A comparative study of the vegetation composition inside and outside a century-old protected area in the Alps

Bachelor Thesis at the Universität Greifswald

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Date	13.08.2025

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Content

Abstract

Several studies addressed the impact of ceased pastoral and silvicultural practices in the last decades in the Alps. They indicate especially on former pastures a homogenization of vegetation with competitive species expanding to the detriment of diverse ruderal and light demanding communities when grazing ceases. In contrast, herb layers in forests showed more diverse responses depending on land-use history and site conditions. Yet, few studies profited from long-term abandoned areas to compare which processes and successional stages establish under natural dynamics in an ecosystem. From the perspective of nature conservation, evidence of these comparisons might be important when deciding how to deal with land-abandonment. Thus, this thesis investigated differences in vegetation composition of the herb layer on pastures and in forests inside and outside the Swiss National Park. The focus has been set on species diversity at alpha and gamma scale, Landolt Indicator Values for Light, Nutrients and Soil Reaction as well as competitive strategies according to Grime. For this, paired vegetation surveys with similar topographical features and land-use history were analysed. On pastures, more competitive but less ruderal species occur in the protected area and α-diversity was lower. In forests, no significant differences could be detected. On landscape level for both grasslands and forests species diversity is higher out- than inside the SNP and the amount of species occurring exclusively outside was twice as high than inside. Firstly, these results imply that ceased extensive pastoral activities alter the pattern of competitive strategies and secondly, that especially in forests, human land-use may create a higher heterogeneity of habitats than natural dynamics. Though, as differences are small and partly no clear tendencies according to previous research could be reported, it may point towards overriding influence of other variables than land-use on vegetation composition. Therefore, further causal analyses of possibly relevant biotic and abiotic factors are recommended.

1. Introduction

The current subalpine landscape is strongly formed by human activities resulting in a distinct pattern of vegetation diversity and composition both on grasslands and in forests (e. g. Cocca et al., 2012; Tasser and Tappeiner, 2002). Consequently, since land abandonment increased in the last decades, natural succession on pastures and meadows and therefore a supposed loss of biodiversity have received ongoing attention (Bonari et al., 2025; Chemini and Rizzoli, 2003; Spatz, 1980). In contrast, a less intense use of mountain forests was partly undertaken deliberately to ensure the maintenance of biodiversity and protective function of these forests (Mather and Fairbain, 2000, as cited in Bebi et al., 2017). Yet, for both ecosystems it is crucial to gain knowledge about the effect of land-use abandonment on vegetation composition in long term to develop appropriate measures for biodiversity conservation.

Since the 1950s, globalization and industrialisation lead to decreasing land-use in the Alps. As the extensive use of summer pastures and meadows became unprofitable, people increasingly gave up traditional agricultural practices marked by concentration of livestock on fewer more productive sites and partially full abandonment (MacDonald et al., 2000). In Switzerland, these developments lead to a 7 % decrease of alpine pastures turning into shrubland and other unproductive area between 1985 and 2018 (Federal Statistical Office, 2024). Consequently, several studies addressed the effect of land abandonment in mountain regions on vegetation to characterize successional pathways and disentangle the effect of land-use versus other topographical and environmental factors. The focus has been set on forest succession at landscape level, predicting an increase of forests on abandoned sites (e. g. Gehrig-Fasel et al., 2007; Tasser et al., 2007) as well as on community level in grasslands. Vegetation surveys on pastures and meadows under different management intensities or grazing exclosure experiments confirm successional pathways comprising a decrease of species richness and shift in species composition towards competitive grasses to the detriment of ruderal herbal species (Mayer et al., 2008; Orlandi et al., 2016; Prévosto et al., 2011). These results have been related to the "Intermediate Disturbance Hypothesis" postulating that medium disturbances lead to a high species diversity (Grime, 1973): In this case, grazing acts as disturbance so that less vigorous but disturbance adapted species can thrive. Under more productive and undisturbed conditions competitive exclusion comes into play: Competitive species will dominate and exclude species with similar environmental requirements. This relates to another important factor altered by land-use: Soil conditions with respect to nutrients and pH value. Especially the abandonment of grazing has been shown to reduce soil pH value and increase C/N ratios. This disadvantages nitrophilous species and promotes acid tolerant grasses (Gavrichkova et al., 2022; Seeber and Seeber, 2005). Though, other studies could not confirm the successional pathways mentioned above and emphasize the importance of other variables than land-abandonment for vegetation composition. On the one hand, these comprise biotic factors such as grazing by wild herbivores (Wildi and Schütz, 2000), on the other hand, also abiotic factors such as soil conditions (Orlandi et al., 2016), climate and elevation (Pittarello et al., 2020) which can all modify or delay succession. Accordingly, Mayer et al. (2012) showed that succession of former pastures takes several decades during which species diversity can stay relatively stable.

Similar to grasslands, mountain forests in the Alps ceased to be used as intensively as before from the 20th century on. Already at the end of the 19th century, the importance of the mountain forests for protection against erosion was recognised, leading to stricter regulations for silviculture. In addition, industrialisation and globalization induced a decreasing use of forests as other forms of energy resources than timber arose (Mather and Fairbairn 2000 in Bebi et al., 2017). Together with the abandonment of

grasslands, these developments led to an increase in forest cover and density (Bebi et al., 2017). Since the beginning of the 20th century, concerns about a sustainable use of the forests and maintenance of biodiversity in them are articulated in Switzerland (Schärer and Jacobi, 2000). Although understory vegetation plays an important role in forest ecosystems (Haritika and Negi, 2025), few subsequent studies focused on biodiversity of the herb layer of mountain forests in the Alps. Studies addressing changes in the herb layer with altered management practices report in part a lower diversity in unmanaged forests stands with closed canopy cover (Duguid and Ashton, 2013), yet, the interplaying impact of stand structure and age as well as herbivory on vegetation composition is highlighted (Chevaux et al., 2022; Meier et al., 2017). In addition, a study in the Italian Alps emphasizes the importance of the starting point of forest regeneration for the later species composition (Marengo et al., 2025). In contrast to the diverging findings for the management´s impact on diversity and vegetation composition, more definite tendencies for its influence on soil conditions are reported: e. g. Christophel et al. (2013) showed that timber extraction practices disturb the upper soil and thereby hinder accumulation of biomass and stocks of nitrogen in the topsoil. Therefore, species with higher nutrient demand and tolerance for lower soil pH values are expected to occur inside the protected area.

Although these observations suggest that the effects of land abandonment in the subalpine (here referred to the zone below the climatic treeline) and alpine landscape is not straight forward and may vary considerably especially in forests´ herb layer, there are few direct comparisons of the flora inside and outside of large abandoned areas. The implementation of the Swiss National Park (SNP) in 1914 and the consequent cessation of pastoral and silvicultural use gives the opportunity to observe the impact of ceased land-use on pastures and in forests undisturbed from major human influences. A further advantage of the study area is the large size and long time passed since implementation allowing to study the subsequent processes under the unfolding of natural dynamics. In the light of the theories and findings mentioned above, this thesis investigates the impact of land-abandonment on species diversity, Landolt Indicator Values (LIV) for Light, Nutrient and Reaction and strategy type according to Grime as major changes are expected for these. This is done by comparing paired survey sites with the same environmental conditions and land-use history in the SNP and surrounding area on grassland and in forests (hereafter referred to as “in-plots” and “out-plots”). This may contribute to the understanding of land abandonment´s impact on vegetation when natural dynamics are given space and time to occur. Moreover, it can provide knowledge for setting priorities in biodiversity conservation.

Following hypothesis are tested:

1) Species richness and Shannon Diversity on alpha scale is different inside and outside of the SNP.
2) Vegetation composition is different inside and outside of the SNP.
3) Vegetation inside and outside the SNP differ in LIVs for Light, Nutrients and Reaction.
4) The share of competitive, ruderal and stress tolerating traits according to Grime is different inside and outside of the SNP.

2. Methods

Study area

The study area comprises the Swiss National Park and mainly the Val Müstair and Val Mora belonging to the Biosfera Val Müstair (see Fig. 1). The Swiss National Park is located in south-eastern Switzerland in the Canton Grison in the Central Eastern Alps. The region is characterized by low precipitation rates of in average 920 mm per year with a maximum in summer. The highest mean air temperature in summer is at 12 °C and lowest in winter at – 9.6 °C. Mean annual air temperatures are around 1.7 °C (Data from the last 10 years at the weather station Buffalora, 1971 m.a.s.l. at the eastern end of the SNP ((Federal Office of Meteorology and Climatology MeteoSwiss, 2025). Snowfall occurs on 149 days per year in Buffalora with decreasing trend (Marty and Suter, 2014). Mainly alkaline bedrock types dominate in the study area (Federal Office of Topography swisstopo, 2024a).

The Swiss National Park was founded 1914 and since then any land-use ceased with minor exceptions in the first years for grazing and timber logging (Parolini, 2012). Today, the parks´ 170 km^2 are to one third covered by former pastures and alpine grasslands, one third is covered by forest dominated by *Pinus mugo* and one third consists of scree and rocks. Most of the former pastures are situated below the current treeline of 2200 m.a.s.l and were primarily grazed by sheep and secondary cattle (Parolini, 2012). The pastures outside are nowadays grazed by mostly cattle in summer (personal observation). The forests in the whole study area ceased to be used intensively at the beginning of the 20th century, the last clear cuts on the area of the Swiss National Park took place at the end of the 19th century. Since the beginning of the last century, the use of the forests outside of the Park continues under cantonal regulations for timber production and to a smaller part as wood pasture (Parolini, 2012) and are dominated by *Pinus mugo* and *Picea abies* (Amt für Wald und Naturgefahren, 2025a).

On subalpine and alpine grasslands, the 29 plot pairs range between 1676 m.a.s.l. and 2295 m.a.s.l. of which two pairs are situated above the current treeline. Most of the plots inside the SNP are on the formerly grazed pastures Alp la Schera (2060-2100 m.a.s.l.), Alp Grimmels (2060-2080 m.a.s.l.) and Alp Stabelchod (1930-1980 m.a.s.l.) and are surrounded by forest. The corresponding plots outside are mainly situated on the grazed Alp Buffalora (1960-2080 m.a.s.l.), Alp Mora (2060-2100 m.a.s.l.) and one on Alp Sprella (2120 m.a.s.l) and are likewise enclosed by forest. The 25 plot pairs in the forest mainly range between 1850 and 2100 m.a.s.l. with the lowest at 1828 m.a.s.l. and highest at 2244 m.a.s.l. situated in the ecotone of the current tree line (For detailed information see App. Tab. 1). Nine of the forest-plots outside are situated in grazed forests (Amt für Wald und Naturgefahren, 2025b).

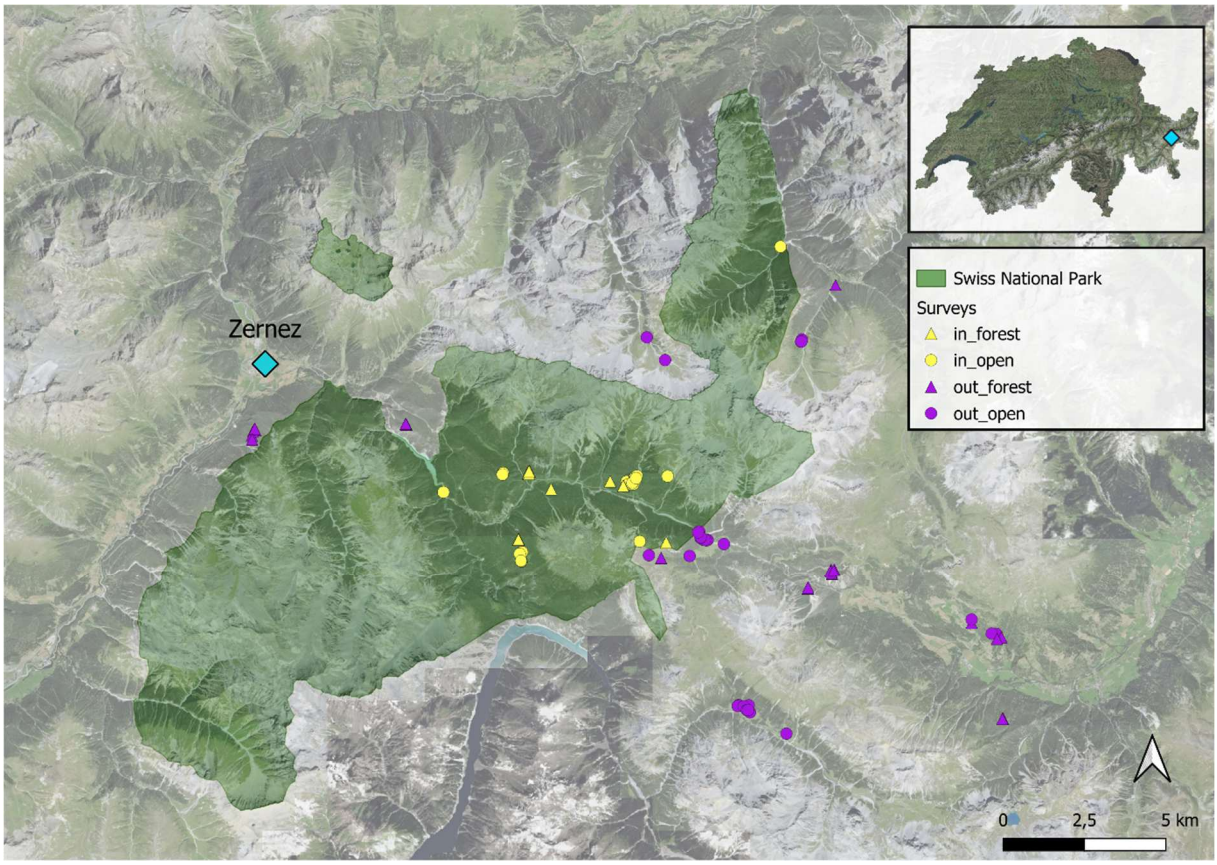

Figure 1: The Swiss National Park is located in south-eastern Switzerland in the Central-Eastern Alps. 104 vegetation surveys were conducted inside the Swiss National Park and the surrounding area, 58 on grassland and 46 in forests (Map of the Swiss National Park and Switzerland derived from Bundesamt für Landestopografie swisstopo, 2025).

Vegetation records

Data for the plots inside the SNP are derived from vegetation surveys on permanent plots from 2023, 2020 and for forests also from 2019. If these plots were not of a size of 1 m^2, 1 m^2 subplots in the existing plots were created and surveyed 2024. To obtain pair plots to these sites, in advance of this thesis following procedure has been applied (description adapted from R. S. von Büren, personal communication, 26.07.2025): firstly, plots in a distance <10 km around the SNP have been created randomly. Secondly, matching sites to the in-plots were selected including following factors: elevation, slope, exposition, the Topographical Index, geology and historical land use so that e. g. in-plots in formerly grazed areas receive also pair-plots on grazed locations. If no pair-plot could be generated, less strict conditions were applied. (For a detailed description of conditions, see App. Tab. 2.). Afterwards, the plots were manually selected according to their accessibility in the field. The vegetation surveys of these out-plots took place from June to the beginning of September 2024. In the 1 m^2 plots, all vascular plants were determined on species level following the nomenclature of Flora Helvetica (Lauber et al., 2024) and their cover was estimated in 1 percent steps or below 2 % in decimal steps, respectively. Additionally, the cover of trees, shrubs, scree, mosses, lichens, litter and bare ground was recorded. The assignment of Landolt Indicator Values for Light, Nutrients and Soil Reaction as well as Grime´s C-S-R strategies was based on the data of Info Flora (Info Flora, n.d.). Landolt Indicator Values assign scores ranging from 1 (low) to 5 (high) to plant species representing their association to environmental

conditions (Landolt et al., 2010). Grime Strategies associate plant traits to Competitiveness, Stress tolerance and Ruderality. According to their predominance, a strategy type can be assigned to each taxon (Grime, 1988).

Data analysis

All calculations were done in the program Rstudio, version 4.4.3 2024 (R Core Team, 2024).

For each plot, the species number and Shannon-Index *H´* for diversity was calculated in the package "vegan" (Oksanen et al., 2025). For testing the difference of the groups concerning LIVs and Grime Strategies, the arithmetic mean of them was calculated for every plot. To calculate means for the Grime Strategy, each prevailing strategy component (C, S, R) in a species´ strategy type was expressed as proportion of hundred (e. g. CCR: C 66 %, R 3 3%). Normal distribution was tested by Shapiro-Wilk-Test. Subsequently, the means were tested for difference by a two-sided Student´s T-Test or non-parametric Wilcoxon Signed Rank Test if a normal distribution of the data was not given. The obtained p-values were Holm-Bonferroni corrected. Additionally, Cohen´s or Wilcoxon´s effect size depending on the distribution of the data was calculated. Test statistics were conducted in the packages "stats" (R Core Team, 2024) and "rstatix" (Kassambara, 2023).

To characterize species richness at a large scale, it was calculated how many species occur in sum on grasslands and in forests inside and outside the SNP as well as how many species occur exclusively in- and outside. Additionally, gamma-diversity based on the Shannon-Index in the package "vegan" (Oksanen et al., 2025) was calculated for pastures and forests inside and outside the SNP.

To explore visually differences in vegetation composition between the surveys inside and outside of the SNP, a Non-metric Multidimensional Scaling (NMDS) based on a distance matrix calculated with the Jaccard index was applied in the package "vegan" (Oksanen et al., 2025). If stress values below 2 are obtained for the ordination, interpretation of the graphic is considered as reliable (Clarke, 1993). LIVs and Grime strategies were plotted as vectors onto the ordination to gain advanced understanding of the relationship of the variables towards each other. Yet, significance of the explanatory power for the contribution to differences in vegetation composition was not tested as the LIVs and CSR values are autocorrelated to the species matrix (Wildi, 2016). The significance of the difference in vegetation composition was tested with the permutational test PERMANOVA (999 permutations) based on the species distance matrix (Anderson, 2008). Ahead, the homogeneity of the group´s variances was tested with the permutational approach PERMDISP (999 permutations) by Anderson (2006) whereby a significant p-value (< 0.05) indicates that difference in vegetation composition may be influenced by unequal dispersions.

Moreover, an Indicator Species Analysis (ISA) based on presence-/absence-data was applied to further characterize the difference in vegetation composition. The Indicator Value (IV) of the species on which the test statistic is based on, is calculated as follows in the R package "indicspecies" (De Cáceres and Legendre, 2009):

$$IV_{ij} = A_{ij} \times B_{ij} \times 100$$

whereby A_{ij} is specificity (the number of plots in a given group *j* harbouring the species *i* as share of all plots harbouring species *i)*. B_{ij} is the relative frequency of species *i* in the given group *j.* The square

rooted IV ranges between 0 and 1 whereby a species receiving a value above 0.25 is perceived as a strong indicator of a group (Dufrêne and Legendre, 1997).

3. Results

3.1 Grassland

Species number and Diversity

The distribution of mean species richness and the Shannon-Index on grasslands inside and outside of the SNP does not differ significantly. Species number range from 14 to 45 inside and 16 to 49 outside. Highest species´ numbers occurred in out-plots and lowest inside on the Alp la Schera. Mean species number is slightly higher in the out-plots, yet this difference is not significant (Tab. 1). The Shannon-Index range from 0.76 to 2.9 inside and 1.47 to 3.08 outside. Here, a significant difference can be stated, though, the effect size indicates only a small difference between the groups (Tab. 1). Vegetation surveys with the lowest diversity almost exclusively occur on Alp la Schera. At a landscape scale too, species number outside is higher than inside: outside 171 species occur, 65 of them exclusively outside (31.70 % of all species on grassland). Inside 140 species occur, 34 of them exclusively inside (16.59 % of all species on grassland). The gamma diversity based on the Shannon-Index for all the grassland plots is also higher outside with 4.19 versus 3.48 inside.

Table 1: Results for mean species number and Shannon-Index on α-scale for vegetation surveys on grasslands inside (in) and outside (out) the Swiss National Park. Significance (p-value < 0.05) is marked by an asterisk.

	Species number		**Shannon-Index**	
Location	in	out	in	out
Mean	28.41	31.1	2.03	2.24
Effect size	- 0.32		0.17	
Test	T-Test		Wilcoxon	
P raw	0.26		0.02*	
P adjusted	1		0.14	
Confidence Limits (95 %)	-7.07 1.97		-0.59 -0.05	

Landolt Indicator Values and Grime Strategies

For all LIVs, no significant differences between the groups´ means have been found (Tab. 2). In general, vegetation outside shows a wider range than inside for Light and Nutrients (Fig. 2). The lowest values for Nutrients and the highest values for Light appear in the out-plot group on Alp Buffalora and in an alpine plot in- and outside the SNP. The lowest Soil Reaction values result from the in-plots on Alp la Schera, highest values are reached by the same alpine plot-pair as mentioned and on plots on Alp Buffalora.

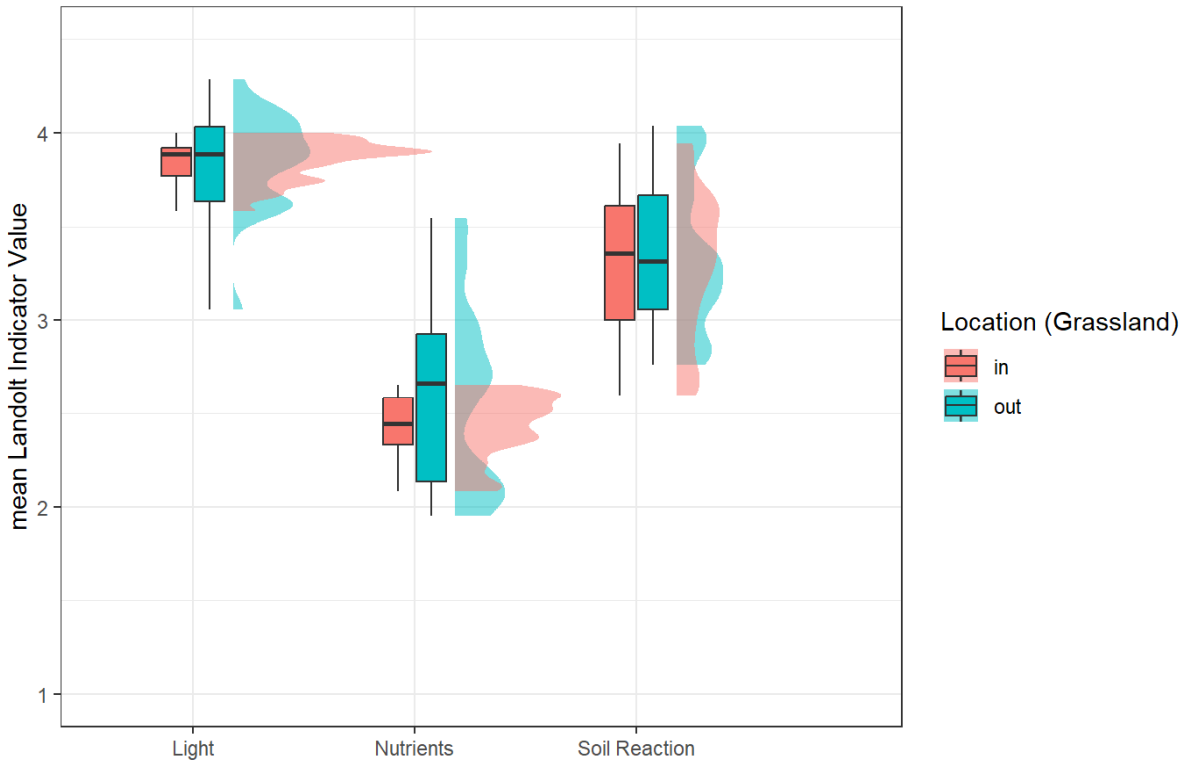

Figure 2: The boxplots show mean Landolt Indicator Values for Light, Nutrients and Soil Reaction for vegetation surveys inside (in) and outside (out) the Swiss National Park on grasslands. They comprise the median (central line) as well as 25th and 75th percentiles (whisker). The clouds represent the amount of data points at the x-axis.

Regarding the C-S-R components, in-plots display higher values for competitiveness than out-plots (Fig. 3). The difference between the locations is significant (p-value unadjusted 0.047, CI 95 %, T-Test), yet, the effect size is small. Also, for Ruderality, a significant difference between vegetation in- and outside has been shown (p-value unadjusted 0.0018, CI 95 %, Wilcoxon-Test), whereby outside a higher share of ruderals is reported. Highest values occur on different locations outside, lowest values inside among others on alpine plots. The distribution of mean values for Stress Tolerance shows no significant difference. Highest values outside are reported for the Buffalora plot-group, lowest values inside mostly for the Alp la Schera.

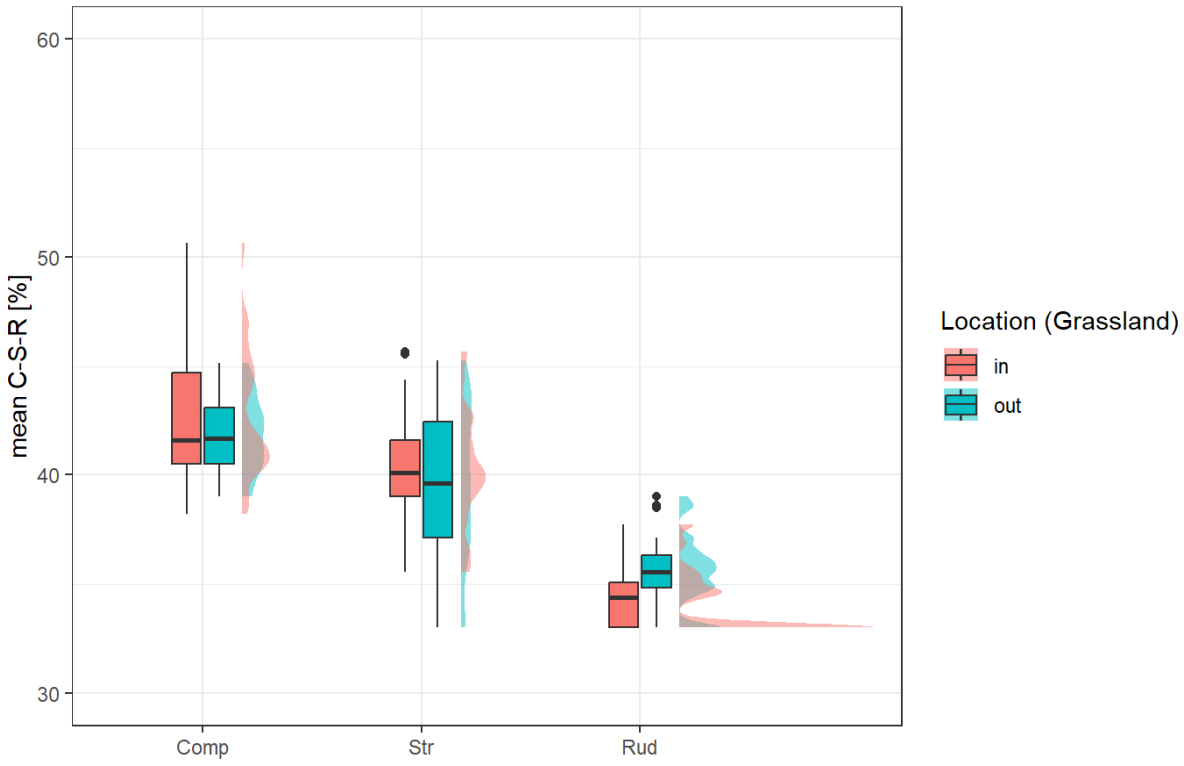

Figure 3: Mean components of Grime Strategies Competitiveness (Comp), Stress Tolerance (Str), Ruderality (Rud) for vegetation surveys inside (in) and outside (out) the Swiss National Park on grassland. They comprise the median (central line) as well as 25th and 75th percentiles (whisker). The clouds represent the amount of data points at the x-axis. Components are computed as share of 100 % of the strategy type.

Table 2: Results for mean Landolt Indicator Values Light, Nutrients and Reaction and Grime Strategies Competitiveness (C), Stress tolerance (S), Ruderality (R) for vegetation surveys inside (in) and outside (out) the Swiss National Park on grasslands. Significance (p-value < 0.05) is marked by an asterisk.

	Light		**Nutrients**		**Reaction**		**C**		**S**		**R**	
Location	in	out	in	out	in	out	in	out	in	out	in	out
Mean	3.85	3.86	2.42	2.58	3.31	3.34	41.6	40.1	40.2	39.7	34.25	35.52
Effect size	- 0.02		- 0.42		- 0.08		0.30		0.1		0.41	
Test	T-Test		T-Test		T-Test		T-Test		T-Test		Wilcoxon	
P raw	0.95		0.12		0.75		0.047*		0.54		0.0018*	
P adjusted	1		0.6		1		0.28		1		0.014	
Confidence Limits (95 %)	-0.11 0.1		-0.35 0.04		-0.24 0.18		0.016 2.96		-1.18 1.21		-2.06 -0.33	

All in all, the analysis of the vegetation composition resulted in a significant difference between locations inside and outside the SNP (p-value 0.001, CI 95 %, PERMANOVA, 999 permutations) with non-significant difference in variance (p-value 0.4, CI 95 %, PERMDISP, 999 permutations). The fitted LIVs and Grime Strategy components onto the ordination display an analogous pattern for the relationship of the variables towards each as mentioned above (Fig. 4): Ruderal traits are mostly related the centroid of the surveys outside the SNP, whereby it also accounts for a group of in-plots. Yet, Competitiveness is overall more related to in-plots. Nutrient demand is correlated negatively to Stress tolerance and Light and Soil Reaction values whereby both groups of variables point towards different out-plot groups. The results of the Indicator Species Analysis show similar trends as they identify character species for nutrient-rich and disturbed pastures as strong indicators for the vegetation outside. But also character species for stress and disturbance influenced habitats with low nutrient supply on alkaline soils are displayed as indictors. For the vegetation inside, character species for nutrient-poor mountain grasslands are identified as strong indicators as well as for nutrient-rich meadows (for the list of Indicator Species see App. Tab. 3, 4.).

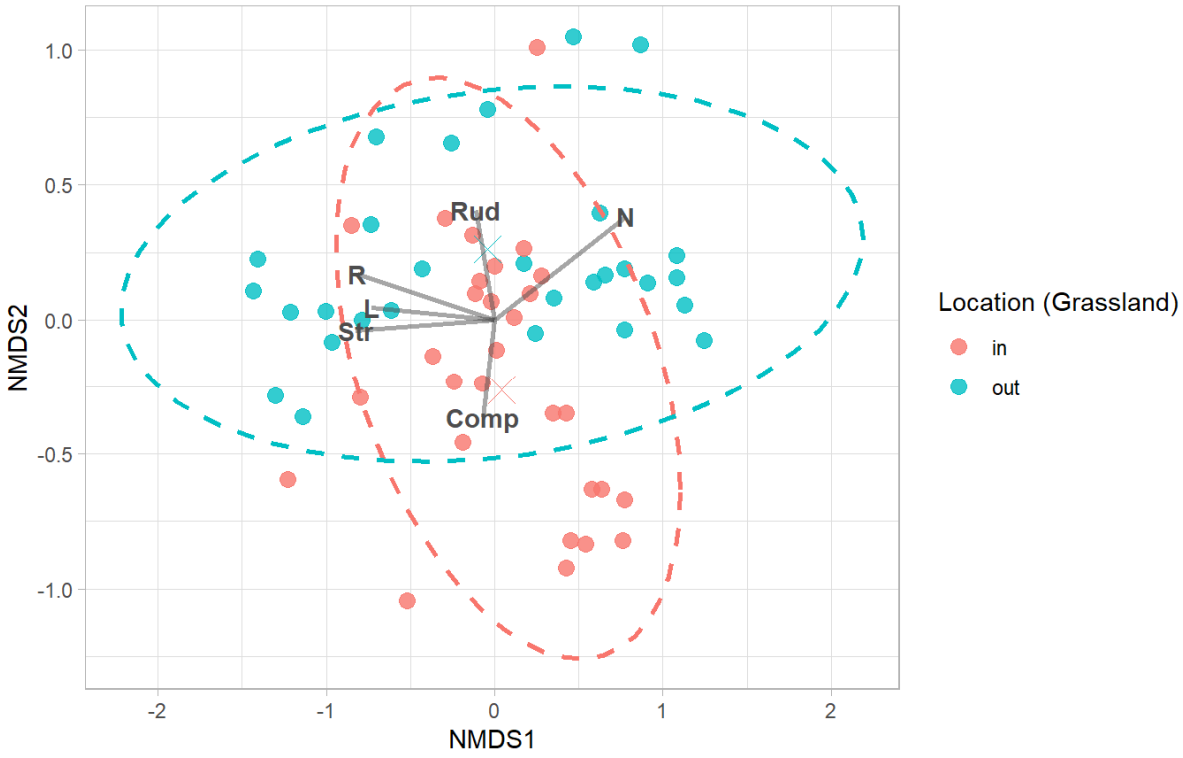

Figure 4: The Non-metric Multidimensional Scaling (NMDS) of vegetation composition on grasslands inside (in) and outside (out) the Swiss National Park displays vegetation surveys as points and the groups´ centroids as crosses in the ordinal space. (Final stress: 0.17 after 20 tries). The Confidence Ellipsis is at 95 %. Landolt Indicator Values for Light (L), Nutrients (N) and Soil Reaction (R) as well as Grime Strategies Competitiveness (Comp), Stress Tolerance (Str) and Ruderality (Rud) are fitted onto the ordination.

3.2 Forest

Species number and Diversity

For species richness and the Shannon-Index of the herb-layer in forests, no significant difference between the locations can be stated (Tab. 3). The range of species number is similar – outside it stretches from 6 to 32 species, inside from 7 to 33. Outside, highest species numbers occur in the plots located in forests with silvopastoralism and a plot situated in the forest ecotone. Inside, the corresponding ecotone-plot shows high species number together with a plot group in the forests at Alp la Schera. For the Shannon-Index, the vegetation surveys outside reach slightly lower values than the in-plots: They range from 0.2 to 2.7 outside versus 0.9 to 2.5 inside. At landscape level scale, there are more species outside: 138 species occur outside, 53 of them just outside (18.86 % of all species in forests) versus 85 species inside, 27 of them occurring just inside (9.61 % of all species in forests). Also, the Shannon-Index on gamma scale is higher outside (3.15) than inside (2.41).

Table 3: Results for mean species number and Shannon-Index on α-scale for vegetation surveys in forests inside (in) and outside (out) the Swiss National Park.

	Species number		**Shannon-Index**	
Location	in	out	in	out
Mean	18	17	1.59	1.65
Effect Size	0.03		-0.09	
Test	Wilcoxon		T-Test	
P raw	0.84		0.76	
P adjusted	1.00		1.00	
Confidence Limits (95 %)	-4 4		-0.45 0.33	

Landolt Indicator Values and Grime Strategies

The univariate tests showed a nearly significant difference for the LIV Light (p-value unadjusted 0.05, CI 95 %, T-Test) with a moderate Effect Size (Tab. 3). The six lowest values for Light occur outside on different locations. Highest values are reached by both the in and out ecotone-plots, the in-plots near Alp la Schera as well as plots in wood-pastures. These two first plot-groups also show highest values for mean Reaction values. Lowest Reaction values distinctively occur for most plots in *Piecea abies* forests outside and the plot-group near Alp la Schera inside the SNP. Regarding nutrient demand, the groups in and out exhibit a similar distribution (Fig. 5) whereby highest values are reached outside.

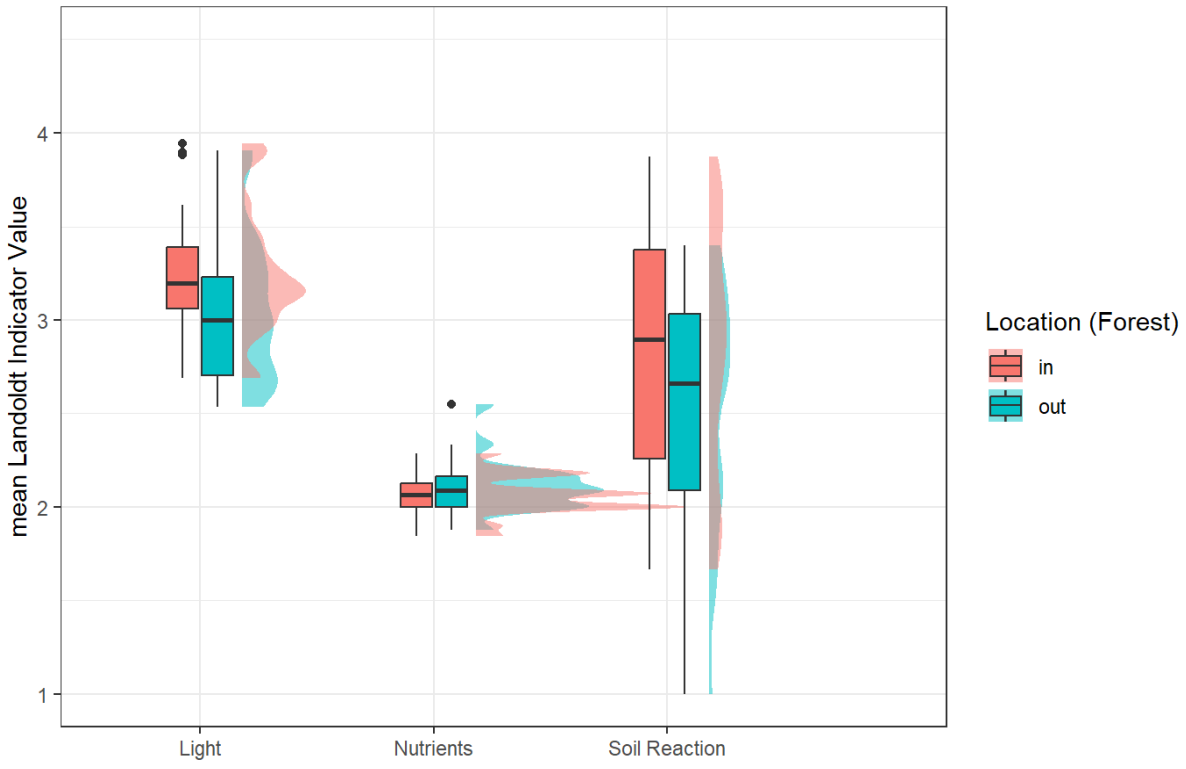

Figure 5: Mean Landolt Indicator Values for Light, Nutrients and Soil Reaction for vegetation surveys inside (in) and outside (out) the Swiss National Park in forests. They comprise the median (central line) as well as 25th and 75th percentiles (whisker). The clouds represent the amount of data points at the x-axis.

Regarding Grime Strategies, no significant differences between the locations can be reported. Though, Competitiveness has a moderate Effect Size and shows a tendency towards significant difference in means (p-value 0.08, CI 95 %, T-Test). Both the share of competitive and ruderal traits have a wider range in the vegetation surveys outside than inside, whereby the seven highest values for Ruderality are reached exclusively from out-plots. Among those are the plots in grazed forests. Values for Stress tolerance display an equal distribution for both groups (Tab. 4).

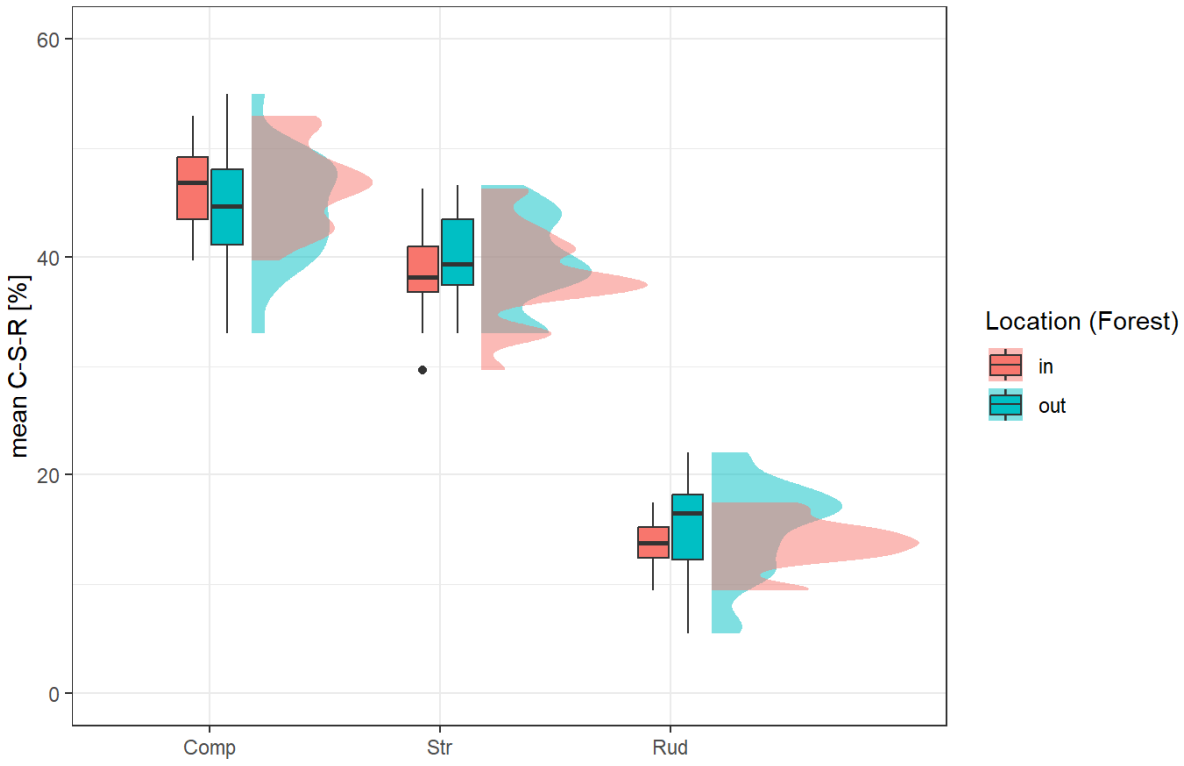

Figure 6: Mean components of Grime Strategies Competitiveness (Comp), Stress Tolerance (Str), Ruderality (Rud) for vegetation surveys inside (in) and outside (out) the Swiss National Park in forests. They comprise the median (central line) as well as 25th and 75th percentiles (whisker). The clouds represent the amount of data points at the x-axis. Components are computed as share of 100 % of the strategy type.

Table 4: Results for mean Landolt Indicator Values Light, Nutrients and Soil Reaction and Grime Strategies Competitiveness (C), Stress tolerance (S), Ruderality (R) for vegetation surveys inside (in) and outside (out) the Swiss National Park in forests. Significance (p-value < 0.05) is marked by an asterisk.

	Light		**Nutrients**		**Reaction**		**C**		**S**		**R**	
Location	in	out	in	out	in	out	in	out	in	out	in	out
Mean	3.25	3.04	2.06	2.12	2.82	2.53	46.8	44.4	38.6	39.6	13.7	15.1
Effect Size	0.58		0.19		0.44		0.54		-0.22		-0.41	
Test	T-Test		Wilcoxon		T-Test		T-Test		T-Test		T-Test	
P raw	0.05		0.21		0.14		0.08		0.45		0.18	
P adjusted	0.40		0.90		0.84		0.56		1.00		0.90	
Confidence	-0.005		-0.09		-0.10		-0.26		-3.47		-3.54	
Limits	0.42		0.01		0.69		5.11		1.57		0.67	
(95 %)												

The fitted means of LIVs and Grime´s strategies also show a negative correlation between Competitiveness and Ruderality, whereby competitiveness increases towards vegetation surveys inside the SNP and Ruderality towards out-plots. Moreover, Reaction and Light are positively correlated and point towards an in-plot group. In opposite, the nutrient´s vector increases away from the in-plots´ centroid. Also, the Indicator Species Analysis identified character species of alkaline and lightful habitats as strong indicators for the vegetation in forests inside of the SNP and species occurring on acid soils with raw humus for the out-plots. Yet, few indicator species have been identified (5 inside, 3 outside, for the list of Indicator Species see App. Tab. 5, 6). The analysis of vegetation composition showed a significant difference of variance between the groups (p-value 0.003, CI 95 %, PERMDISP, 999 permutations) which is also seen in Fig. 7 as the out-vegetation surveys are distributed more widely over the ordinal space than the in-plots. I. e. the obtained significant p-value of 0.01 (CI 95 %, PERMANOVA, 999 permutations) for a difference in species composition may be due to divergent variances.

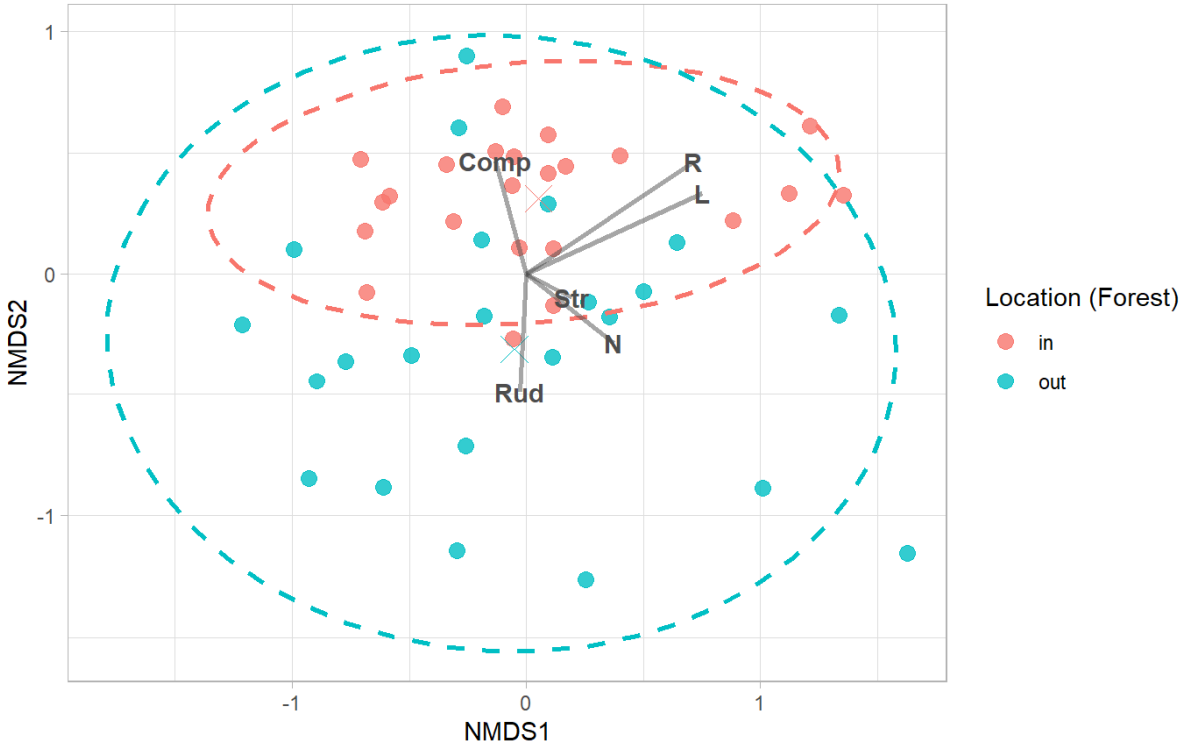

Figure 7: The Non-metric Multidimensional Scaling (NMDS) of vegetation composition in forests inside (in) and outside (out) the Swiss National Park displays vegetation surveys as points and the groups´ centroids as crosses in the ordinal space. (Final stress: 0.19 after 20 tries). The Confidence Ellipsis is at 95 %. Landolt Indicator Values for Light (L), Nutrients (N) and Soil Reaction (R) as well as Grime Strategies Competitiveness (Comp), Stress Tolerance (Str) and Ruderality (Rud) are fitted onto the ordination.

4. Discussion

This study compares the effect of long-term abandonment on herb-layer´s species richness and composition of subalpine pastures and forests. Against hypotheses, mean species numbers, LIVs and Grime strategy components are in general similar on pastures and forests inside and outside the SNP. At local scale, significant differences have been found for grasslands regarding species diversity as well as Competitiveness and Ruderality. At landscape level, species diversity and richness were lower inside the SNP. This was especially pronounced in forests, where overall a higher variance in the vegetation composition was displayed.

4.1 Grassland

Vegetation diversity and composition on a local scale

As I assumed grazing by cattle to be an important factor shaping vegetation, I expected according to the Intermediate Disturbance Hypothesis, changes towards a more homogenous vegetation dominated by shade tolerant competitive species to the detriment of ruderal species inside the SNP. In addition, after grazing cessation rising C:N ratios in increasing biomass accumulation was reported (Gavrichkova et al., 2022; Seeber and Seeber, 2005). Also Tappeiner and Cernusca (1993) observed this and inferred lower nutrient availability as they are stored in the slowly decomposed organic matter. Hence, I expected more species with low nutrient demand in the SNP. Yet, significant differences have only been demonstrated for diversity on local scale and the Grime Strategies Competitiveness and Ruderality but these variables could contribute especially to the difference in vegetation composition in- and outside the SNP considering results of the NMDS. A higher share of competitive species and lower diversity inside the SNP are in line with other studies reporting that competitive and vegetatively propagating species expand to the disadvantage of generatively propagating when grazing ceases (Hard, 1976 in Maag et al. 2001). Especially grasses are observed to become dominant (Prévosto et al., 2011; Rudmann-Maurer et al., 2008) not only due to fast clonal growth but also fast production of leaves (Firn et al., 2016) and by reducing light availability on the ground because of their high growth (Dudova et al., 2019). A high share of ruderal species in grazed communities is also shown by others, whereby the main factors of how cattle impact vegetation can be summarized as dung deposition, herbage removal and disturbance by trampling (Kohler et al., 2006). In accordance, Pierce et al. (2007) showed that in grazed communities the share of ruderals rises as not only the disturbance by grazing and trampling advantages them but also the redistribution of nutrients and therefore their heterogenous local abundance. This favours species that are able to develop and reproduce fast before nutrients become depleted (Craine, 2005) which may explain that some plots with a high share of ruderal traits also exhibit a high share of species with elevated nutrient demand. At the same time, nutrient-poor patches with high light availability are created when biomass is removed by extensive grazing, supporting high species diversity (Poschlod and WallisDeVries, 2002). Also several studies in the subalpine zone reported a decrease of plants with low nutrient demand when grazing ceases (Mayer et al., 2008; Prévosto et al., 2011; Tasser and Tappeiner, 2002). The authors explain the decrease not only by the heterogenous nutrient input in space and time, but also to be due to selective grazing removing biomass especially of nutritive plants. Thus, both rather high and low nutrient values occur under grazing by cattle while values inside the SNP have a narrower range indicating rather nutrient poor site conditions. This might explain why the arithmetic mean shows no major difference between the SNP and surrounding area. The same pattern may be the case for the observed distribution of Light-values.

Findings of Schütz et al. (2003) might explain why successional patterns are not found to be as pronounced as presumed. The authors revealed different successional pathways for abandoned pastures in the SNP depending on their successional starting point and herbivory by wild ungulates: They showed that due to a rising red deer (*Cervus elaphus*) density following the establishment of the SNP, grazing pressure on abandoned pastures increased again and so did species richness as well as small light demanding species. Vegetation composition subjected to high grazing pressure by wild herbivores exhibited small changes when the vegetation at the starting point of succession belonged to the *Poion alpinae* association, but rising species numbers on formerly intensively grazed and nutrient rich areas as red deer hinds prefer these (Schütz et al., 2000). On the nutrient poor edges of former pastures, grazing by wild herbivores occurs less intensive and grassland dominated by *Nardus stricta* develops. This a typical successional stage on nutrient-poor soils when grazing ceases (Spatz, 1980) as *Nardus stricta* is able to resist grazing and trampling and can expand when grazing ceases due to its competitive force. Moreover, it can compete with acidification after grazing cessation (Mayer et al., 2012). This successional pathway is e. g. reported for Alp la Schera (Schütz et al., 2000) for which this study´s data also confirm the suggested pattern of low diversity and high proportion of competitive traits on acidic soil. As the ISA identified both species of nutrient-poor grasslands as well as species of the *Poion alpinae*-community as Indicator Species for the vegetation inside the SNP, it supports the trend of these two successional pathways. The current successional stages of *Poion-alpinae*-communities and nutrient-poor grasslands are thereby considered to be still relatively species rich (Spatz, 1980). These findings highlight, that besides starting point and biotic factors also time passed since abandonment needs to be considered when comparing species richness and composition of abandoned to those of constantly used areas.

In addition to the presumed strong influence of grazing, also abiotic conditions may shape the observed pattern in vegetation composition. Ferré et al. (2020) showed chemical and physical soil properties to be evenly important for the occurrence of Grime Strategies as grazing. They found shallow subalkaline soils under dry conditions to support increased stress tolerators and diversity, a pattern which is also in this study visible especially for the Buffalora plot group regarding Soil Reaction, Light and Diversity. Also, in grazing exclusion experiments, the response of diversity and vegetation composition was shown to differ depending on soil type and elevation (Mayer and Erschbamer, 2017). In addition, especially in habitats with strong environmental constraints as they occur in the subalpine to alpine zone, some studies showed that these affect plant diversity more than management intensity (Orlandi et al., 2016; Pittarello et al., 2020). Here, Ferré et al. (2020) emphasize that environmental conditions of low productivity and short growing season in the high mountain zone favour stress tolerating plants. For example, *Sesleria* grasslands as they are indicated to occur in the SNP, display an overall inclination towards stress tolerating species (Ferré et al., 2020; Kammer and Möhl, 2002). That the environmental conditions themselves might not be substantially altered by land-use could especially be the case for Soil Reaction values exhibiting a very similar distribution. Mountain soil properties are considered to be influenced besides land-use and bedrock, which was controlled in this study, by a variety of variables such as climate, geomorphic processes and time (Egli and Poulenard, 2016). The importance of other factors than land-use in determining habitat conditions and therefore vegetation composition could also account for the alpine in- and out-plots as both are characterized by calcareous lightful and nutrient-poor conditions with a low share of ruderal traits. This may rather mirror conditions in alpine habitats than the effect of grazing. These considerations might also explain, why vegetation inside and outside the SNP exhibits especially for Stress Tolerance and Reaction Values no conspicuous different patterns. To

clarify both the importance of land-use versus other abiotic factors for vegetation composition and the impact of land-use on abiotic factors themselves, further factor analyses are recommended.

Effects at landscape scale

That the vegetation surveys outside the SNP display a wider range of nutrient and light requirements in addition to a higher species richness and diversity outside than inside at landscape level than at mean plot level, points towards observations of Dullinger et al. (2003). They report declining species richness and diversity at landscape level interpreting that pattern as rather a homogenization of the landscape when land-use ceases than a loss of biodiversity on small scale. Therefore, a main effect of the continued land-use may be the creation of heterogenous conditions regarding nutrient and light conditions on a landscape scale.

4.2 Forest

Vegetation diversity and composition on a local scale

As on grasslands, I expected human activities to act as disturbance in mountain forests. According to the Intermediate Disturbance Hypothesis and models predicting a closer canopy-cover within three decades after ceased disturbances in mountain forests (Stritih et al., 2023), I assumed a shift towards shade tolerant and competitive species inside the SNP. Regarding understory species richness, it was shown that in later successional stages species richness rises after an initial drop in the stem exclusion stage (Thom and Seidl, 2022). These tendencies could partly be observed in this study. Dugiud and Ashton (2013) were unable too, to report clear differences in species richness during the initial and stem exclusion stage after 50 years based on a review on the effect of management on understory vegetation in temperate forests with un-logged stands as controls. The authors emphasise therefore to consider successional age when analysing understory species richness. Regarding Grime Strategies, a tendency towards higher competitive and lower ruderal strategists inside the SNP was found to characterize the difference of vegetation composition in- and outside the SNP. One factor driving this pattern might be the use of forests as wood-pastures. Buttler (2014) summarized similar effects of cattle activity in forests as on grasslands: Wood-pastures harbour high species numbers and allow less competitive, light demanding species to grow. Also in this study, plots in wood-pastures exhibited a rather high share of stress and disturbance tolerating species. They also exhibited partly a high share of nutrient demanding species, yet the distribution of N-values is similar inside and outside the SNP. This finding contrasts expectations as studies in the Bavarian Alps on managed forests revealed a degradation of calcareous soils after silvicultural practices such as selective harvesting and clear-cutting (Christophel et al., 2013; Katzensteiner, 2003). The authors conclude that biomass extraction and faster litter decomposition after opening of the soil decrease nutrient stocks. Here, further research on current harvesting practices and intensity may clarify observed pattern in nutrient availability. For the LIVs Light and Reaction the opposite trend as expected was found: higher values occurred inside the SNP. That especially for Light unexpected tendencies are shown, may, as on grasslands, be partly caused by grazing of wild ungulates. It is assumed to play a major role in altering species composition as it creates open patches in the forest and therefore favours species diversity and light demanding species (Meier et al., 2017). As the density of ungulates rose considerably also in the forests of the SNP after its implementation (Fluri et al., 2023), they might contribute to the observed high share of light demanding species and maintenance of diversity on a similar level as outside at local scale.

Besides the direct impact of land-use, it is also for forests that the successional starting point and therefore stand age and structure are important for the current herb-layer vegetation composition. Marengo et al. (2025) found the understory composition of forests on former grassland to exhibit a higher share of heliophilous and ruderal species than those developing on former wooded areas. In addition, Kreyling et al. (2008) showed for coniferous forests in Canada that after two to three decades, understory vegetation of secondary grown forests developed slowly and was still similar to that of clear-cuts. As most of the forests in the SNP established on clear-cuts, this legacy might therefore contribute to the little differences seen now in vegetation composition. Concerning stand structure, Chevaux et al. (2022) reported the indirect effect of management on crown cover, hence, light availability, to be more important for understory species diversity than its direct impact by disturbance. A closer canopy cover in unmanaged stands disfavours thereby species richness and light demanding species. Yet, in the SNP the current successional stage is marked by dying of crowns of dominating *Pinus mugo* (Hauenstein, 2011) which may lead to patches of higher light availability and therefore contribute to the higher share of light demanding species in the SNP. Here, further analysis on successional stages is needed to better understand underlying mechanisms for the current vegetation patterns.

At last, also in forests natural environmental conditions may be equally important as the effect of land-use for vegetation composition. Stähli et al. (2006) showed that forests on the area of the Swiss National Park are long-term dominated by *Pinus mugo* whereas forests in the region of Fuldera, where pair plots are located, consist mainly of *Picea abies*. While *Pinus mugo* forests naturally occur on rather dry and lightful habitats and show lowest crown closure in contrast to *Picea abies* and *Larix decidua*, *Picea abies* tolerates shady conditions (Risch et al., 2003). In addition, *Picea abies* is shown to lower the pH value in the topsoil by its needles (Ewald, 2000). This might be also the case in this study as most of plots in *Picea abies* forests indicate acidic conditions. Though, human land-use is considered to have maintained that pattern as *Pinus mugo* profited from the anthropogenic disturbances (Parolini, 2012). This may explain results of the ISA identifying lightful and calcareous habitats favouring species in the SNP versus rather to acidic conditions belonging species outside as characteristic. Yet these results should be interpreted carefully as only few indicator species are identified. Again, also small-scale environmental conditions might have a dominant effect on species composition as e. g. a distinct in-plot group in the forest near Alp la Schera display very low Soil Reaction values but in-plots near Alp Stabelchod high ones with also high Light-values and high diversity. One factor might be elevation since for example both ecotone-plots in- and outside of the SNP display a high share of light demanding and stress tolerating species favouring neutral to alkaline soil. This may reflect a more open canopy cover and harsher growing conditions in higher elevations what also Stritih et al. (2023) modelled for mountain forests. As on grassland, restricted growing conditions in the subalpine zone might also contribute to the un-pronounced differences of stress tolerating plants. Thus, already existing site conditions intermingled with land-use may be mirrored especially in the observed LIVs regarding high light demand inside and lower soil reaction values outside of the SNP.

Effects at landscape scale

In forests, the difference of nearly even species richness at local scale but higher species numbers at landscape level outside the SNP than inside is even more pronounced as on grasslands. The higher species richness on large scale is thereby in line with the very high variance in species composition outside. This presumably mostly contributes to the significant difference in vegetation composition in- and outside the SNP as the fitted LIVs are just partly related to distinctive plot-groups in- and outside

the SNP. This may suggest again that the most pronounced effect of land-use captured in this study might be the creation of heterogeneity favouring different species compositions.

5. Conclusion

This study showed for herb layer on pastures and in forests minor differences in vegetation composition regarding habitat requirements in- and outside the SNP but a divergent distribution of the share of competitive and ruderal strategies, especially pronounced on pastures. This indicates that extensive pastoral and silvicultural practices alter more unidirectional the distribution of competitive strategies than habitat conditions. The thereby higher species richness and diversity at a landscape scale with especially in forests conspicuous higher variance in vegetation surveys outside the protected area, point to a more heterogeneity creating effect of land-use than of natural dynamics on a large scale. Since changes expected to happen after long-term land-abandonment could only partly been reported in the protected area, it implies the importance to examine further processes in an ecosystem to clarify the impact of land-abandonment. This may comprise to conduct causal investigations on the role of abiotic conditions since fine scale topography and elevation as well as biotic factors such as influence of wild herbivores or forest stand dynamics. These causal analyses may further contribute to understand which processes take place when pastoral and silvicultural use ceases and therefore where and when to concentrate efforts for biodiversity conservation.

Acknowledgment

I want to thank especially Raphael von Büren for his full support and confidence from the field work on until writing the last sections. Thanks to Sonja Wipf who helped getting the work off the ground and Jürgen Kreyling for his reliable availability for questions of any kind. I very value Maria´s sharp thoughts and Harry for sharing his skills and knowledge with much patience.

References

Amt für Wald und Naturgefahren, 2025a. Waldstandorte. Geoportal des Kantons Graubünden. https://geo.gr.ch/karten/interaktive-karten (acessed 12.08.2025)

Amt für Wald und Naturgefahren, 2025b. Wald-Weide. Geoportal des Kantons Graubünden. https://geo.gr.ch/karten/interaktive-karten (acessed 12.08.2025)

Anderson, M.J., 2008. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Anderson, M.J., 2006. Distance-Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62, 245–253. https://doi.org/doi.org/10.1111/j.1541-0420.2005.00440.x

Bebi, P., Seidl, R., Motta, R., Fuhr, M., Firm, M., Krumm, F., Condera, M., Ginzler, C., Wolgemuth, T., Kulakowski, D., 2017. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. For. Ecol. Manag. 388, 43–56.

Bonari, G., Bricca, A., Tomasi, G., Dorigatti, L., Bertolli, A., Andretta, D., Sabatini, F.M., Di Musciano, M., Prosser, F., 2025. Grassland Changes in the Eastern Alps Over Four Decades: Unveiling Patterns Along an Elevation Gradient. Appl. Veg. Sience 28:e70012. https://doi.org/10.1111/avsc.70012

Buttler, A., 2014. Grasslands in silvopastoral mountain ecosystems, in: Grassland Biodiversity and Conservation in a Changing World, Environmental Science, Engineering and Technology. Nova Science Publishers, United Kingdom.

Chemini, C., Rizzoli, A., 2003. Land use change and biodiversity conservation in the Alps. J. Mt. Ecol. 7 (Suppl.), 1–7.

Chevaux, L., Mårell, A., Baltzinger, C., Boulanger, V., Cadet, S., Chevalier, R., Debaive, N., Dumas, Y., Gosselin, M., Gosselin, F., Rocquencourt, A., Paillet, Y., 2022. Effects of stand structure and ungulates on understory vegetation in managed and unmanaged forests. Ecol. Appl. 32, e2531. https://doi.org/doi.org/10.1002/eap.2531

Christophel, D., Spengler, S., Schmidt, B., Ewald, J., Prietzel, J., 2013. Customary selective harvesting has considerably decreased organic carbon and nitrogen stocks in forest soils of the Bavarian Limestone Alps. For. Ecol. Manag. 305, 167–176. https://doi.org/10.1016/j.foreco.2013.05.054

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Cocca, G., Sturaro, E., Gallo, L., Ramanzin, M., 2012. Is the abandonment of traditional livestock farming systems the main driver of mountain landscape change in Alpine areas? Land Use Policy 29, 878–886. https://doi.org/10.1016/j.landusepol.2012.01.005

Craine, J.M., 2005. Reconciling plant strategy theories of Grime and Tilman. J. Ecol. 93, 1041–1052. https://doi.org/10.1111/j.1365-2745.2005.01043.x

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574. https://doi.org/10.1890/08-1823.1

Dudova, K.V., Dzhatdoeva, T.M., Dudov, S.V., Akhmetzhanova, A.A., Tekeev, D.K., Onipchenko, V.G., 2019. Competitive Strategy of Subalpine Tall-Grass Species of the Northwestern Caucasus. Mosc. Univ. Biol. Sci. Bull. 74, 179–187. https://doi.org/10.3103/S0096392519030039

Dufrêne, M., Legendre, P., 1997. Species assamblages and indicator species: the need for a flexible and asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Duguid, M.C., Ashton, M.S., 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. For. Ecol. Manag. 303, 81–90. https://doi.org/10.1016/j.foreco.2013.04.009
Dullinger, S., Dirnbröck, T., Greimler, J., Grabherr, G., 2003. A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. J. Veg. Sci. 14, 243–252. https://doi.org/10.1111/j.1654-1103.2003.tb02149.x
Egli, M., Poulenard, J., 2016. Soils of Mountainous Landscapes. Int. Encycl. Geogr. People Earth Environ. Technol.
Ewald, J., 2000. The influence of coniferous canopies on understorey vegetation and soils in mountain forests of the northern Calcareous Alps. Appl. Veg. Sience 3, 123–134. https://doi.org/10.2307/1478926
Federal Office of Meteorology and Climatology MeteoSwiss, 2025. Authomatic weather stations. MeteoSchweiz. URL https://www.meteoswiss.admin.ch/services-and-publications/applications/measurement-values-and-measuring-networks.html#param=messnetz-automatisch&table=false&station=BUF (accessed 15.06.2025).
Federal Office of Topography swisstopo, 2024a. Lithology 500.
Federal Office of Topography swisstopo, 2024b. National Park.
Federal Statistical Office, 2024. Land use and land cover. URL https://www.bfs.admin.ch/bfs/en/home/statistics/territory-environment/land-use-cover.html (accessed 25.11.2024).
Ferré, C., Caccianiga, M., Zanzottera, M., Comolli, R., 2020. Soil–plant interactions in a pasture of the Italian Alps. J. Plant Interact. 15, 39–49. https://doi.org/10.1080/17429145.2020.1738570
Firn, J., Schütz, M., Nguyen, H., Risch, A.C., 2016. Herbivores sculpt leaf traits differently in grasslands depending on life form and land-use histories. Ecology 98, 239–252. https://doi.org/10.1002/ecy.1637
Fluri, J., Anderwald, P., Korner-Nievergelt, F., Wipf, S., Amrhein, V., 2023. The Influence of Wild Ungulates on Forest Regeneration in an Alpine National Park. Forests 14, 1272. https://doi.org/doi.org/10.3390/ f14061272
Gavrichkova, O., Pretto, G., Brugnoli, E., Chiti, T., Ivashchenko, K.V., Mattioni, M., Moscatelli, M.C., Scartazza, A., Calfapietra, C., 2022. Consequences of Grazing Cessation for Soil Environment and Vegetation in a Subalpine Grassland Ecosystem. Plants 11. https://doi.org/10.3390/plants11162121
Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? J. Veg. Sci. 18, 571–582. https://doi.org/10.1111/j.1654-1103.2007.tb02571.x
Grime, J.P., 1988. The C-S-R model of primary plant strategies — origins, implications and tests, in: Plant Evolutionary Biology. Springer, Dordrecht.
Grime, J.P., 1973. Competitive Exclusion in Herbaceous Vegetation. Nature 242, 344–347. https://doi.org/10.1038/242344a0
Haritika, Negi, A.K., 2025. The underestimated role of understory vegetation dynamics for forest ecosystem resilience: a review. Plant Ecol.
Hauenstein, P., 2011. Phänomenales Totholz - Friedhof, Geburtsstätte und Lebensraum zugleich, in: Haller, H., Eisenhut, A., Haller, R. (Eds.), Atlas Des Schweizerischen Nationalparks - Die Ersten 100 Jahre, Nationalpark Forschung in Der Schweiz. Haupt Verlag, Bern.
Info Flora, n.d.
Kammer, P.M., Möhl, A., 2002. Factors Controlling Species Richness in Alpine Plant Communities: An Assessment of the Importance of Stress and Disturbance. Arct. Antarct. Alp. Res. 34, 398–407. https://doi.org/10.1080/15230430.2002.12003510
Kassambara, A., 2023. rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package.
Katzensteiner, K., 2003. Effects of harvesting on nutrient leaching in a Norway spruce (Picea abies Karst.) ecosystem on a Lithic Leptosol in the Northern Limestone Alps. Plant Soil 250, 59–73. https://doi.org/10.1023/A:1022821913932
Kohler, F., Gillet, F., Gobat, J.-M., Buttler, A., 2006. Effect of cattle activities on gap colonization in mountain pastures. Folia Geobot. 41, 289–304. https://doi.org/10.1007/BF02904943

Kreyling, J., Schmiedinger, A., Macdonald, E., Beierkuhnlein, C., 2008. Slow understory redevelopment after clearcutting in high mountain forests. Biodivers. Conserv. 17, 2339–2355. https://doi.org/10.1007/s10531-008-9385-5

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., 2010. Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt, Bern.

Lauber, K., Wagner, G., Gygax, A., 2024. Flora Helvetica - Illustrierte Flora der Schweiz, 7th ed. Haupt Verlag.

MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. J. Environ. Manage. 59, 47–69. https://doi.org/10.1006/jema.1999.0335

Marengo, G., Anselmotto, N., Barberis, D., Lombardi, G., Lonati, M., Garbarino, M., 2025. Land-use legacy drives post-abandonment forest structure and understory in the western Alps. Landsc. Urban Plan. 259, 105357.

Marty, C., Suter, C., 2014. Schneehöhen im SNP. Abnehmende Tendenz und grosse Schwankungen, in: Haller, H., Eisenhut, A., Haller, R. (Eds.), Atlas Des Schweizerischen Nationalparks. Die Ersten 100 Jahre, Nationalpark-Forschung in Der Schweiz. Haupt Verlag, Bern.

Mayer, R., Erschbamer, B., 2017. Long-term effects of grazing on subalpine and alpine grasslands in the Central Alps, Austria. Basic Appl. Ecol. 24, 9–18. http://dx.doi.org/10.1016/j.baae.2017.07.005

Mayer, R., Kaufmann, R., Vorhauser, K., Erschbamer, B., 2008. Effects of grazing exclusion on species composition in high-altitude grasslands of the Central Alps. Basic Appl. Ecol. 10, 447–455. https://doi.org/10.1016/j.baae.2008.10.004

Mayer, R., Nagl, F., Erschbamer, B., 2012. Subalpine Wiesen und Weiden - die Kulturlandschaften der subalpinen Stufe, in: Cattoen, E.-M., Erschbamer, B. (Eds.), An Den Grenzen Des Waldes Und Der Menschlichen Siedlung, Alpine Forschungsstelle Obergurgl. innsbruck university press, Innnsbruck, pp. 11–37.

Meier, M., Stöhr, D., Walde, J., Tasser, E., 2017. Influence of ungulates on the vegetation composition and diversity of mixed deciduous and coniferous mountain forest in Austria. Eur. J. Wildl. Res. 36, 29. https://doi.org/10.1007/s10344-017-1087-4

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O´Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Carceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Oulette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., Borman, T., 2025. vegan: Community Ecology Package. R package.

Orlandi, S., Probo, M., Sitzia, T., Trentanovi, G., Garbarino, M., Lombardi, G., Lonati, M., 2016. Environmental and land use determinants of grassland patch diversity in the western and eastern Alps under agro-pastoral abandonment. Biodivers. Conserv. 25, 275–293. https://doi.org/10.1007/s10531-016-1046-5

Parolini, J.D., 2012. Vom Kahlschlag zum Naturreservat. Geschichte der Waldnutzung im Gebiet des Schweizerischen Nationalparks, Nationalpark Forschung Schweiz. Haupt Berne.

Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R.M., Cerabolini, B., 2007. Disturbance is the principal α-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. J. Ecol. 95, 698–706. https://doi.org/10.1111/j.1365-2745.2007.01242.x

Pittarello, M., Lonati, M., Enri, S.R., Lombardi, G., 2020. Environmental factors and management intensity affect in different ways plant diversity and pastoral value of alpine pastures. Ecol. Indic. 115, 106429.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. Biol. Conserv. 104, 361–376. https://doi.org/10.1016/S0006-3207(01)00201-4

Prévosto, B., Kuiters, L., Bernhardt-Römermann, M., Dölle, M., Schmidt, W., Hoffmann, M., Van Uytvanck, J., Bohner, A., Kreiner, D., Stadler, J., Klotz, S., Brandle, R., 2011. Impacts of Land Abandonment on Vegetation: Successional Pathways in European Habitats. Folia Geobot. 46, 303–325. https://doi.org/10.1007/s12224-010-9096-z

R Core Team, 2024. A language and Environment for Statistical Computing.
Risch, A.C., Nagel, L.M., Schütz, M., Krüsi, B.O., Kienast, F., Bugmann, H., 2003. Structure and long-term development of subalpine Pinus montana Miller and Pinus cembra L. forests in the Central European Alps. Forstwiss. Cent. 122. https://doi.org/doi.org/10.1046/j.1439-0337.2003.03011.x
Rudmann-Maurer, K., Weyand, A., Fischer, M., Stöcklin, J., 2008. The role of landuse and natural determinants for grassland vegetation composition in the Swiss Alps. Basic Appl. Ecol. 9, 494–503. https://doi.org/10.1016/j.baae.2007.08.005
Schärer, W., Jacobi, C., 2000. Assessment zur Nachhaltigkeit der Schweizer Forstpolitik – Die Sicht der Eidgenössischen Forstdirektion | The Sustainability Assessment of the Swiss Forest Policy from the Point of View of the Swiss Forest Agency. Schweiz. Z. Für Forstwes. 151, 484–488. https://doi.org/10.3188/szf.2000.0484
Schütz, M., Risch, A.C., Leuzinger, E., Krüsi, B.O., Achermann, G., 2003. Impact of herbivory by red deer (Cervus elaphus L.) on patterns and processes in subalpine grasslands in the Swiss National Park. For. Ecol. Manag. 181, 177–188. https://doi.org/10.1016/S0378-1127(03)00131-2
Schütz, M., Wildi, O., Achermann, G., Krüsi, B.O., 2000. Predicting the development of subalpine grassland in the Swiss National Park: how to build a succession model based on data from long-term permanent plots, in: Schütz, M., Krüsi, B.O., Edwards, P.J. (Eds.), Sukzessionsforschung Im Schweizerischen Nationalpark: Von Braun-Blanquet's Dauerflächen Zur Modellierung Langfristiger Ökologischer Entwicklungen, Nationalpark Forschung in Der Schweiz.
Seeber, J., Seeber, G.U.H., 2005. Effects of land-use changes on humus forms on alpine pastureland (Central Alps, Tyrol). Geoderma 124, 215–222.
Spatz, G., 1980. Succession patterns on mountain pastures. Vegetatio 43, 39–41.
Stähli, M., Finsinger, W., Tinner, W., Allgöwer, B., 2006. Wildfire history and fire ecology of the Swiss National Park (Central Alps): new evidence from charcoal, pollen and plant macrofossils. The Holocene 805–817. https://doi.org/10.1191/0959683606hol967rp
Stritih, A., Seidl, R., Senf, C., 2023. Alternative states in the structure of mountain forests across the Alps and the role of disturbance and recovery. Landsc. Ecol. 38, 933–947. https://doi.org/10.1007/s10980-023-01597-y
Tappeiner, U., Cernusca, A., 1993. Alpine Meadows and pastures after abandonment - Results of the Austrian MaB-programme and the EC-STEP project INTEGRALP. Pirineos 141–142, 97–118. https://doi.org/10.3989/pirineos.1993.v141-142.166
Tasser, E., Tappeiner, U., 2002. Impact of land use changes on mountain vegetation. Appl. Veg. Sience 5, 173–184.
Tasser, E., Walde, J., Tappeiner, U., Teutsch, A., Noggler, W., 2007. Land-use changes and natural reforestation in the Eastern Central Alps. Agric. Ecosyst. Environ. 118, 115–129. https://doi.org/10.1016/j.agee.2006.05.004
Thom, D., Seidl, R., 2022. Accelerating Mountain Forest Dynamics in the Alps. Ecosystems 25, 603–617. https://doi.org/doi.org/10.1007/s10021-021-00674-0
Weiss, A., 2001. Topographic Positions and Landforms Analysis.
Wildi, O., 2016. Why mean indicator values are not biased. J. Veg. Sci. 27, 40–49. https://doi.org/10.1111/jvs.12336
Wildi, O., Schütz, M., 2000. Reconstruction of a long-term recovery process from pasture to forest. Community Ecol. 1, 25–32.

Appendix

Table 1: Properties of the surveyed plots. Plots on grassland within or outside the Swiss National Park are referred to as in- or out_open, respectively. Plots in forests as in- or out_forest.

Plot	Longitude (LV95)	Latitude (LV95)	Altitude m.a.s.l.	Location
Bp1_B	2814208.04	1171751.69	1930.2	in_open
Bp1_pair	2825581.39	1167049.96	1930.9	out_open
CiN1	2810973.81	1169309.83	2060	in_open
CiN1_pair	2817655.37	1164864.64	2050.9	out_open
CiN2	2810972.47	1169306.92	2065	in_open
CiN2_pair	2817622.94	1164833.04	2042.9	out_open
Cxs1	2814456.44	1171888.38	1958.5	in_open
Cxs1_pair	2816700.26	1169965.7	1973.6	out_open
Cxs2	2814256.97	1171671.77	1931	in_open
Cxs2_pair	2825436	1167061.66	1925.3	out_open
Fe1a	2814468.58	1171889.13	1959.4	in_open
Fe1a_pair	2816663.97	1169952.48	1971	out_open
Fe2	2814524.72	1171926.13	1966.5	in_open
Fe2_pair	2816556.75	1169973.01	1969.4	out_open
FN1	2810989.11	1169589.39	2117	in_open
FN1_pair	2814827.23	1176173.98	2120	out_open
FN2	2810989.34	1169592.49	2117	in_open
FN2_pair	2817963.6	1164857.12	2094.8	out_open
FN3	2810958.1	1169311.5	2066	in_open
FN3_pair	2817805.35	1164821.97	2057.5	out_open
Gri1_C	2810406.23	1172005.91	2051.1	in_open
Gri1_pair	2819596.17	1176103.6	2072.8	out_open
Gri2_D	2810393.35	1171969.72	2058.2	in_open
Gri2_pair	2816144.41	1169474.81	2060.8	out_open
Gri3_C	2810404.81	1172016.07	2060.8	in_open
Gri3_pair	2819569.52	1176039.14	2077.3	out_open
Gri4_D	2810386.68	1171971.18	2040	in_open
Gri4_pair	2819581.82	1176044.45	2069.6	out_open
HiN1	2810961.75	1169350.2	2080	in_open
HiN1_pair	2817906.33	1164706.33	2056.4	out_open
IlPra_D	2814464.9	1171779.04	1947.4	in_open
IlPra_pair	2816609.66	1169968.5	1970.4	out_open
Lav1	2810878.49	1169985.07	2062.7	in_forest
Lav1_pair	2820597.68	1169041.81	2079.8	out_forest
Lav2	2810885.43	1169983.22	2047.4	in_forest
Lav2_pair	2820521.98	1168905.04	2081.7	out_forest
Lav3	2810880.61	1169979.96	2062.7	in_forest
Lav3_pair	2820503.08	1168969.59	2076.8	out_forest
Lav4	2810876.42	1169982.37	2055.2	in_forest
Lav4_pair	2820494.26	1169041.98	2071	out_forest
Lav5	2810875.38	1169980.74	2058.3	in_forest
Lav5_pair	2820471.05	1169000.95	2068	out_forest
Lav6	2810877.59	1169978.26	2062.7	in_forest

Lav6_pair	2820571.04	1169020.65	2078.7	out_forest
Mi15a	2818939.54	1178986.52	1710	in_open
Mi15a_pair	281465.12	1167820.8	1727.9	out_open
Mu1_C	2815466.43	1171918.06	2244.3	in_open
Mu1_pair	2815388.86	1175474.93	2258.6	out_open
Mu4_A	2815421.94	1169894.35	2228	in_forest
Mu4_pair	2815266.8	1169413.41	2244.6	out_forest
Mu5_A	2814609.3	1169921.06	2286.7	in_open
Mu5_pair	2814892.17	1169496.36	2295.3	out_open
PF1	2810960.32	1169332.95	2071	in_open
PF1_pair	2818001.94	1164640.15	2053.9	out_open
PF13_B	2810918.31	1169538.45	2086.6	in_open
PF13_pair	2819122.18	1163984.54	2097.3	out_open
PF2	2810955.71	1169328.84	2071	in_open
PF2_pair	2817939.46	1164709.39	2058.9	out_open
Pin1a	2814102.89	1171628.11	1916	in_forest
Pin1a_pair	2825734.27	1166945.61	1909.1	out_forest
Pin1b	2814105.44	1171626.36	1916	in_forest
Pin1b_pair	2825599.21	1166896.87	1891	out_forest
Pin2_A	2814101.29	1171619.47	1912.4	in_forest
Pin3_A	2813698.28	1171758.84	1899.9	in_forest
Pin3a_pair	2819775.94	1168445.47	1880.6	out_forest
Pin3b_pair	2819788.66	1168485.18	1880.8	out_forest
S2_A	2808570.4	1171428.14	1676.2	in_open
S2_pair	282871.23	1167722.62	1700.1	out_open
S30a	2811179.45	1172036.35	1898	in_forest
S30a_pair	2802743.49	1173333.03	1878.6	out_forest
S30b	2811177.65	1172033.2	1898	in_forest
S30b_pair	2802781.27	1173331.86	1901.6	out_forest
S30c	2811181.86	1172034.76	1898	in_forest
S30c_pair	2802715.89	1173296.05	1880.6	out_forest
S30d	2811181.24	1172031.67	1898	in_forest
S30d_pair	2802679.44	1173161.11	1892	out_forest
S30e	2811180.34	1172029.8	1898	in_forest
S30e_pair	2802767.32	1173372.59	1872.8	out_forest
S31a	2811189.75	1171991.66	1909	in_forest
S31a_pair	2825784.5	1164439.2	1891.7	out_forest
S31b	2811192.13	1171989.72	1908	in_forest
S31b_pair	2825764.23	1164438.56	1897.1	out_forest
S32a	2811201.1	1171990.82	1909	in_forest
S32a_pair	2824820.87	1167386.55	1914.2	out_forest
S39	2811219.91	1172068.87	1892	in_forest
S39_pair	2807430.3	1173502.13	1913.1	out_forest
S40	2811204.57	1172066.11	1891	in_forest
S40_pair	2807410.04	1173523.65	1902.1	out_forest
S41	2811202.19	1172066.11	1891	in_forest
S41_pair	2802685.94	1173043.25	1911.7	out_forest
S45_C	2811882.23	1171521.6	1843.3	in_forest
S45_pair	2820629.81	1177790.47	1828.1	out_forest
Tr1_A	2814417.62	1171762.54	1946.6	in_open

Tr1_pair	2816478.83	1170029.31	1966.9	out_open
Tr2_A	2814407.74	1171673.68	1940.2	in_open
Tr2_pair_2	2824816.34	1167494.29	1940.4	out_open
Tr3_A	2814393.28	1171734.49	1943.9	in_open
Tr3_pair	2816439.09	1170225.38	1965.1	out_open
Tr4_A	2814413.2	1171753.36	1936.3	in_open
Tr4_pair	2816484.33	1170050.26	1967.5	out_open
Tr5	2814381.51	1171714.52	1939.8	in_open
Tr5_pair	2816404.4	1170199.68	1960	out_open
Tr6_D	2814494.26	1171859.04	1955.1	in_open
Tr6_pair	2817200.72	1169837.94	1985.9	out_open

Table 2: Procedure for the creation of paired plots to the existing plots in the Swiss National Park.

Factor	**Resolution[1]**	**Conditions[2]**		
		1st iteration	2nd iteration	3rd iteration
Elevation	4 m	± 20 m		
Slope	4 m	± 10°		
Slope	20 m	± 10°		
Aspect	4 m	± 45°		
Aspect	20 m	± 45°		
TPI[3]	4 m	± 0.4 m		± 1 m
TPI	20 m	± 2 m		± 5 m
Geology		same TEKT_CODE[4]	same geology_simplify[5]	
Forest or no forest		forest = forest/no forest = no forest		
Historically grazed		historically grazed = historically grazed		no condition

[1]**Resolution**: The used elevation model has a resolution of 2 m. It was interpolated to 4 m or 20 m respectively. Both models were used to create pair-plots with the same factors at fine-scale (4 m) and broad-scale (20 m).
[2]**Conditions**: Pair-plots were created in 3 iterations. In the 1st one, the strictest conditions were applied. For those plots for which no pair-plots could be obtained, less strict conditions were applied in the 2nd and if needed 3rd iteration as displayed in the table.
[3]**TPI (Topographic Condition Index)**: The difference between the elevation of a central cell and the average height of the 8 surrounding cells based on Weiss (2001).
[4]**TEKT_CODE**: 22 tectonic categories based on a tectonic map of the Swiss National Park
[5]**geology_simplify**: the 22 tectonic categories have been simplified into: calcareous, dolomite, verrucano, lakes

Note: Table and comments adapted from R. S. von Büren (personal communication, 26.07.2025)

Table 3: Results of the presence/absence-based Indicator Species Analysis displaying all species being significant Indicator Species (p-value < 0.05) for the vegetation on grasslands inside of the Swiss National Park. A square rooted Indicator Value (IV) > 0.50 is considered as strong indicator. The frequency is indicated for inside (in) and outside (out).

Indicator Species in	$\sqrt{\mathbf{IV}}$	**p-value**	**Frequency**	
			in	out
Galium anisophyllon	0.81	0.005	28	13
Achillea millefolium	0.73	0.025	25	16
Potentilla crantzii	0.69	0.005	17	4
Cerastium arvense	0.68	0.005	16	3
Carex sempervirens	0.66	0.005	16	4
Cirsium acaule	0.64	0.020	17	7
Botrychium lunaria	0.62	0.005	13	2
Senecio abrotanifolius	0.56	0.005	10	1
Ranunculus acris	0.55	0.035	11	3
Phleum alpinum	0.46	0.015	7	1
Poa pratensis	0.42	0.05	5	0
Taraxacum officinale aggr.	0.42	0.05	5	0

Table 4: Results of the presence/absence-based Species Indicator Analysis displaying all species being a significant Indicator Species (p-value < 0.05) for the vegetation on grasslands outside of the Swiss National Park. A square rooted Indicator Value (IV) > 0.50 is considered as strong indicator. The frequency is indicated for inside (in) and outside (out).

Indicator Species out	$\sqrt{\mathbf{IV}}$	**p-value**	**Frequency**	
			in	out
Ligusticum mutellina	0.65	0.005	1	13
Leontodon hispidus	0.63	0.010	6	16
Taraxacum alpinum aggr.	0.59	0.005	0	10
Polygonum viviparum	0.56	0.050	4	12
Anthyllis vulneraria	0.55	0.035	3	11
Gentiana campestris	0.55	0.035	3	11
Agrostis alpina	0.53	0.005	1	9
Leontopodium alpinum	0.53	0.005	0	8
Rumex alpestris	0.53	0.015	0	8
Euphrasia salisburgensis	0.50	0.035	2	9
Antennaria dioica	0.50	0.025	1	8
Selaginella selaginoides	0.50	0.050	1	8
Trifolium thalii	0.49	0.025	0	7
Elyna myosuroides	0.46	0.045	1	7
Globularia cordifolia	0.46	0.025	0	6

Table 5: Results of the presence/absence-based Species Indicator Analysis displaying all species being a significant Indicator Species (p-value < 0.05) for the vegetation in forests inside of the Swiss National Park. A square rooted Indicator Value (IV) > 0.50 is considered as strong indicator. The frequency is indicated for inside (in) and outside (out).

Indicator Species in	$\sqrt{\mathbf{IV}}$	**p-value**	**Frequency**	
			in	out
Melampyrum pratense	0.81	0.005	17	2
Pinus mugo	0.78	0.005	18	5
Erica carnea	0.77	0.020	21	11
Galium anisophyllon	0.55	0.020	7	0
Luzula sieberi	0.51	0.025	6	0

Table 6: Results of the presence/absence-based Species Indicator Analysis displaying all species being a significant Indicator Species (p-value < 0.05) for the vegetation in forests outside of the Swiss National Park. A square rooted Indicator Value (IV) > 0.50 is considered as strong indicator. The frequency is indicated for inside (in) and outside (out).

Indicator Species out	$\sqrt{\mathbf{IV}}$	**p-value**	**Frequency**	
			in	out
Melampyrum sylavticum	0.75	0.005	0	13
Calamagrostis villosa	0.7	0.15	2	13
Galium pumilium	0.52	0.025	1	7