compared with those of the year 2018 to identify species with a significant change in its frequency. The relevés of the year in between were used to test after which year a significant change is observable for those species.

3. Results

Five groups of vegetation types were aggregated based on the plant sociological mapping (Oberdorfer, 1992a; Oberdorfer, 1992b; Oberdorfer, 1993) done during the first relevé and the matching of the supervised classification in VEGEDAZ for the relevés of the year 2000 (see appendix 2).

Table 2: Grouped vegetation types according plant sociological mapping of all plots during first relevé.

Vegetation types	Included plant sociological association (A) or sub association (S)	Plot ID
Crepido-Festucetum rubrae vegetation **'CF'** ("Milchkrautweiden")	– *Crepido-Festucetum rubrae* (A) – *Crepido-Festucetum rubrae* with snow valley species (S)	3, 4, 5, 9, 11, 22, 23, 27, 28, 29, 30, 31, 33
Rumicetum alpinae vegetation **'RA'** ("Alpenampfer- & Alpenkreuzkrautflur")	– *Rumicetum alpini typicum* (S) – *Rumicetum alpini senecionetosum alpine* (S)	1, 2, 10, 16, 26
Seslerio-Caricetum sempervirentis vegetation '**SC**' ("Blaugrasrasen")	– *Seslerio-Caricetum sempervirentis* (A) – Combinations of *Seslerio-Caricetum sempervirentis* (A) and *Crepido-Festucetum rubrae* (A) or *Alchemillo-Deschampsietum caespitosi* (A)	6, 14, 18, 19, 25, 32, 34
Nutritious lawn and meadow vegetation '**NM**' ("nährstoffreiche Flur- & Rasenvegetationen")	– *Alchemillo-Deschampsietum caespitosi* (A) – *Alchemillo-Poetum supinae* (A) – *Festuco-Agrostietum* (A)	7, 13, 15, 17, 21, 24
Rhododendron vegetation '**RE**' ("Alpenrosengebüsche")	– *Rhododendro ferruginei-Vaccinietum* (A) – *Erico-Rhododendretum hirsuti* without *Pinus mugo* (S)	8, 12, 20

A DCA ordination for the five vegetation types was done for the relevés of the year 2000 and for those of the year 2018 (see figure 2). The first axis explains 12.8% and the second axis explains 11.9% of the variation of species composition in 2000. In 2018, the first and second axis explain 12.6% and 8.8% of the variation. The plots with *Rumicetum alpine* vegetation (RA) of the year 2000 are well separated from the other plots. All the other plots of this year are not as clearly isolated and have overlapping areas. In 2018, the plots with *Seslerio-Caricetum sempervirentis* and *Rhododendron* vegetation tend to be more separated compared to the corresponding relevés in 2000. Environmentally variables were fitted post hoc to the two axes and revealed a strong significance for indicator value of light (r^2=0.4180, p=0.001), humidity (r^2=0.6694, p=0.001) and nutrients (r^2=0.9133, p=0.001). Elevation was only slightly significant (r^2=0.1356, p=0.056) and exposition is not significant correlated the axis of the DCA.

The ANOVA of vegetation types and diversity followed by Tukey's post hoc test revealed a significantly higher richness of the *Seslerio-Caricetum sempervirentis* vegetation compared to the other distinguished vegetation types in the year 2000 ($p \leq 0.034$, see Figure 3).

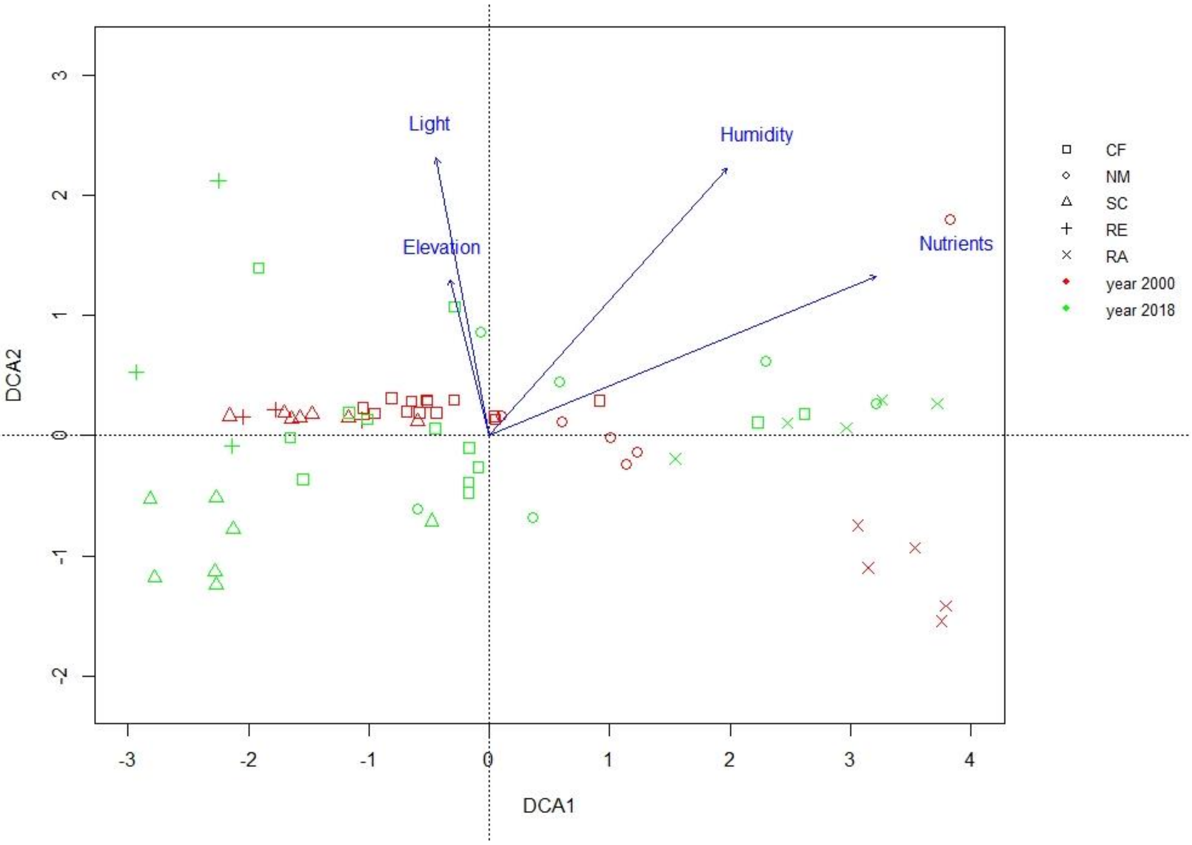

Figure 2: Joint detrended correspondence analysis (DCA) of the old and new plots differentiated into the vegetation types. CF: *Crepido-Festucetum rubrae* vegetation, NM: Nutritious lawn and meadow vegetation, SC: *Seslerio-Caricetum sempervirentis* vegetation, RE: *Rhododendron* vegetation, RA: *Rumicetum alpinae* vegetation. Red symbols represent relevés of year 2000, green symbols those of 2018. Significantly correlated variables were fitted post hoc to the two axes.

On the contrary, *Rumicetum alpine* vegetation had a significantly lower diversity in terms of richness and Shannon-Index compared to vegetation types ($p \leq 0.048$) except for Nutritious lawn and meadow vegetation. These differences in diversity between the vegetation types diminished partly in the year 2018. Richness and the Shannon-Index of the *Seslerio-Caricetum sempervirentis* vegetation were still significantly higher to most of the other vegetation types ($p \leq 0.045$) but the significant difference to *Rhododendron* vegetation disappeared. The *Rumicetum alpinae* vegetation had for all diversity indices no significant differences any more compared to all the other vegetation types except for the *Seslerio-Caricetum sempervirentis* vegetation ($p<0.001$ for richness and Shannon-Index, $p=0.049$ for evenness).

The two-factor ANOVA with year and vegetation type as factors showed significant differences for the vegetation type, the year as well as the interaction of year and vegetation type for both groups of plots (plots 1 - 26 and 1 - 34) for all three diversity indices (see table 2). Over time, in *Crepido-Festucetum rubrae* vegetation a significant lower richness in 2011 and 2018 was detected compared to the other years ($F_{5,72}=7.81$, $p<0.001$ for plots 1 - 26, post-hoc Tukey HSD tested). The relevés starting from the year 2000 were analysed for each year separately to further identify the differences in diversity between the five vegetation types (one-way ANOVA with post-hoc Tukey HSD tests). The richness of *Seslerio-Caricetum sempervirentis* vegetation 'SC' was significantly higher compared to all other vegetation types in all sampled years except for the last relevé in 2018, where the difference in richness to *Rhododendron* vegetation disappeared.

Rumicetum alpinae vegetation ‘RA’ had the significantly lowest richness compared to most of the other vegetation types. However, the difference in richness to Nutritious lawn and meadow vegetation ‘NM’ was not for all sampled years significant. Shannon and evenness showed a similar pattern but with less significant differences between the vegetation types (see figure 3 and appendix 3).

Table 2: Results (*F*- and *p*-value) of two-factor ANOVA analysis (year* vegetation type + Error (plot ID)) for the diversity indices richness, Shannon, and evenness. The analysis was done for the plot sets 1 - 26 and 1 - 34 separately.

Plot groups	Factor	Statistics	Richness	Shannon	Evenness
plots 1-26	vegetation type	$F_{4,21}$	19.82	10.08	4.22
		p	<0.001 ***	<0.001 ***	0.012 *
	year	$F_{9,189}$	6.48	8.48	5.33
		p	<0.001 ***	<0.001 ***	<0.001 ***
	interaction	$F_{36,189}$	2.48	3.09	1.91
		p	<0.001 ***	<0.001 ***	0.003 **
plots 1-34	vegetation type	$F_{4,29}$	28.46	16.68	7.68
		p	<0.001 ***	<0.001 ***	<0.001 ***
	year	$F_{5,145}$	4.90	18.31	13.18
		p	<0.001 ***	<0.001 ***	<0.001 ***
	interaction	$F_{20,145}$	2.37	3.80	2.91
		p	0.002 **	0.002 **	<0.001 ***

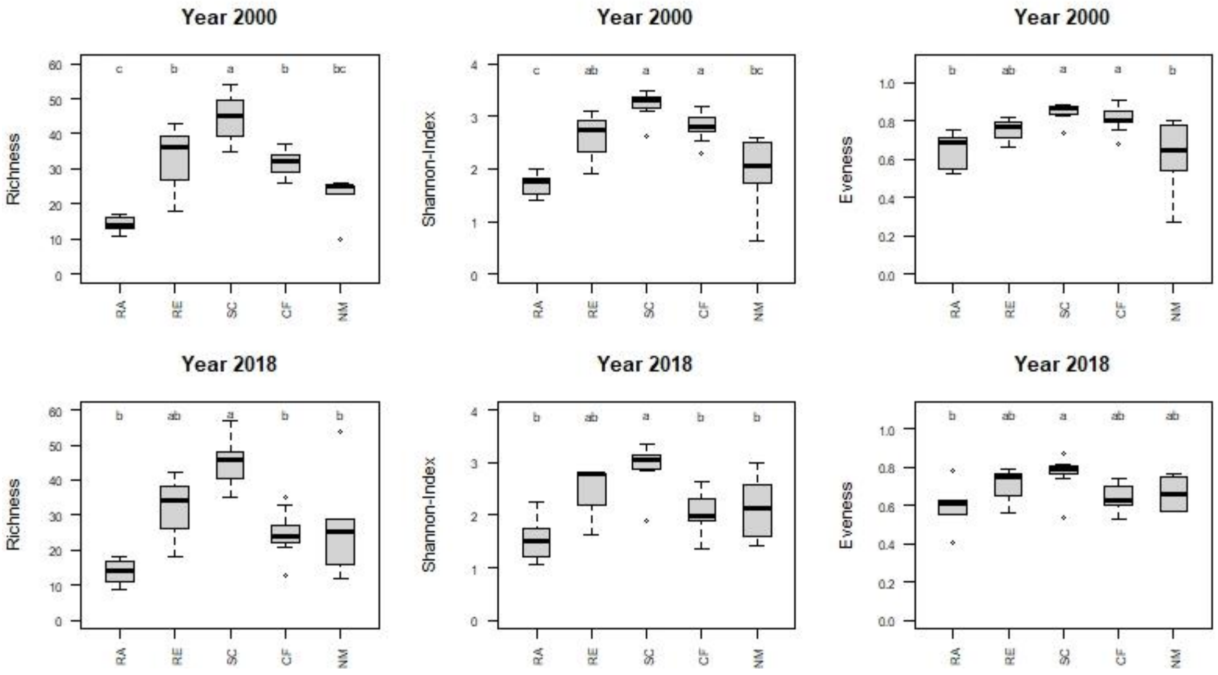

Figure 3: Diversity (richness, Shannon, and evenness) of the different vegetation groups in the year 2000 and 2018. CF: *Crepido-Festucetum rubrae* vegetation, NM: Nutritious lawn and meadow vegetation, SC: *Seslerio-Caricetum sempervirentis* vegetation, RE: *Rhododendron* vegetation, RA: *Rumicetum alpinae* vegetation. Letters indicate result of Tukey HSD tests (significance 95%).

Table 3: Results (*F*- and *p*-value) of ANOVA analysis of richness with year as factor (richness~year + Error (plot ID)) for each vegetation type (CF: *Crepido-Festucetum rubrae* vegetation, NM: Nutritious lawn and meadow vegetation, SC: *Seslerio-Caricetum sempervirentis* vegetation, RE: *Rhododendron* vegetation, RA: *Rumicetum alpinae* vegetation). The analysis was done for the plot sets 1 - 26 and 1 - 34 separately.

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Vegetation type	**Plots 1 - 26**		**Plots 1 - 34**	
	***F*-value**	***p*-value**	***F*-value**	***p*-value**
CF	$F_{9,54}$=8.837	<0.001 ***	$F_{5,60}$=11.75	<0.001 ***
RA	$F_{9.36}$=0.994	0.462	$F_{5,20}$=1.236	0.329
SC	$F_{9,36}$=3.364	0.004 **	$F_{5,26}$=1.362	0.271
NM	$F_{9,45}$=2.177	0.042 *	$F_{5,25}$=1.1	0.385
RE	$F_{9,18}$=2.479	0.048 *	$F_{5,10}$=2.737	0.082

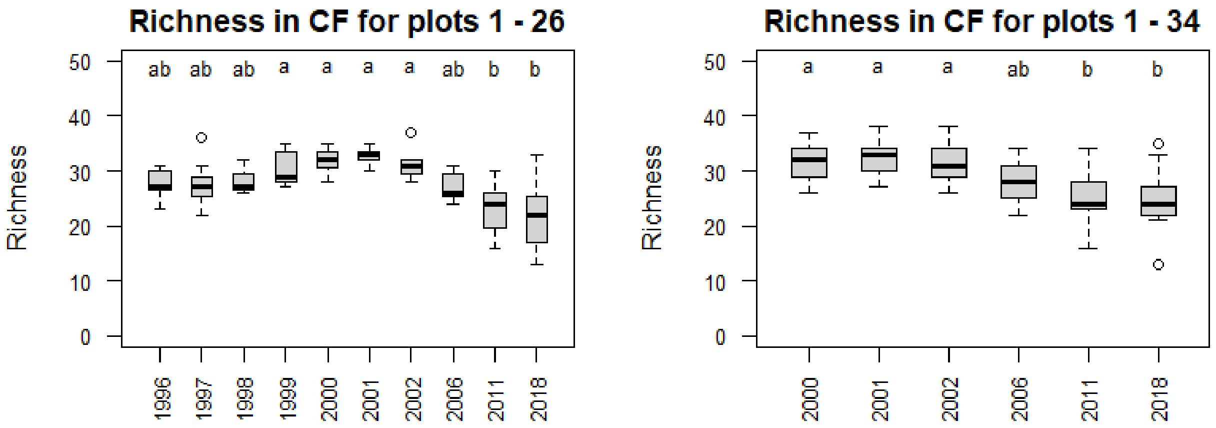

Figure 4: Richness of *Crepido-Festucetum rubrae* vegetation (CF) calculated for the two plot groups separately (plots 1 - 26 for relevés 1996 - 2018 and plots 1- 34 for relevés 2000 - 2018). Letters indicate result of Tukey HSD tests (significance 95%).

Further one-way ANOVAs were performed to identify significant differences in richness and the different sampled years within each vegetation type. Those results revealed for the *Crepido-Festucetum rubrae* vegetation the strongest significance whereas *Rumicetum alpinae* vegetation had no significant differences throughout the sampled years (see table 3).
A post-hoc analysis for the *Crepido-Festucetum rubrae* vegetation showed that the richness in the sampled years 2000, 2001 and 2002 was significantly higher than the richness sampled during the relevés in 2011 and 2018 (see figure 4).

The two-factor ANOVA analysis of arcsine transformed cover of herb, moss, and litter as well as uncovered soil showed in most cases significant differences in the year of the relevé (except for herb and moss cover for plots 1 - 34, see table 4). The interaction between year and vegetation type was also in most cases significant. Significant differences between vegetation type were for plots 1 – 26 only for the arcsine transformation of uncovered soil detected. For plots 1 – 34, the vegetation type was in most cases significant (see table 4 for details).
Detailed analysis of the arcsine transformed herb cover showed only for the vegetation type of *Crepido-Festucetum rubrae* for the plots 1 – 26 and year ($F_{9,60}$=3.12, *p*= 0.004) a significant difference between 1999 and 2018 (post-hoc Tukey HSD *p* adjusted = 0.040). The analysis of the arcsine transformed moss cover could not detect further significant differences in year nor

Table 4: Results (*F*- and *p*-value) of ANOVA analysis of arcsine transformed cover of herb, moss, and litter as well as uncovered soil (~vegetation type * year + Error (plot ID)). The analysis was done for the plot sets 1 - 26 and 1 - 34 separately.

Plot groups	Factor	Statistics	herb cover	moss cover	litter cover	uncovered soil
plots 1-26	vegetation type	$F_{4,21}$	2.11	0.29	0.87	8.84
		p	0.115	1.349	0.501	<0.001 ***
	year	$F_{9,189}$	4.37	2.91	42.52	9.53
		p	<0.001 ***	0.003 **	<0.001 ***	<0.001 ***
	interaction	$F_{36,189}$	1.90	3.10	2.373	3.04
		p	0.003 **	<0.001 ***	<0.001 ***	<0.001 ***
plots 1-34	vegetation type	$F_{4,29}$	6.21	2.71	2.51	8.42
		p	<0.001 ***	0.049*	0.064	<0.001 ***
	year	$F_{5,145/165}$ 1)	0.46	0.92	34.79	7.41
		p	0.087	0.47	<0.001 ***	<0.001 ***
	interaction	$F_{20,145}$	-	2.48	3.54	3.53
		p	-	0.001 **	<0.001 ***	<0.001 ***

1) Second value for residuals indicates value without interaction

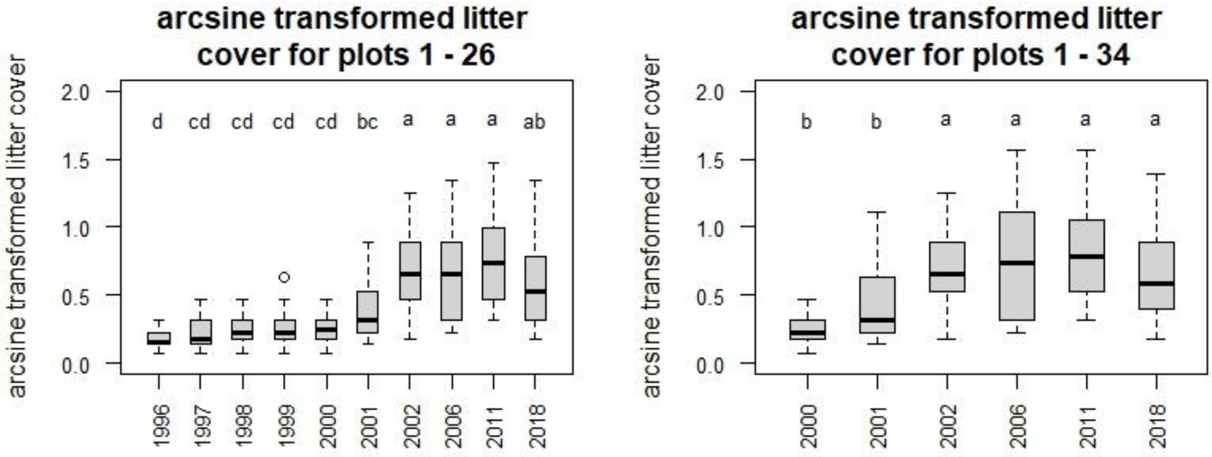

Figure 5: Arcsine transformed litter cover for plots 1 - 26 and 1 - 34. Letters indicate result of Tukey HSD tests (significance 95%).

in the different vegetation types. Litter cover in contrast increased significantly over the years of study indifferent of the vegetation type (see figure 5).

The arcsine transformed cover of uncovered soil differed significantly between the years 1999 and 2018 for plots 1 – 26 and between 2000 and 2018 for the plots 1 – 34. The arcsine transformed cover of uncovered soil and the vegetation types showed significant differences between *Rumicetum alpinae* vegetation, *Seslerio-Caricetum sempervirentis* vegetation and *Crepido-Festucetum rubrae* vegetation. The *Rumicetum alpinae* vegetation had the highest value for uncovered soil which was significantly higher than all other vegetation types (see figure 6).

The two-factor ANOVA analysis of arcsine transformed cover of the different vegetation layers (ground layer: 0 - 5 cm, lower layer: 5 – 25 cm, middle layer: 25 – 50 cm, upper layer: 50 – 120 cm) showed in all cases significant differences for the year of the relevé as well as for the vegetation type (see table 5). The interaction between year and vegetation type was in all cases

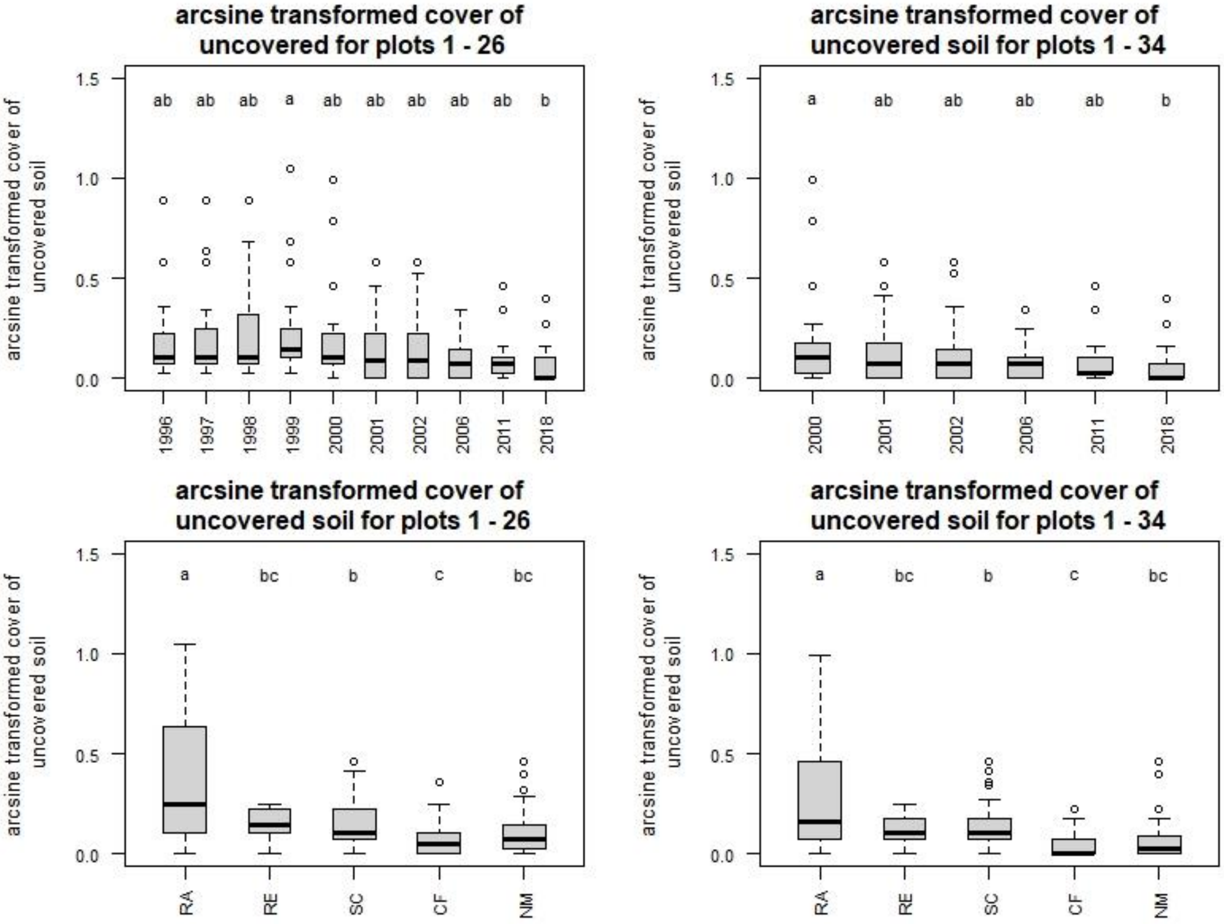

Figure 6: Arcsine transformed cover for uncovered soil in plots 1 - 26 and 1 - 34. Year of relevé and vegetation type was analysed in separately. CF: *Crepido-Festucetum rubrae* vegetation, NM: Nutritious lawn and meadow vegetation, SC: *Seslerio-Caricetum sempervirentis* vegetation, RE: *Rhododendron* vegetation, RA: *Rumicetum alpinae* vegetation. Letters indicate result of Tukey HSD tests (significance 95%).

significant for the ground and lower layer. No significance was detected for the interaction in the middle layer. For the upper layer it was only significant for plots 1 – 26 (see table 5).

Detailed analysis of the arcsine transformed ground layer showed that the year had a significant influence on its cover ($F_{9,250}$=3.53, p=<0.001) with a significant lower value in 2018 compared to the years before 2011 (post-hoc Tukey HSD p adjusted = 0.006 and lower) in plots 1 – 26. The analysis of the vegetation type revealed for *Rumicetum alpinae* vegetation a significant lower value than for most other vegetation types ($F_{4,199}$=7.74, p<0.001 for plots 1 – 34, post-hoc Tukey HSD tested), except for *Rhododendron* vegetation in plots 1 – 34. The arcsine transformed lower layer showed nearly no significant differences between the different years. The value of *Seslerio-Caricetum sempervirentis* vegetation was significantly lower than all other vegetation types for plots 1 – 34 ($F_{4,199}$=18.71, p<0.001, post-hoc Tukey HSD tested) whereas this significance was not as high for plots 1 - 26. The arcsine transformed cover of the middle layer showed a steady increase over the years with a significant difference between 2018 and the year 1999 and before ($F_{9,250}$=4.57, p<0.001 for plots 1 – 26, post-hoc Tukey HSD tested).

Table 5: Results (*F*- and *p*-value) of ANOVA analysis of arcsine transformed vegetation layer (ground, lower, middle, and upper layer) for vegetation type and year (~vegetation type * year + Error (plot ID)). The analysis was done for the plot sets 1 – 26 and 1 – 34 separately.

Plot groups	Factor	Statistics	veg. layer 0- 5 cm	veg. layer 5- 25 cm	veg. layer 25- 50 cm	veg. layer 50- 120 cm
plots 1-26	vegetation type	$F_{4,21}$	6.08	3.50	19.9	37.8
		p	0.002 **	0.025 *	<0.001 ***	<0.001 ***
	year	$F_{9,189/225}$[1)]	7.63	11.22	12.73	10.56
		p	<0.001 ***	<0.001 ***	<0.001 ***	<0.001 ***
	interaction	$F_{36,189}$	2.03	4.10	-	2.17
		p	<0.001 ***	<0.001 ***	-	<0.001 ***
plots 1-34	vegetation type	$F_{4,29}$	3.81	5.79	17.02	46.83
		p	0.013 *	0.001 **	<0.001 ***	<0.001 ***
	year	$F_{5,145/165}$[1)]	13.65	3.45	7.49	7.03
		p	<0.001 ***	0.006 **	<0.001 ***	<0.001 ***
	interaction	$F_{20,145}$	2.59	2.76	-	-
		p	<0.001 ***	<0.001 ***	-	-

1) Second value for residuals indicates value without interaction

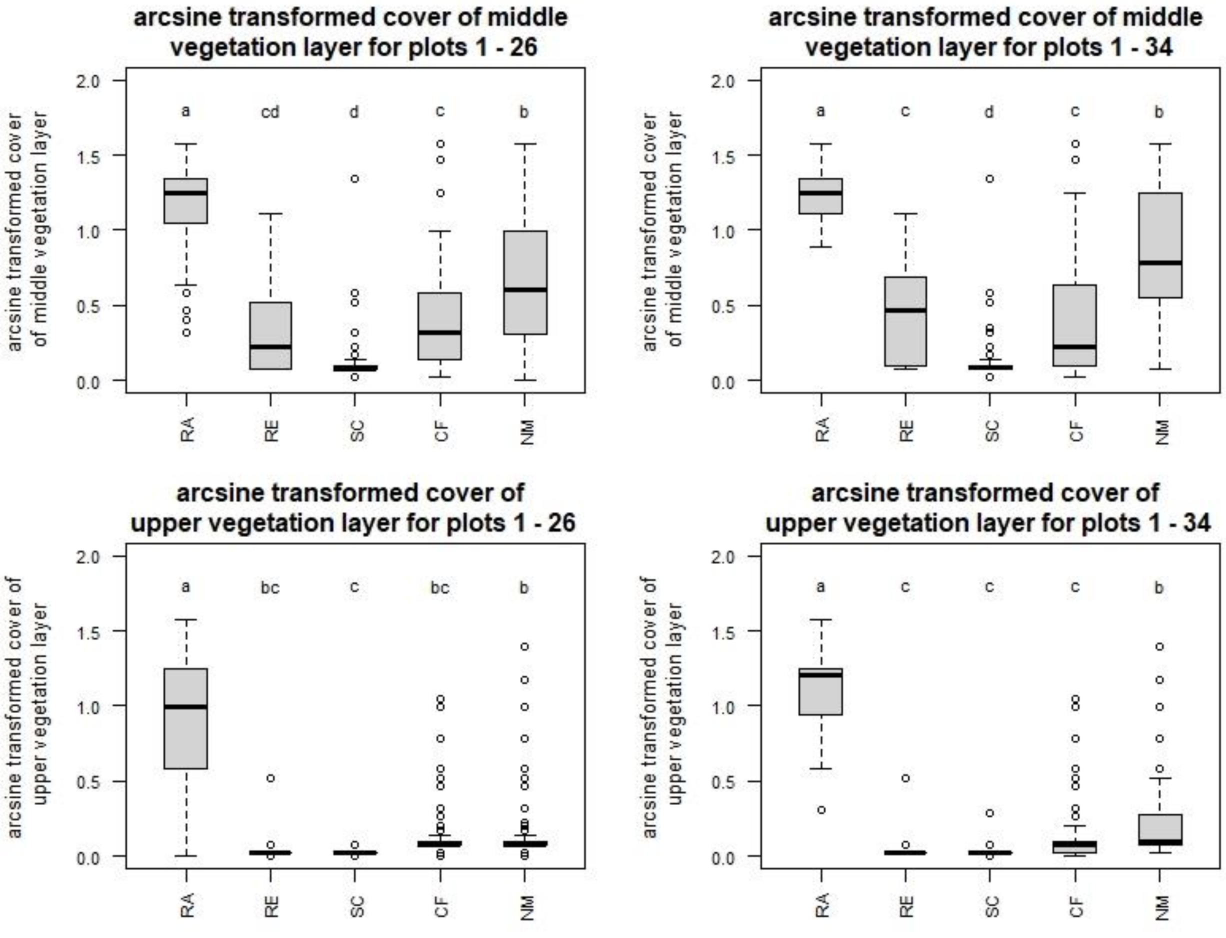

Figure 7: Arcsine transformed cover of the middle (25 – 50 cm) and upper vegetation layer (50 – 120 cm) in plots 1 – 26 and 1 – 34. CF: *Crepido-Festucetum rubrae* vegetation, NM: Nutritious lawn and meadow vegetation, SC: *Seslerio-Caricetum sempervirentis* vegetation, RE: *Rhododendron* vegetation, RA: *Rumicetum alpinae* vegetation. Letters indicate result of Tukey HSD tests (significance 95%).

The arcsine transformed middle and upper vegetation layer showed strong significance between the different vegetation types. *Rumicetum alpinae* vegetation had in both layers significant higher values than the other vegetation types (see figure 7).

The frequency of two species increased significantly from 2000 to 2018 (*Rhinanthus alectorolophus* and *Epilobium alpestre*) in the overall species list of the plots 1 – 34 (see table 6). A significant decrease in the frequency was identified for a total of ten species (*Poa alpina*, *Euphrasia minima*, *Cerastium fontanum* subsp. *vulgare*, *Taraxacum alpinum* aggr., *Cerastium strictum*, *Agrostis rupestris*, *Gentiana verna*, *Selaginella selaginoides*, *Veronica alpina*, *Trifolium repens*). The test for significant differences in species frequency between 1996 and 2018 for the plots 1 to 26 confirmed all mentioned species and no other significant change in frequency was found. Further analysis showed that *Euphrasia minima* was already in 2006 significantly lower in frequency compared to the relevés in 2000 (p<0.001). Additionally, *Poa alpina* (p=0.004), *Cerastium fontanum* subsp. *vulgare* (p=0.004) and *Veronica alpina* (p=0.031) had also a lower frequency of abundance at this time compared to the year 2000. All other species in table 6 showed only in 2018 a significant difference in abundance compared to the year 2000.

Table 6: Result of sign test (frequencies and *p*-values of binomial test) for change in species abundance frequency of all sampled plots in 2000 compared to 2018.

Species	**Frequency 2000**	**Frequency 2018**	***p*-value**
Winners			
Rhinanthus alectorolophus	2	10	0.008
Epilobium alpestre	4	13	0.012
Losers			
Poa alpina	20	4	<0.001
Euphrasia minima	21	7	0.001
Cerastium fontanum subsp. *vulgare*	10	1	0.012
Taraxacum alpinum aggr.	13	4	0.012
Cerastium strictum	12	5	0.016
Agrostis rupestris	11	3	0.021
Gentiana verna	9	3	0.031
Selaginella selaginoides	13	7	0.031
Veronica alpina	7	1	0.031
Trifolium repens	12	5	0.039

4. Discussion

Plant sociological mapping

The permanently marked plots of this study site were situated in a wide range of different vegetation types. Besides plant composition, the vegetation types differed mainly in terms of nutrients (high availability of nutrients in Nutritious lawn and meadow vegetation and *Rumicetum alpinae* vegetation) and vegetation structure (dominating shrub layer in *Rhododendron* vegetation). The initial plant sociological mapping was not always undoubted and transitions between different vegetation types occurred. Nevertheless, more than half of the plant sociological mapping could be confirmed by a supervised classification (see appendix 2). However, the two applied method for the supervised classification (Eggenberg system and Jaccard coefficient) agreed only in half of the cases with each other. Other studies support that the assignment to the Swiss classification scheme by Eggenberg is quite insufficient at least for some vegetation types (Dengler, et al., 2019). The equivocal results of plant sociological mapping are well reflected in the performed DCA (see figure 2). Only *Rumicetum alpinae* vegetation is clearly separated from the other vegetation types. All other vegetation types show at least some overlapping with each other. The plots in the DCA are more spread in 2018 compared to 2000, indicating a divergence of vegetation composition in the vegetation types. After 18 years of the summer pasture abandonment, the vegetation composition in the plots seem to be more unlikely to each other than before. This result contradicts the findings of other studies, that suggest a homogenization of the vegetation cover (Dullinger, et al., 2003). However, the study side was intensely grazed for many years before the vegetation surveys of this study started (Gilgen, et al., 2003). This over-use might have homogenized the different vegetation types beforehand. In consequence, the abandonment of grazing could have restored the initial differences of the vegetation composition in the vegetation types.

Changes in biodiversity

The biodiversity remained surprisingly constant within the different vegetation types over the sampled years (see table 2 and appendix 3). The *Seslerio-Caricetum sempervirentis* vegetation had significant higher biodiversity indices to most of the other vegetation types in the year 2000. This difference was still detectable in 2018 but with less significance to the other vegetation types. *Seslerio* vegetation are in general high in biodiversity (Delarze, et al., 2015). The major change in species richness was found in *Crepido-Festucetum rubrae* vegetation with a significant decline in richness between 2000 and 2018. This vegetation type is created by human use and depends regular grazing by farm animals (Delarze, et al., 2015). Therefore, an abandonment of grazing leads to major changes and an establishment of a new vegetation type might be the long-term consequence. In the *Rumicetum alpinae* vegetation, no significance at all was found in richness depending on year (see table 3), indicating a stable composition of plants low in biodiversity.

It is debated if abandonment of grazing sites leads to a loss of biodiversity. For example, one study did not find any effect in species richness of abandonment vs. pasture in the of steppes of the inner alpine dry valleys in Switzerland (Boch, et al., 2019). Also, no effect on species richness was found in an exclosure experiment in Central Alps in Austria after 15 years (Mayer & Erschbamer, 2017) as well as along a 19-year chonosequence study of an abandoned vs. intensively grazed site in the Canton St. Gallen in Switzerland (Widmer, et al., 2020), suggesting a very slow response of alpine grasslands to changes in the grazing regime. Other studies suggest a decrease of vascular plant species as a long-term effect of pasture abandonment (Dullinger, et al., 2003; Orlandi, et al., 2016; Pornaro, et al., 2013). Species richness can also rise in short-term as an effect of pasture abandonment (Pornaro, et al., 2013). Therefore, it is likely that the biodiversity in the observed plots is further changing and effects on plant biodiversity must be studied over decades for further conclusions. However, this study supports the idea that the effect of abandonment depends strongly on the vegetation type and suggest the strongest effects on *Crepido-Festucetum rubrae* vegetation.

Changes in vegetation parameters

The arcsine transformed herb cover showed only in *Crepido-Festucetum rubrae* vegetation a significant increase between 1999 and 2018 suggesting again the strongest response for this vegetation type. Arcsine transformed litter cover increased in all plots significantly over the years indifferent of the vegetation type. Since grazing may accelerate litter decomposition rates (Luo, et al., 2010; Chuan, et al., 2018), the absence of grazing sheep explains therefore the observed accumulation of litter cover.

The arcsine transformed percentage of uncovered soil decreased over the years and differed significantly between the vegetation types. Uncovered soil might have been an effect of overgrazing (Wiesmair, et al., 2017). Grazing also limits the amount of litter as less plant material can accumulate over a season, leading to less uncovered soil. The influence of both factors may depend on the different vegetation type, which explains the observed differences in vegetation type. The observed decrease of uncovered soil might be a sign for recovering and restoration of overgrazing (Wang, et al., 2019).

Analysis of the vegetation layers showed in most cases high significances between vegetation type, year, and its interaction (see table 5). Most differences were detected between middle (25 – 50 cm) and upper layer (50 – 120 cm) of different vegetation types with the highest value for the *Rumicetum alpinae* vegetation. The middle layer also showed a steady increase over the years, meaning that the vegetation grew higher and got denser in this layer.

Changes in species frequencies

All species with a significant lower abundance in 2018 than in the year 2000 are small growing plant species. Abandonment of a grazing side leads to a higher concurrence for light favouring tall growing species which goes along the results of density of the vegetation layers (see discussion part before). This reaction is expected to be seen the fastest at annual plants which explains that *Euphrasia minima* was already in 2006 significantly lower in frequency compared to the relevés in 2000. Another relatively fast responding species is *Poa alpina*, often a dominant species of Crepido-*Festucetum rubrae* vegetation (Delarze, et al., 2015). It is grazing tolerant, and this selective advantage disappears in an abandoned pasture.

The two winner species with a significant higher abundance in 2018 (*Rhinanthus alectorolophus*, *Epilobium alpestre*) are relatively tall growing species. Both plant species have a higher temperature index (Landolt, et al., 2010) than most plants with lower abundance, indicating that the warming climate might favour the abundance of these species in subalpine grasslands (Vittoz, et al., 2009). *E. alpestre* has a relatively low indicator value for light. This shading tolerance gives an advantage in a taller growing vegetation. The significantly higher abundance *R. alectorolophus* might be also linked to the lower abundance of *E. minima* since both species are unspecialized hemiparasites and the wide host range *R. alectorolophus* may facilitate their migration under warmer conditions (Phoenix & Press, 2005; Vittoz, et al., 2009).

5. Conclusion

This study shows that the restoration of an overgrazed site in an alpine region might take decades to recover. Vegetation types created by intensive grazing (*Rumicetum alpinae* and Nutritious lawn and meadow vegetation) are surprisingly stable and if at all only slowly changing after 18 years of pasture abandoning and therefore still low in biodiversity.

However, an extensive summer pasture might help to prevent a loss of non-forest habitats for alpine species (Dirnböck, et al., 2003). A moderate extensive grazing regime is beneficial for biodiversity (Dullinger, et al., 2003) and can help to prevent soil erosion (Cislaghi, et al., 2019). Grazing can lead in general to a greater special heterogeneity of vegetation and therefore for a higher biodiversity (Adler, et al., 2001; Wrage, et al., 2011). A regulation of the shrub cover by mowing can help to prevent a plant species loss due to reforestation and may maintain the highest biodiversity (Pornaro, et al., 2013). However, different vegetation types react differently to grazing and are very different in their sensitivity to overgrazing (Fragnière, et al., 2022). Excluding such areas from a summer pasture will help to protect those sites of high conservational value.

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Appendices

Appendix 1: Modified version of the cover-abundances scale of Braun-Blanquet used in the relevés with corresponding transformed percentages.

Symbology	Individuals	Cover	Transformed percentages
r	very few (1)	<< 1%	0.01%
r+	very few (1-2)	< 1%	0.05%
+	few (2-5)	< 1%	0.1%
1-	few (6-7)	1 - 5%	2%
1	numerous (8-18)	1 - 5%	3%
1+	numerous (19-20)	1 - 5%	4%
2m-	numerous (21-22)	< 5%	4.25%
2m	numerous (>22)	< 5%	4.5%
2m+	plenty	< 5%	4.75%
2a-	any	<= 5%	5%
2a	any	6 - 14%	10%
2a+	any	<= 15%	14.5%
2b-	any	<= 15%	15%
2b	any	16 - 24%	20%
2b+	any	<= 25%	24.5%
3-	any	<= 25%	25%
3	any	26 - 49%	37.5%
3+	any	<= 50%	49.5%
4-	any	<= 50%	50%
4	any	51 - 74%	62.5%
4+	any	<= 75%	74.5%
5-	any	<= 75%	75%
5	any	76 - 99%	87.5%
5+	any	100%	100%
*	species nearby, outside the plot		-

Appendix 2: VEGEDAZ supervised classification: Grouping of relevés to TypoCH_UTF8. Green rows symbolise matching results.

Plot ID	Plant (sub-) association	Vegetation type	TypoCode Eggenberg 1)	Punkte nach Eggenberg 1)	TypoCode Jaccard 1)	Jaccard-Index 1)
1	K	RA	4.3.5.	*Nardion*	4.3.2.	*Caricion firmae*
2	A	RA	7.1.7.	*Rumicion alpini*	7.1.7.	*Rumicion alpini*
3	M	CF	4.5.4.	*Poion alpinae*	4.5.4.	*Poion alpinae*
4	M	CF	4.5.4.	*Poion alpinae*	4.5.4.	*Poion alpinae*
5	M	CF	4.3.5.	*Nardion*	4.3.5.	*Nardion*
6	B	SC	4.3.1.	*Seslerion*	4.3.2.	*Caricion firmae*
7	P	NM	7.1.3.	*Poion supinae*	7.1.3.	*Poion supinae*
8	E	RE	5.4.3.	*Ericion*	6.6.4.	-
9	M	CF	4.3.5.	*Nardion*	4.3.5.	*Nardion*
10	K	RA	7.1.8.	*Arction*	7.1.7.	*Rumicion alpini*
11	M	CF	4.5.4.	*Poion alpinae*	4.5.4.	*Poion alpinae*
12	V	RE	6.6.4.	-	6.6.4.	-
13	D	NM	2.2.2.	*Caricion fuscae*	4.0.	-
14	B/M	SC	4.5.4.	*Poion alpinae*	4.3.3.	*Caricion ferrugineae*
15	D	NM	7.1.7.	*Rumicion alpini*	4.0.	-
16	A	RA	7.1.7.	*Rumicion alpini*	5.2.4.	*Adenostylion*
17	D	NM	7.1.7.	*Rumicion alpini*	4.5.2.	*Polygono-Trisetion*
18	B/D	SC	4.3.1.	*Seslerion*	4.3.2.	*Caricion firmae*
19	B	SC	4.3.2.	*Caricion firmae*	4.3.2.	*Caricion firmae*
20	E	RE	4.3.2.	*Caricion firmae*	4.3.2.	*Caricion firmae*
21	D	NM	4.5.4.	*Poion alpinae*	4.5.4.	*Poion alpinae*
22	Ms	CF	4.5.4.	*Poion alpinae*	4.4.1.	*Arabidion caeruleae*
23	M	CF	4.3.7.	*Caricion curvulae*	4.3.7.	*Caricion curvulae*
24	R	NM	4.5.2.	*Polygono-Trisetion*	4.5.2.	*Polygono-Trisetion*
25	B	SC	4.3.1.	*Seslerion*	4.3.2.	*Caricion firmae*
26	A	RA	7.1.7.	*Rumicion alpini*	7.1.7.	*Rumicion alpini*
27	M	CF	4.5.4.	*Poion alpinae*	4.5.4.	*Poion alpinae*
28	M	CF	4.5.4.	*Poion alpinae*	4.5.4.	*Poion alpinae*
29	M	CF	4.5.4.	*Poion alpinae*	4.3.3.	*Caricion ferrugineae*
30	M	CF	4.3.3.	*Caricion ferrugineae*	4.3.3.	*Caricion ferrugineae*
31	M	CF	4.5.4.	*Poion alpinae*	6.6.4.	-
32	Bn	SC	4.3.5.	*Nardion*	6.6.4.	-
33	M	CF	4.5.4.	Poion alpinae	4.5.4.	*Poion alpinae*
34	B	SC	4.3.1.	Seslerion	4.3.2.	*Caricion firmae*

Appendix 3: Boxplots of diversity indices for the different vegetation types of the year 2000 - 2018