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Restoration methods promote plant diversity of semi-natural grasslands in the Swiss Plateau

Master Thesis

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Environment and Natural Resources

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Abstract

Traditionally managed grasslands are well-known biodiversity hotspots in the European cultural landscape. Though, despite continuous extensive management, many show their plant diversity decreasing. The restoration of these degraded grasslands has gained importance in recent years due to the ongoing loss of farmland biodiversity, but remains, nevertheless, a challenge. Many active restoration methods exist – such as reseeding using hay transfer or with a regional natural or commercial seed mixtures – and have been shown to improve plant diversity successfully when applied in combination with soil disturbance. However, the outcome of grassland restoration is difficult to predict as it strongly depends on regional conditions and these methods have not yet been studied Switzerland. In this study, we experimentally tested at the field (i.e., meadow) scale four active restoration methods that included without any seed addition or soil disturbance. This was replicated in 12 regions spread over the Swiss Plateau. Each region was assigned to one species-rich donor meadow where natural seeds and green hay were harvested and distributed on the restoration meadows. All vascular plants and their cover were recorded in two permanent plots (8 m^2 each) one year before restoration (in 2018) and two years after restoration (in 2021, restoration occurred in spring 2019). In addition, the number of QII plant indicator species were recorded in a 3-m diameter plot (QII for quality two level, based on the Swiss ecological quality assessment method, see main text for more details). Total species richness of both permanent plots increased by 9 ± 1 species per meadow. Restoration was even more successful when measured in terms of QII plant indicators, with an increase of 5.7 ± 0.4 indicators and higher explained variance estimated by restoration treatment ($R^2 = 0.57$). Meadows restored with SC harboured both the highest plant species richness and the most QII species. Beta diversity, however, was lower in SC than in HP or SN. The HH treatment resulted in a smaller increase in plant species richness than the HP treatment, which was related to less soil disturbance during the restoration process. We tested if some environmental parameters affected the restoration and found that soil phosphate content negatively correlated with species richness. Using community-weighted mean analyses, we found that specific leaf area (SLA) was low in SC and SN. In SN also the month of first flowering was significantly later. The number of seeds and seed mass showed significant differences between treatments and was particularly high in HP whereas seed mass was low in C. These short-term effects (after two years) of grassland restoration are promising but we expect that plant communities will undergo further changes in species composition and plant species richness within the next few years. We recommend that the evaluation is repeated in two and four years.

1 Introduction

Semi-natural grasslands managed as hay meadows are an essential element of plant diversity and the cultural landscape not just in Switzerland but in all of Europe (Dengler et al., 2014). This valuable habitat is exposed to several threats, such as intensification, abandonment, eutrophication, climate change and invasive species (Squires et al., 2018). The almost complete transformation of extensive hay meadows into intensive grassland since the 1950s has led to dramatic losses of plant species in the Swiss Plateau (Bosshard, 2015). Compared to the agricultural landscape at higher altitudes, plant diversity on the Swiss Plateau is considerably lower (Meier et al., 2021). The intensified land use and nitrogen input as a contribution to the over-fertilization is increasing the homogenization of many near-natural habitats and has led to dwindling populations of habitat specialists and rising populations of nitrophilous generalists (Fischer et al., 2015; FOEN, 2017; Kosonen et al., 2019). This highlights an urgent need to restore plant diversity in semi-natural grasslands wherever possible (Freitag et al., 2021). Biodiversity Promotion Areas (BPAs) were introduced in Switzerland with the aim of maintaining and promoting biodiversity in the agricultural landscape and financially compensating farmers for the adapted use of their land (Guntern et al., 2020). BPAs are agricultural areas with a high importance for biodiversity, such as wildflower strips or hedgerows (Guntern et al., 2020; Herzog & Walter, 2005). The BPA extensively managed meadows are the most popular type of BPA in Switzerland and represent 64% of all BPA and 121’558 ha in 2019 (FOAG, 2020a). In order to receive the basic direct payments, Swiss farmers must manage at least 7% of their land as BPA, i.e., meet the minimum cross-compliance requirements of their land as BPA (FOAG, 2020b). In addition to the input-based payments (QI, for quality level one payments), Swiss farmers are rewarded financially for BPA hay meadows reaching a certain level of botanical quality (QII, for quality level two). This quality level is assessed by plant indicators, specifically the presence of at least six given plant species from a list of indicators (FOAG, 2020b). Even though the amount of QII-meadows has steadily increased in recent years, only 23% of extensively managed meadows reached quality level II in the lowlands (FOAG, 2020a). The management of extensively managed meadows often matches the standard use requirement (first mowing not before June 15 and no fertilization). The aim of this management is to delay the first cut so that plants are able to germinate and plant diversity can increase with time. Specific changes in the mowing regime on these extensively-managed meadows can result in positive effects on invertebrate diversity, but vascular plant diversity did not increase within a study time of 5 years, even though most meadows were managed extensively for much longer (van Klink et al., 2017). Plant diversity may not have increased because of seed limitations resulting from a poor seed bank (Bossuyt & Honnay, 2008) and missing propagules from the landscape (Helsen et al., 2013).

Hay meadows can be restored successfully by seed introduction through natural seed dispersal in regions with ancient and species-rich grasslands (Resch et al., 2021). In a homogeneous landscape like the Swiss Plateau, without a large species pool in the surrounding areas, seed limitation must be overcome by active restoration methods (Helsen et al., 2013; Kiehl et al., 2010). Many studies on grassland restoration report a successful enhancement of species richness and ecosystem functionality by different restoration methods throughout Europe (Albert et al., 2021; Baasch et al., 2016; Fritch et al., 2011). Predicting restoration success is rather difficult and needs to be adapted to local site conditions (Freitag et al., 2021). Spontaneous succession of ex-arable land worked well in dry grasslands where species richness mainly increased with age of the meadow (Prach et al., 2014). Seeding with a commercial seed mixture had a significant positive effect on the establishment of target species in the study of Baasch et al., (2016). However, Albert et al., (2019) suggests using locally harvested seeds or hay transfer from donor meadows. All these restoration methods followed soil disturbance in an existing grassland or were applied on arable land. Soil disturbance has been proven to be crucial because pre-existing vegetation prevents target species from establishing themselves (Bischoff et al., 2018).

Knowing only how species richness changed will never enable us to analyse why some meadows end up with higher species richness or a stable plant community. If we want to better understand why some species establish and others do not, we need to understand what site parameters and functional characteristics the established community has (Hedberg & Kotowski, 2010). Generally, species richness and seed density of seed mixtures are key variables in predicting restoration success (Scotton, 2016). However, the harvested seeds per species have been best explained by method, seed mass, specific leaf area (SLA) and phenology (Albert et al., 2019). Albert et al., (2021) further suggests that higher seed number, lower seed mass and lower reliance on pollinators in restored grasslands indicate a different ecosystem functionality compared to ancient grasslands. SLA is usually positively correlated with the potential relative growth rate and negatively correlated with the investment in leaf protection. So species with a high SLA are more competitive, while species with a low SLA are more stress-tolerant (Mudrák et al., 2018; Westoby, 1998).

The relative effectiveness of different active restoration methods has not been quantitatively studied in Switzerland. And despite the frequent use of grassland restoration in conservation practice, few restoration studies have been conducted on field scale (but see Prach et al., 2014). The advantage of large scale restoration over plot scale is the lower edge effect as propagules from outside are less likely to impact the outcome, and permanent plots can be chosen randomly inside a restored area. Many studies used target species to assess restoration success, which is a comparable approach to the QII species list used in Switzerland (Bischoff et al., 2018; FOAG, 2020b; Kiehl et al., 2010). Nonetheless, studies linked directly to agricultural practice are of high importance in applied ecology. In this thesis we will thus address changes in species richness, QII plant indicators, and plant functional traits of meadows restored by these seed addition methods combined with soil disturbance: Hay transfer and harrowing, hay transfer and ploughing, commercial seed mixture and a naturally collected local seed mixture.

The main questions were: What are the short-term effects of different active restoration methods on vascular plant species richness in extensively-managed meadows? What is the quantitative assessment of QII-indicators on the restoration meadows before and after restoration? Which plant characteristics and functional traits are important for grassland restoration? We expect that restoration should successfully increase species richness and QII indicator richness. In addition, functional traits may show differences between restoration methods that are not reflected by species richness.

This Master thesis is part of a long-term project of the University of Bern. The grassland restoration project, lowland module, of the Division of Conservation Biology was launched in 2018 by Prof. Dr. Raphaël Arlettaz and Dr. Jean-Yves Humbert. In this larger project, the effects of restoration on plant diversity as well as the development of invertebrate diversity, including spiders, ground beetles and pollinators, are studied (e.g. Slodowicz et al., 2019; Stöckli et al., 2021). My contribution to this project was the field work in 2021. Together with Daniel Slodovicz, we sampled all permanent plots and all the QII plots in the restoration meadows. Further, I managed the data collection and the statistical analysis of the first short-term results on vegetation.

2 Methods

2.1 Study sites

The study regions (n=12) were distributed over the western part of the Swiss Plateau with a minimal distance of 10 km between each region (see Fig. 1). Each study region contains five restoration meadows and one donor meadow. This results in a total of 12 x 6 = 72 meadows included in this study, with 12 donor meadows and 60 restoration meadows. All meadows in this study were BPAs extensively managed meadows. The donor meadows were required to host high botanical diversity, which was defined by as a minimum of ten QII indicators present in the entire meadow (see Chap. 2.3). In contrast, restoration meadows had a low botanical diversity, with less than six QII indicators in a plot, despite extensive management for a minimum of 5 years. Note that grazing in autumn was permitted. All meadows are on farmland with productive soils and relatively low inclination by Swiss standards (mean slope = 5° ± 1). The size of the restoration meadows varies from 0.14 ha to 1.1 ha, with a mean of 0.5 ha. Most meadows were formerly used as cropland, intensively managed meadow or pasture.

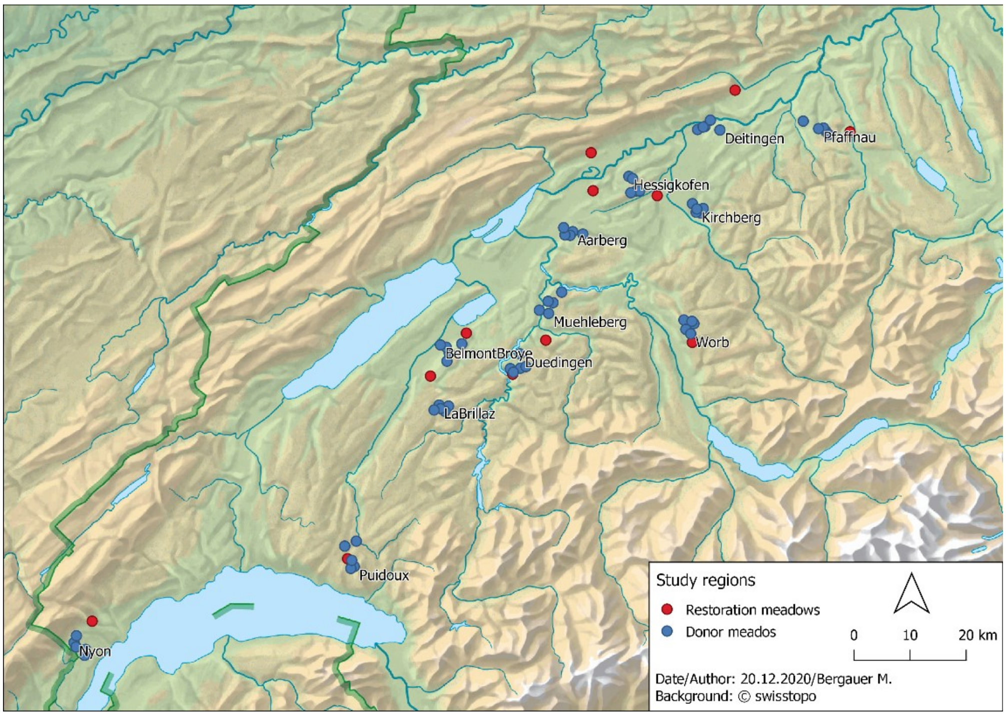


Fig. 1: Map of the 72 study sites with five restoration meadows (blue) and one donor meadow (red) for each of the 12 regions.

2.2 *Experimental design*

Five restoration treatments were randomly assigned and applied to the restoration meadows in early summer 2019. Treatments were carried out on field scale (i.e., one treatment per meadow). The five treatments were:

(i) Control: no seed addition and no soil disturbance (C)

(ii) Hay transfer from a species-rich donor meadow on a harrowed receiver meadow (HH)

(iii) Hay transfer from a species-rich donor meadow on a ploughed receiver meadow (HP)

(iv) Sowing of a commercial seed mixture on a ploughed receiver meadow (SC)

(v) Sowing of a hand-collected seed mixture on a ploughed receiver meadow (SN)

For SC, SN and HP treatments, the meadows were ploughed in early spring. They were then harrowed regularly (every four to six weeks), and shortly before sowing or transferring the hay in May/June, the meadows were harrowed again to level the soil. In the harrowed meadows, the grass was mown about a week before the treatment and a few days before sowing. The soil was then surface harrowed two or three times. For the hay transfer, green hay was cut early in the day on the donor meadows and directly distributed on the restoration meadows. The natural seeds were harvested on the same donor meadows one year prior to the hay transfer, and seeded by hand in 2019. The commercial seed mixture “UFA Salvia CH-G” was seeded using a seed distributor of the provider “UFA Samen”. The seed amount was around 10 g/m^2 and for the species composition see Appendix C.

2.3 Data collection

In 2018, two permanent vegetation plots of 2 m × 4 m (8 m^2) were placed 8 m apart from each other in the restoration meadows and in the donor meadows (Fig. 2). The corner of the first plot was randomly placed with a distance of at least 10 m from the edge of the restored area to avoid edge effects. The corner of the second plot was placed 14 m away from the first corner in a random direction (north, east, south or west). Both corners were permanently marked by a buried magnet. In total, 144 vegetation plots were recorded as baseline data in 2018. Inside each plot, full vegetation relevées were recorded, including all vascular plant species and species cover estimated in percent, with shoot presence. In 2021, we resurveyed the vegetation and species cover in all permanent plots within the restoration meadows. One of the 60 restoration meadows was lost because the level of bare ground was over 70% after restoration and most of the scarce vegetation consisted of the species *Rumex obtusifolius.* Due to heavy rains in 2019, and the comparably steep slope, most of the seeds must have been washed away. This meadow did not resemble any other restoration meadows and was therefore excluded from the study.

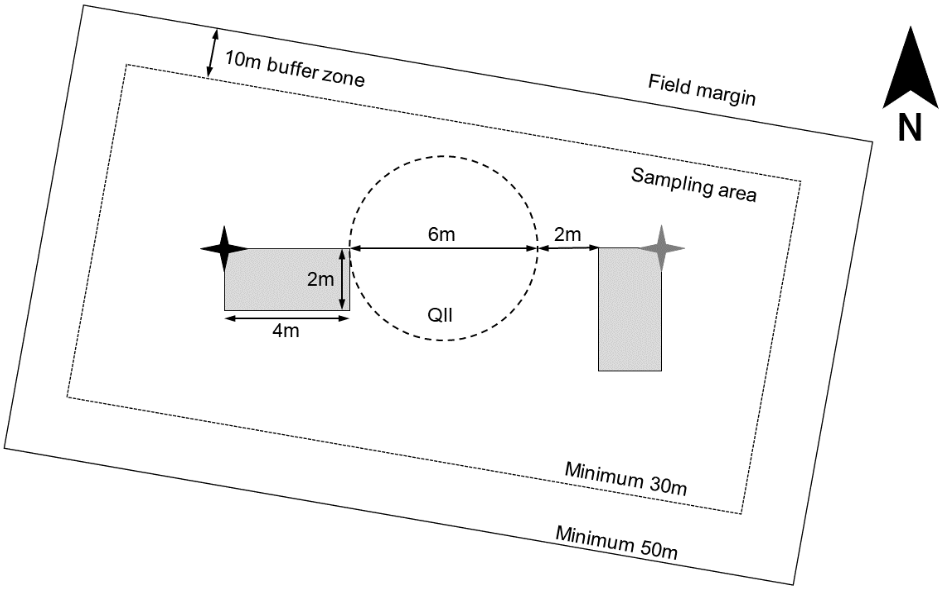


Fig. 2: Sampling scheme. The placement of the permanent plots inside a restoration- or donor meadow. Random point 1 (black star) was set 10 m away from the field border. Random point two (gray star) was placed 14 m away from random point 1 in a random direction (north, east, south or west). In between the centre of the QII plot was placed in a straight line, 7m apart from random point 1.

In addition to the vegetation relevés in the two permanent rectangle plots, the botanical quality of the meadow was assessed using the official quality assessment methods (FOAG, 2020b). This was done by sampling one randomly placed plot between the two permanent plots in all restoration meadows. These QII plots were circular with a radius of 3 m (28 m^2), and the names of present QII indicators were noted. Where this random plot was representative of the whole meadow, no second plot was sampled. However, if the meadow was heterogenous, we individually placed a second plot where the vegetation differed from the first plot. A list of all QII indicators can be found in the quality survey regulations of the Swiss confederation (List B; northern alps, FOAG, 2020b).

Soil samples were extracted in 2018 with a tubular soil core with a diameter of 3.5 cm and a depth of 10 cm on each corner of the vegetation plots. Measured soil properties of the combined samples were: Total nitrogen content (N), total organic carbon (C), C/N ratio, soil phosphorous converted into phosphate content (P), soil pH measured in $CaCl^2$ solution along with clay, silt and sand content (see also Ettlin, 2019).

2.4 Statistical analysis

All statistical analysis were performed using R version 4.0.3 (R Core Team, 2020). For the linear mixed-effect models (LMM) we used the package "lme4" (Bates et al., 2015) and model assumptions were tested using the package "DHARMa" (Hartig, 2020).

The species richness of restoration meadows was calculated by merging the two permanent plots using the cumulative number of species in both plots. This approach was applied to both the baseline data of 2018 and the resurvey of 2021. In addition to species richness per plot (alpha diversity), we also calculated beta diversity using the following formula: $\beta = \gamma - \alpha$ with γ being the total number of species of the same treatment in the 12 regions and α the total number of species per merged plots in a meadow.

The QII indicators list of the quality survey regulations includes species pooled in groups containing difficult distinguishable plants with similar quality characteristics (e.g., *Asteraceae*, yellow, multiple flower heads). Multiple species in one pool are counted as one QII indicator. To create an accurate QII assessment, we pooled the species accordingly. In this analysis only the random plots in between the two vegetation plots were used, and the additional second plots placed on a representative spot were discarded from further analysis since weighted means of these subjectively placed plots and the random plots show a strong correlation (Weinrich, 2018). The number of QII indicators (QII indicator richness) per plot was used as the response variable.

We checked whether environmental parameters had an effect on species richness and QII indicator richness in the restoration meadows, excluding the control. This was done for parameters that are expected to be linked to plant species richness in grasslands: Total nitrogen content (N), soil pH, phosphate (P), time of extensive management in years, species richness of donor meadow, C/N ratio and sand content. The effect of these parameters on species richness was fitted either by linear regression or by polynomial regression. Similarly, the correlation between plant species richness and QII indicator richness was fitted by the most parsimonious model. If a polynomial or non-linear model was suggested by the data, we compared it to the linear model using AICc (Package MuMIn; Barton, 2020) and used the model with the lower AICc value.

The effect of the treatments on species richness, beta diversity and QII indicator richness was tested using a linear mixed-effect model (LMM), with regions as random effect and Gaussian distribution. We checked for differences between control and treatments, as well as among treatments by comparing least-squares means

(Package emmeans; Lenth, 2021). The environmental parameters (see above) were excluded from these models. Model assumptions were tested for normal distribution of residuals was well as zero-inflation by dispersion test, a QQ-Plot of the residuals, and the residual plot vs. predicted treatments (Hartig, 2020). We tested for the presence of spatial autocorrelation using Moran's I but it was never significant.

In addition to species richness and QII indicator richness, a trait-based approach was applied to find differences in restoration methods based on community weighted means of plant functional traits. Functional trait data was downloaded from the LEDA trait database (for detailed information on data collection, see Kleyer et al., 2008). Based on data availability, ecological importance and preliminary results, the following traits were analysed: specific leaf area (SLA; leaf area per leaf dry mass [mm^2 /mg]), number of seeds, seed mass [mg], phenology and functional groups. The phenological data (first month of flowering) was provided by the University of Bern, which had data available that was extracted from the Flora Helvetica Lauber et al., 2018; van Klink et al., 2017). Also, all plants found in the permanent plots were categorized into two functional groups: forbs (non-Poales*)* and grasses (Poales; i.e., *Poaceae, Cyperaceae and Juncaceae*). The mean species cover of each plant in the two plots was used to calculate community-weighted means (CWM) using the formula:

$$CWM = \sum_{i=1}^{n} \frac{c_i}{c_{tot}} * F_i$$

Where $c_i$is the cover of the species i, c_{tot} is the summed cover over all species and F_i is the median functional trait value. The categorical value (i.e., grass or forb) was calculated by simply taking the sum of c_i for each category. Altogether, functional trait data was available for 95% for SLA, number of seeds and seed mass whereas phenology was available for 97% of the 129 recorded vascular plants in the restored meadows in 2021.

Similarly to the vegetation data, CWM were modelled as response variables with treatment as predictors using linear mixed-effect models with Gaussian distribution. Region was set as random effect and model assumptions were tested.

3 Results

3.1 Effects of restoration method on species richness

We recorded a total of 150 vascular plant species in the permanent plots, including the donor meadows, in both years. In 2018, we recorded 88 species and a mean species richness of 24.8 (min = 9, max = 32) in the restoration meadows only (C included, plot size = 8 m^2 of two discontinuous plots). After restoration in 2021, we recorded 129 species and a mean species richness of 32.2 (min = 15, max = 44). Mean species richness significantly increased after restoration (i.e., C excluded) by 9.15 species (SE = 0.96, $p < 0.001$). Interestingly, species richness decreased in three restored meadows by a few species. However, the largest increase of species richness after restoration was 19 plant species in one permanent plot.

All treatments had a significantly higher plant species richness than the control in 2021. ΔSpecies richness, i.e., the difference in species richness between the respective treatment and the control, ranged from 4.75 in HH (SE = 1.9, $p = 0.016$) to 11.8 in SC (SE = 1.9, $p < 0.001$) with a mean Δspecies richness of 7.25 (SE = 1.39). Thus, SC resulted in the highest species richness and performed significantly better than all other treatments (see Table 1). The treatments using the seeds of the donor meadow HH, HP and SN did not have a significant difference in species richness to each other, only to C. Treatment explained 41% of the variance of species richness (marginal $R^2 = 0.41$).

Beta diversity was significantly higher for the treatments HP and SN compared to C (HP: SE = 1.9, $p = 0.001$, SE = 1.95, SN: $p = 0.002$, see also Fig. 3). Beta diversity was negatively influenced either by high overall species number or relatively low species number per meadow. In contrast to alpha diversity (i.e., species richness), the treatments HH and SC were not higher in beta diversity than C. Gamma diversity (i.e., total number of species per treatment) was particularly low for HH and C but not for SC, which had a lower beta diversity due to a high alpha diversity.

Soil phosphate content in the restoration meadows ranged from 0.44 to 154 [mg/kg]. Phosphate had a unimodal relationship with species richness fitted by a polynomial regression (Residual SE: 5.03, $p = 0.03$, see Appendix D). The treatment HP showed a higher mean value of phosphate compared to the other treatments. This might have a negative impact, but the difference is not significant ($p = 0.075$).

Nitrogen content had low values on almost all meadows and the three exceptions with higher N concentration do not show a clear pattern. Soil pH ranged from 4.2 to 7.4 and did not correlate with species richness. The time of extensive management measured in years had no effect on species richness (linear model, SE = 0.12, $p = 0.174$), and differences in mean values of the treatments are minimal (mean values range from 17 to 22 years). Sand content ranged from 13% to 57% but did not correlate with species richness. The species richness of the donor meadows might have a minor positive but insignificant effect on species richness of the restored meadows using the seeds of the donor meadows (i.e., HH, HP and SN) with one outlier, where an exceptionally high species-rich donor meadow did not result in high species richness in the corresponding restoration meadows. Most restoration meadows had a low C/N ratio and only three meadows had a higher C/N ratio but intermediate species richness.

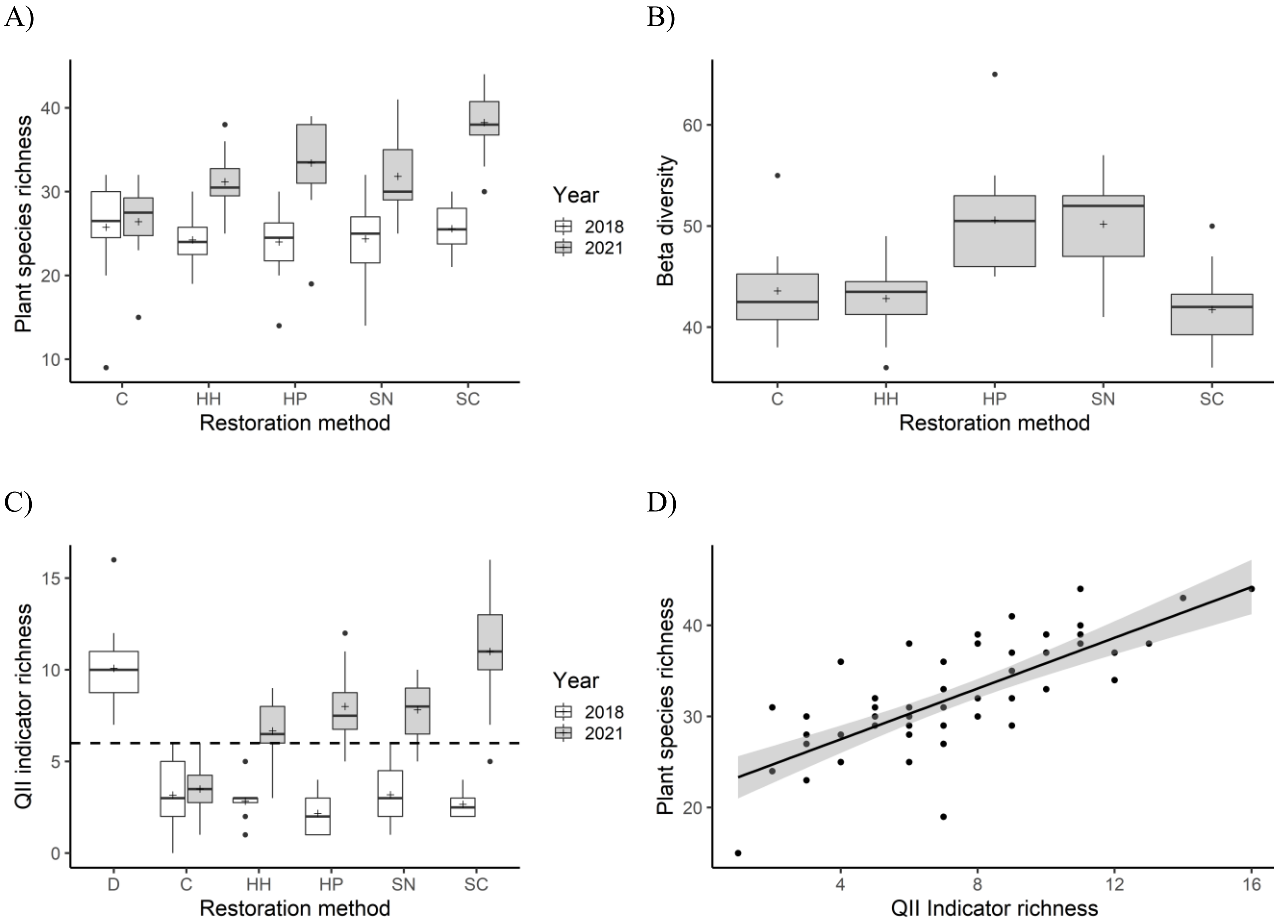


Fig. 3: The effect of restoration methods on A) plant species richness, B) beta diversity, and C) QII indicator richness. In D), the linear regression between plant species richness and QII indicator richness (black line) and 95% confidence intervals. Figures A) and C) include the baseline data of 2018 and resurvey data of 2021 (one year before and two years after restoration). Treatment abbreviations: D = donor, C = control, HH = hay harrow, HP = hay plough, SN = seed natural, and SC = seed commercial.

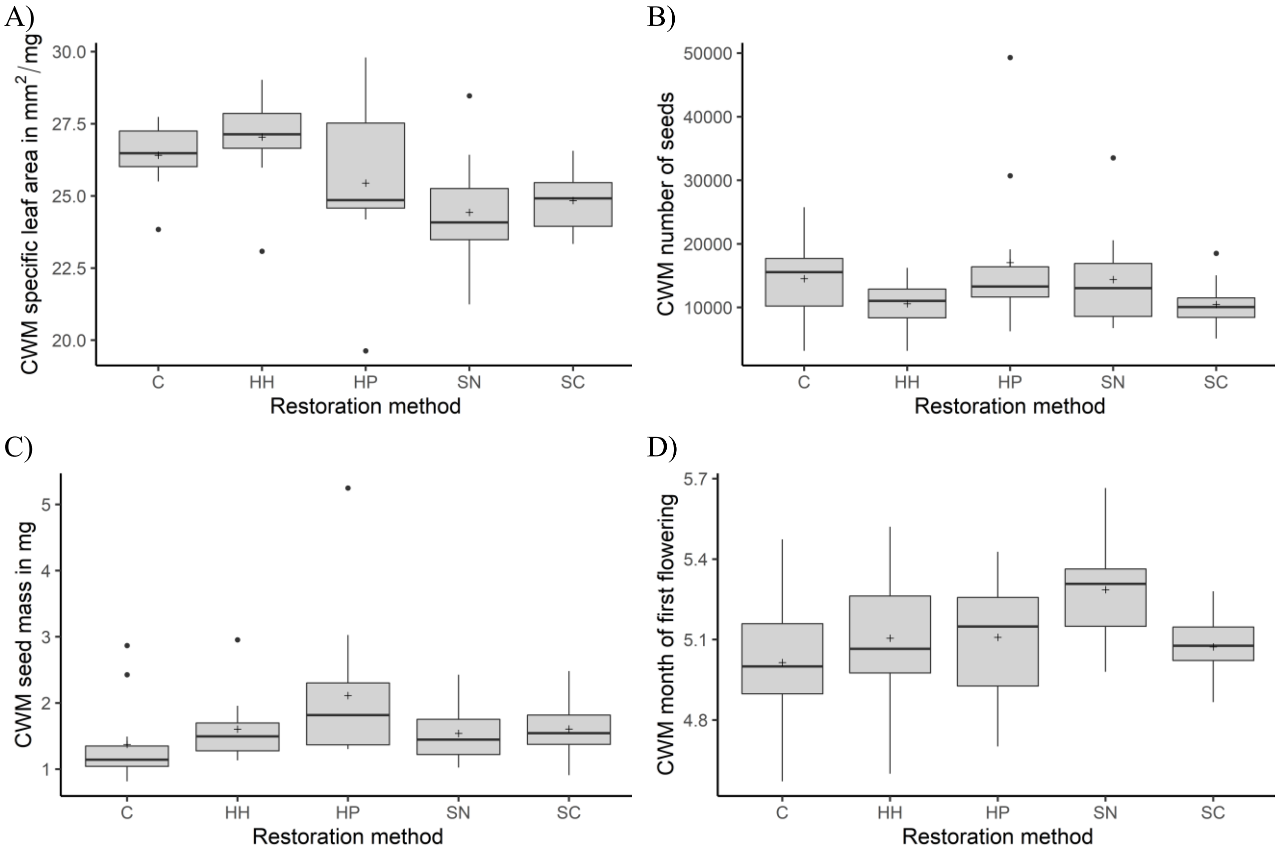
3.2 Effects of restoration method on QII indicator richness

The QII indicator richness per restoration meadow increased from a mean of 2.7 QII indicators in 2018 (min = 1, max = 6) to a mean of 8.4 QII indicators in 2021 (min = 3, max = 16), excluding the treatment C. Thus, the overall increase after restoration was 5.7 QII indicators per meadow (LMM, SE = 0.43, *p* <0.001). The QII indicator richness also showed a positive linear relationship with species richness and both variables correlated with high significance (linear model: marginal $R^2 = 0.56$, *p* <0.001).

All treatments had highly significant more QII indicators than C. Similarly to species richness, the treatment SC was significantly better than the other three treatments, which did not differ from each other. The explained variance of treatments for QII indicators was 57% (marginal $R^2 = 0.57$). The increase due to restoration led to a sufficient amount of indicators to reach ≥ 6 QII indicators per plot in 42 out of 47 restored meadows. Therefore, the restoration had a success rate of 89% in terms of QII indicators. Nonetheless, the restoration meadows that were restored with seed transfer did not reach the level of the donor meadows (i.e., HH, HP and SN). One meadow of the treatment C did reach six QII species while another meadow had six QII species in 2018 and decreased to five species in 2021.

3.3 *Effect of restoration methods on CWMs of functional traits*

CWM of plant functional traits differed significantly among treatments and showed no interaction with considered parameters (e.g., Phosphate). Species with low SLA were predominantly present in treatments using seed mixtures (SC and SN, see Fig. 4). The mean number of seeds produced per plant of C did not differ significantly from the treatments but within the treatments (Table 1). HP had a higher seed number than both HH and SN. CWM of seed mass is lowest in C, although only HP is significantly higher (Table 1). The mean month of first flowering was highest for SN, which is significantly higher than all other treatments. The percentage cover of graminoids showed a high variability but only differed significantly between HH and HP (Fig. 4). Likewise, the summed cover of forbs (non-graminoids) varies strongly but all treatments have similar means (Table 1).



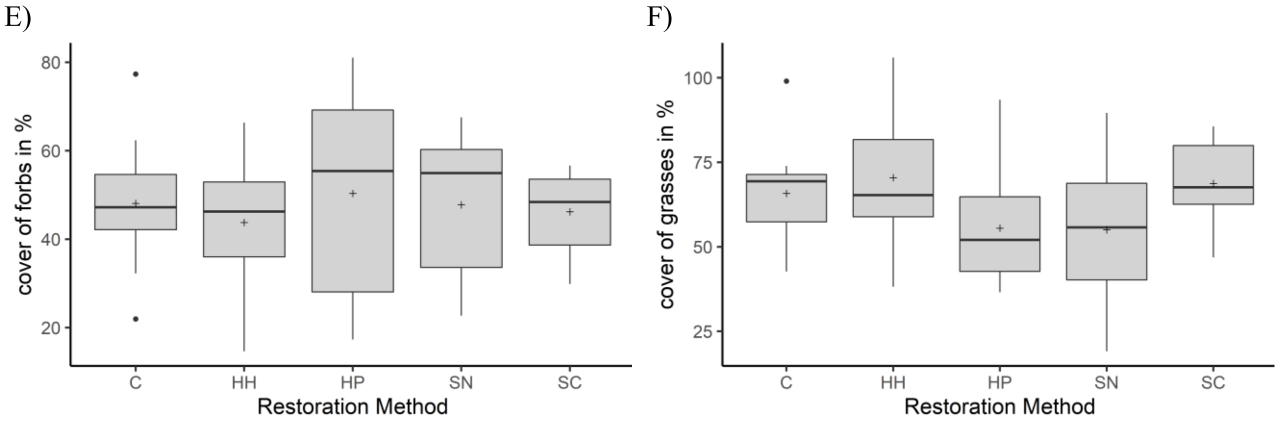


Fig. 4: The effect of restoration methods on community-weighted means of A) specific leaf area, B) number of seeds, C) seed mass and D) month of first flowering (y-axis indicate months of the year as a numeric value, i.e., 5.1 = 03. May). Also on species cover of E) forbs (non-Poales) and F) grasses (Poales). Treatment abbreviations: D = donor, C = control, HH = hay harrow, HP = hay plough, SN = seed natural, and SC = seed commercial.

4 Discussion

The applied restoration methods led to a significant increase in vascular plant species in all four treatments, resulting in a successful restoration in all meadows. This is also reflected in the QII indicator richness where only 5 out of 47 restored meadows did not reach the threshold of six indicators in one QII plot. These positive short-term effects are of high importance for farmers even after two years because Swiss direct payments increase substantially for extensively managed meadows that reach QII (Direktzahlungsverordnung DZV, 2013).

A recent report on the condition of biodiversity in the Swiss agricultural landscape recorded plant richness to range from 18 to 26 species in 10 m^2 plots placed in extensively managed meadows (Meier et al., 2021). These plant richness values are particularly low due to intensification in such meadows (Boch et al., 2020). A slightly higher value was observed by Bosshard (2015), who reported a mean plant richness of 27 in 10 m^2 plots in mesic meadows (*Arrhenatheretum*). This is well in line with our results, as we recorded a mean plant richness of 25 before and 32 after restoration. However, we used non-contiguous elongated plots (total area: 16 m^2), which results in more species than in one quadratic 10 m^2 plot (Dengler & Oldeland, 2010). The advantage of two plots is to optimize the comparison of treatments and to better represent the different microhabitats in a meadow, which is crucial to capture the effects of restoration at field scale.

Evaluation of restoration methods

The treatment with the highest species richness (mean = 38.2 ± 1.3) as well as the most QII indicators (mean = 11 ± 0.6) was SC, the sowing of a commercial seed mixture. We expected this result due to the high number of species (n=38) in the seed mixture and the ideal harvesting and storage conditions by the provider, although we did not expect such a pronounced difference between SC and the other treatments (on average 4.8 species more than HP). The Δspecies richness of SC (11.8) is comparable to the results of Freitag et al., (2021), who restored 4 m^2 – plots by seeding in combination with soil disturbance and had a Δspecies richness of 8.77 after 5 years (Δspecies richness = treatment – control). Beta diversity was significantly lower for SC compared to HP and SN which might be an indication that despite higher species richness, the similarity of meadows restored with SC is high. It is well-known that some of the commercially sown plant species decrease in cover or even disappear while other restoration methods result in a more stable plant community (Kiehl et al., 2010; Prach et al., 2014). Many studies underline the importance of introducing regional (autochthonous) seeds to ensure local ecotypes of plant species remain in a region (Albert et al., 2019). However, the quality of regional seed mixtures is different in a landscape with relatively few species-rich donor meadows, as in the Swiss Plateau, compared to the Czech Republic with ancient grasslands hosting some of the most species-rich areas in Europe (Biurrun et al., 2021). The possibility to compare harvested seeds and green hay of the same donor meadow was a goal of this study. Therefore, we only harvested seeds from one donor meadow instead of multiple meadows, which resulted in fewer species in the seed mixtures of SN.

The treatment HP performed best of the restoration methods using regional seeds (on average 1.6 species more than SN). This is in line with studies showing that green hay transfer is a successful restoration method (Albert et al., 2019). Nonetheless it still resulted in significantly fewer species than SC (see Chapter 3.1). In terms of beta diversity, the treatments HP and SN had a higher value than SC. We assume that these plant communities are more stable than SC because species differ from meadow to meadow and they are well adapted to the local conditions. However, genetic isolation by distance is measured in large geographical distances (100km+) and genetic differences are highly species-specific (Durka et al., 2017). For example, the established seed transfer zones in Germany are as big as Switzerland in its entirety (Durka et al., 2017).

The restoration method using green hay transfer was applied twice on restored meadows with low and high soil disturbance (harrow vs. plough). The treatment HH had slightly lower species richness than HP, but the difference was not significant. This is well in line with studies linking an increase of both total species richness and target species to soil disturbance but showing only small differences between low and high disturbance (Bischoff et al., 2018). Other studies on grassland restoration show that soil disturbance combined with seed addition is important, and the absence of soil disturbance does not result in sufficient species richness (Kiehl et al., 2010; Klaus et al., 2017).

The QII indicator richness and the “total” species richness recorded per meadow correlated highly (see Chapter 3.2) . This is an indication that the selected QII indicator list indeed reflects plant diversity in the study region (Riedel et al., 2019; Weinrich, 2018). The explained variance in the applied model is higher for QII indicators than species richness (see above), which suggests that the applied treatments increased the QII indicator richness more than species richness. This might be linked to the treatment SC, in which the seed mixture consists predominantly of QII indicators (68% of seeded species are indicators). Also, the donor meadows had to host at least 10 QII indicators to qualify for this study. Thus, restoration led to a strong increase of QII indicators, not all species could establish successfully, and the three treatments HH, HP and SN still have less QII indicators than the donors (on average HH 3.4, HP 2.1 and SN 2.3 species less). Still, the threshold of six QII indicators was achieved by almost all restored meadows.

Evaluation of environmental parameters

The majority of the measured environmental parameters had no or only minor effects on species richness and QII indicator richness. This is due to the study design aiming to minimize the influence of external factors. In our meadows, N content was generally low for most meadows, and the negative impact on species richness was therefore negligible, which is also true for C/N ratio. In contrast, soil P content varied strongly among restored meadows and had a negative impact at higher concentrations. This result shows that meadows with high P concentrations (i.e., P > 100 mg/kg), species richness might be lower after restoration. However, the species richness increased nonetheless in these meadows, which indicates that restoration is still an improvement, just on a lower level. The same result was found by Schmiede et al., (2012), who found a reduction of plant establishment with elevated P but no such pattern for N or K. Interestingly, the duration of extensive management had no significant impact on species richness after restoration. This partly contradicts other studies that found a positive correlation between age and species richness (Prach et al., 2014). Again, this might be due to the large species pool of the surroundings, in addition to the fact that we only included meadows with age > 8 years in this study, and increase in species richness is expected to occur in the first 10 years of extensive management (Prach et al., 2014). Sand content can be linked to the water holding capacity of the soil, but we found no effect of sand content and species richness. The species richness of the donor meadows was expected to have an impact on meadows restored either by hay transfer or harvested seeds. The positive relationship is visible but not significant, probably due to the variance of the different treatments.

Evaluation of functional traits

The studied functional traits show distinct variability between treatments. This indicates differences in plant composition, which were not detected by analysing species richness or indicators alone. However, we expect further changes in plant composition, and certainly in plant cover (Albert et al., 2019). Nonetheless, some of the observed patterns can be explained. The lower SLA values were mainly observed in treatments with high species richness, which indicates that restoration indeed favoured specialized species rather than fast-growing generalists. This was also observed by similar studies, which found better establishment of species with tougher leaves (low SLA), especially on low-productivity sites (Albert et al., 2019; Freitag et al., 2021). The number of seeds had similar values for restored meadows and the undisturbed control. In contrast to our result, Albert et al., (2021) found much higher seed numbers in ancient grasslands compared to restored sites. Similarly to the findings of Albert et al., (2019) green hay supported the transfer of species with larger seeds. In one treatment (SN), the first flowering was surprisingly late. Apart from harvesting right before the first cut, seeds were collected throughout the summer of 2018 in the uncut refuges of the donor meadows. Among these collected seeds, there might have been later flowering species. In the same study region, van Klink et al.,

(2017) found no differences in month of first flowering between mowing regimes, but flowering was generally later than in our study. Other studies point out that plant phenology is rather important for restoration and linked to establishment on the species level (Engst et al., 2017). We recorded all plots before mowing and our plots were characterized by a dominance of grasses (graminoids) compared to forbs (non-graminoids). This is reflected by findings of Albert et al., (2021) who recorded a dominance of grasses before mowing and forbs after mowing. The differences in grass cover between HH and HP indicate a negative impact of soil disturbance on grass cover, as this is the sole difference between the two treatments.

5 Conclusions and management recommendations

The overall increase of species richness after restoration, and the similarity of meadows even after 20+ years of extensive management, lead me to the conclusion that active restoration measures can be successful and are needed in some parts of the Swiss Plateau. This is especially true where species-rich meadows became scarce and a large species pool of the surroundings are missing. All tested restoration methods successfully enhanced plant species richness as well as the QII indicator richness, and the best performance resulted from the treatment SC, which in turn had a lower beta diversity than HP or SN. These two treatments had similar values in almost all measured variables, with the exception of the first month of flowering, which was significantly later in meadows treated with SN. Differences between restoration methods were not always detectable by species richness alone, and the analysis of environmental parameters and functional traits can be important in assessing restoration success. The treatments using seed mixtures (SN and SC) had a lower SLA than the other treatments, which is linked to long-living specialist species. Lastly, the treatment HH that did not receive a strong soil disturbance had a lower increase in species richness and a low beta diversity in the short-term. However, we anticipate further changes in plant species richness and plant composition in the following years, as not all the seeded species are well adapted to interspecific competition and a decline in species richness has been confirmed by other studies (e.g. Freitag et al., 2021). Therefore, the outcome of the short-term effects of grassland restoration is insufficient to recommend one treatment over the others as all have successfully enhanced species richness. A correct execution is just as important for successful restoration as the right method. This includes the right timing in Spring (both of collection of plant material or seeds and distribution), weather conditions, a cleaning cut to remove fast-growing weeds and repeated weed removal of undesirable species. Treatments with seed mixtures (regional or commercial) have the advantage of flexible timing, as the seeds have already been harvested a year before, whereas hay transfer has to be carried out on the same day as the mowing of the donor meadow. However, the costs of hay transfer methods are considerably lower, as costs for seed material and storage are omitted (Török et al., 2011). Farmers that apply either hay transfer, seeding natural or commercial seed mixtures combined with ploughing and subsequent harrowing, can expect to reach QII two years after restoration, given the restored meadow has similar conditions to our study sites. The maturity of the donor meadows (i.e., the moment of harvesting) is equally important and should be considered when doing grassland restoration. Management contracts for extensively managed meadows have a term of at least eight years. Therefore, further research on the mid- and long-term effects of these restoration methods is essential in order to provide concrete guidance for farmers, local authorities and environmental engineers.

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Appendix A)

Table 1: Model results of response variables predicted with treatments in linear mixed-effect models using Gaussian distribution and Region as random effect. Significant p-values of pairwise differences between treatments are indicated in bold. Degrees-of-freedom method: Kenward-roger, p-value adjustment: none.

Plant species richness

Treatment	*mean*	*std. Error*	*df*	*CI*
C (Intercept)	26.4	1.34	54	23.7 – 29.1
HH	31.2	1.34	54	28.5 – 33.9
HP	33.4	1.34	54	30.7 – 36.1
SC	38.2	1.34	54	35.6 – 40.9
SN	31.8	1.41	54	29 – 34.6
Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	-4.75	1.9	43	**0.016**
C - HP	-7	1.9	43	**0.001**
C - SC	-11.833	1.9	43	**<.0001**
C - SN	-5.402	1.95	43.8	**0.008**
HH - HP	-2.25	1.9	43	0.243
HH - SC	-7.083	1.9	43	**0.001**
HH - SN	-0.652	1.95	43.8	0.739
HP - SC	-4.833	1.9	43	**0.015**
HP - SN	1.598	1.95	43.8	0.416
SC - SN	6.432	1.95	43.8	**0.002**
Marginal R^2	0.41			

QII indicator richness

Treatment	*mean*	*std. Error*	*df*	*CI*
C (Intercept)	3.5	0.61	54	2.27 – 4.73
HH	6.67	0.61	54	5.44 – 7.9
HP	8	0.61	54	6.77 – 9.23
SC	11	0.61	54	9.77 – 12.23
SN	7.82	0.64	54	6.53 – 9.11
Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	-3.167	0.87	43	**0.001**
C - HP	-4.5	0.87	43	**<.0001**
C - SC	-7.5	0.87	43	**<.0001**
C - SN	-4.318	0.89	43.8	**<.0001**
HH - HP	-1.333	0.87	43	0.131
HH - SC	-4.333	0.87	43	**<.0001**
HH - SN	-1.152	0.89	43.8	0.201
HP - SC	-3	0.87	43	**0.001**
HP - SN	0.182	0.89	43.8	0.839
SC - SN	3.182	0.89	43.8	**0.001**
Marginal R^2	0.573			

Beta diversity

Predictors [Treatment]	*mean*	*std. Error*	*df*	*CI*
C (Intercept)	43.6	1.34	54	40.9 – 46.3
HH	42.8	1.34	54	40.1 – 45.5
HP	50.6	1.34	54	47.9 – 53.3
SC	41.8	1.34	54	39.1 – 44.4
SN	50.2	1.34	54	47.4 – 53
Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	0.75	1.9	43.0	0.695
C - HP	-7	1.9	43.0	**0.001**
C - SC	1.833	1.9	43.0	0.340
C - SN	-6.598	1.95	43.8	**0.002**
HH - HP	-7.75	1.9	43.0	**0.000**
HH - SC	1.083	1.9	43.0	0.572
HH - SN	-7.348	1.95	43.8	**0.001**
HP - SC	8.833	1.9	43.0	**<.0001**
HP - SN	0.402	1.95	43.8	0.838
SC - SN	-8.432	1.95	43.8	**<.0001**
Marginal R^2	0.403			

CWM SLA

Predictors [Treatment]	*mean*	*std. Error*	*df*	*CI*
C (Intercept)	26.4	0.502	54	25.4 – 27.4
HH	27	0.502	54	26 – 28
HP	25.4	0.502	54	24.4 – 26.5
SC	24.8	0.502	54	23.8 – 25.8
SN	24.4	0.526	54	23.4 – 25.5
Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	-0.631	0.711	43	0.380
C - HP	0.965	0.711	43	0.182
C - SC	1.569	0.711	43	**0.033**
C - SN	1.98	0.728	43.8	**0.009**
HH - HP	1.595	0.711	43	**0.030**
HH - SC	2.2	0.711	43	**0.003**
HH - SN	2.611	0.728	43.8	**0.001**
HP - SC	0.604	0.711	43	0.400
HP - SN	1.015	0.728	43.8	0.170
SC - SN	0.411	0.728	43.8	0.575
Marginal R^2	0.238			

CWM number of seeds

Predictors [Treatment]	*mean*	*std. Error*	*df*	*CI*
C (Intercept)	14534	2114	51.6	10292 – 18776
HH	10588	2114	51.6	6346 – 14830
HP	17071	2114	51.6	12829 – 21313
SC	10469	2114	51.6	6227 – 14711
SN	14720	2209	52.2	10287 – 19152

CWM flowering start (phenology)

Predictors [Treatment]	*mean [phenology]*	*std. Error*	*df*	*CI*
C (Intercept)	5.01	0.0655	42.8	4.88 – 5.15
HH	5.11	0.0655	42.8	4.97 – 5.24
HP	5.11	0.0655	42.8	4.98 – 5.24
SC	5.07	0.0655	42.8	4.94 – 5.2
SN	5.29	0.0681	44.8	5.15 – 5.42

Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	3946	2822	43	0.169
C - HP	-2537	2822	43	0.374
C - SC	4065	2822	43	0.157
C - SN	-185	2894	43.6	0.949
HH - HP	-6483	2822	43	**0.027**
HH - SC	119	2822	43	0.966
HH - SN	-4131	2894	43.6	0.161
HP - SC	6602	2822	43	**0.024**
HP - SN	2351	2894	43.6	0.421
SC - SN	-4251	2894	43.6	0.149
Marginal R^2	0.11			
Conditional R^2	0.21			

cover of forbs

Predictors [Treatment]	*mean [forb cover]*	*std. Error*	*df*	*CI*
C (Intercept)	48.1	4.59	51.6	38.9 – 57.3
HH	43.8	4.59	51.6	34.6 – 53
HP	50.4	4.59	51.6	41.1 – 59.6
SC	46.2	4.59	51.6	37 – 55.4
SN	47.6	4.8	52.2	38 – 57.2

Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	4.321	6.13	43	0.485
C - HP	-2.267	6.13	43	0.713
C - SC	1.9	6.13	43	0.758
C - SN	0.469	6.29	43.6	0.941
HH - HP	-6.588	6.13	43	0.288
HH - SC	-2.421	6.13	43	0.695
HH - SN	-3.852	6.29	43.6	0.543
HP - SC	4.167	6.13	43	0.500
HP - SN	2.736	6.29	43.6	0.666
SC - SN	-1.431	6.29	43.6	0.821
Marginal R^2	0.019			
Conditional R^2	0.13			

CWM seed mass

Predictors [Treatment]	*mean [seed mass]*	*std. Error*	*df*	*CI*
C (Intercept)	1.37	0.194	54	0.98 – 1.76
HH	1.6	0.194	54	1.21 – 1.99
HP	2.11	0.194	54	1.72 – 2.5
SC	1.61	0.194	54	1.22 – 2
SN	1.54	0.203	54	1.13 – 1.95

Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	-0.2302	0.275	43	0.406
C - HP	-0.7386	0.275	43	**0.010**
C - SC	-0.2327	0.275	43	0.402
C - SN	-0.1659	0.281	43.8	0.558
HH - HP	-0.5084	0.275	43	0.071
HH - SC	-0.0025	0.275	43	0.993
HH - SN	0.0643	0.281	43.8	0.820
HP - SC	0.5060	0.275	43	0.072
HP - SN	0.5727	0.281	43.8	**0.048**
SC - SN	0.0668	0.281	43.8	0.814
Marginal R^2	0.123			

Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	-0.09	0.080	43	0.261
C - HP	-0.09	0.080	43	0.244
C - SC	-0.06	0.080	43	0.466
C - SN	-0.27	0.082	43.4	**0.002**
HH - HP	0.00	0.080	43	0.967
HH - SC	0.03	0.080	43	0.689
HH - SN	-0.18	0.082	43.4	**0.033**
HP - SC	0.04	0.080	43	0.659
HP - SN	-0.18	0.082	43.4	**0.036**
SC - SN	-0.21	0.082	43.4	**0.013**
Marginal R^2	0.135			
Conditional R^2	0.358			

cover of graminoids

Predictors [Treatment]	*mean*	*std. Error*	*df*	*CI*
C (Intercept)	65.8	4.95	53.6	55.9 – 75.7
HH	70.4	4.95	53.6	60.5 – 80.4
HP	55.5	4.95	53.6	45.6 – 65.4
SC	68.7	4.95	53.6	58.8 – 78.6
SN	55.2	5.18	53.7	44.8 – 65.5

Pairwise differences	*Estimates*	*std. Error*	*df*	*p. value*
C - HH	-4.646	6.85	43	0.501
C - HP	10.275	6.85	43	0.141
C - SC	-2.921	6.85	43	0.672
C - SN	10.63	7.02	43.7	0.137
HH - HP	14.921	6.85	43	**0.035**
HH - SC	1.725	6.85	43	0.802
HH - SN	15.275	7.02	43.7	**0.035**
HP - SC	-13.196	6.85	43	0.061
HP - SN	0.355	7.02	43.7	0.960
SC - SN	13.55	7.02	43.7	**0.060**
Marginal R^2	0.128			

Appendix B)

Table 2: Summary of environmental parameters with possible effect on restoration success and the summary of the response variables used in the analysis. SE – standard error.

	Restoration meadows		
Environmental parameter	**Min**	**Max**	**Mean ± SE**
Area [m^2]	1738	52186	9924 ± 1051
Extensive since [Year]	1980	2013	2001 ± 1
Extensive for [N° of Years - 2021]	8	41	20 ± 1
Former management	artificial meadow (3) cropland (26) forest (1) intensive meadow (11) intensive pasture (10) low intensity meadow (19) orchard (1) pasture (1)		
Elevation [m.a.sl.]	420	759	566 ± 11
Slope [°]	0	21	5 ± 1
Nitrogen content [%]	0.14	1.32	0.33 ± 0.02
Total oranic carbon [%]	1.34	16.29	3.46 ± 0.27
C/N Ratio	9	21	10 ± 0.3
pH	4	7	5.5 ± 0.1
Phosphate content [mg/kg]	0	294	51 ± 6
Clay content [%]	6	21	10 ± 0.3
Silt content [%]	37	69	53 ± 1
Sand content [%]	13	57	36 ± 1

Response variables 2021	**Min**	**Max**	**Mean ± SE**
Plant species richness	15	44	32.2 ± 0.8
QII indicator richness	1	16	7.39 ± 0.4
Beta diversity	36	65	45.7 ± 0.8
CWM specific leaf area [mm2 /mg]	20	30	25.7 ± 0.3
CWM number of seeds	3178	49303	13394 ± 977
Graminoid cover [%]	19	106	63.2 ± 2.3
Forb cover [%]	15	81	47.2 ± 2
Flowering start [month]	4.6	5.7	5.1 ± 0.03
Seed mass [mg]	0.8	5.2	1.6 ± 0.09

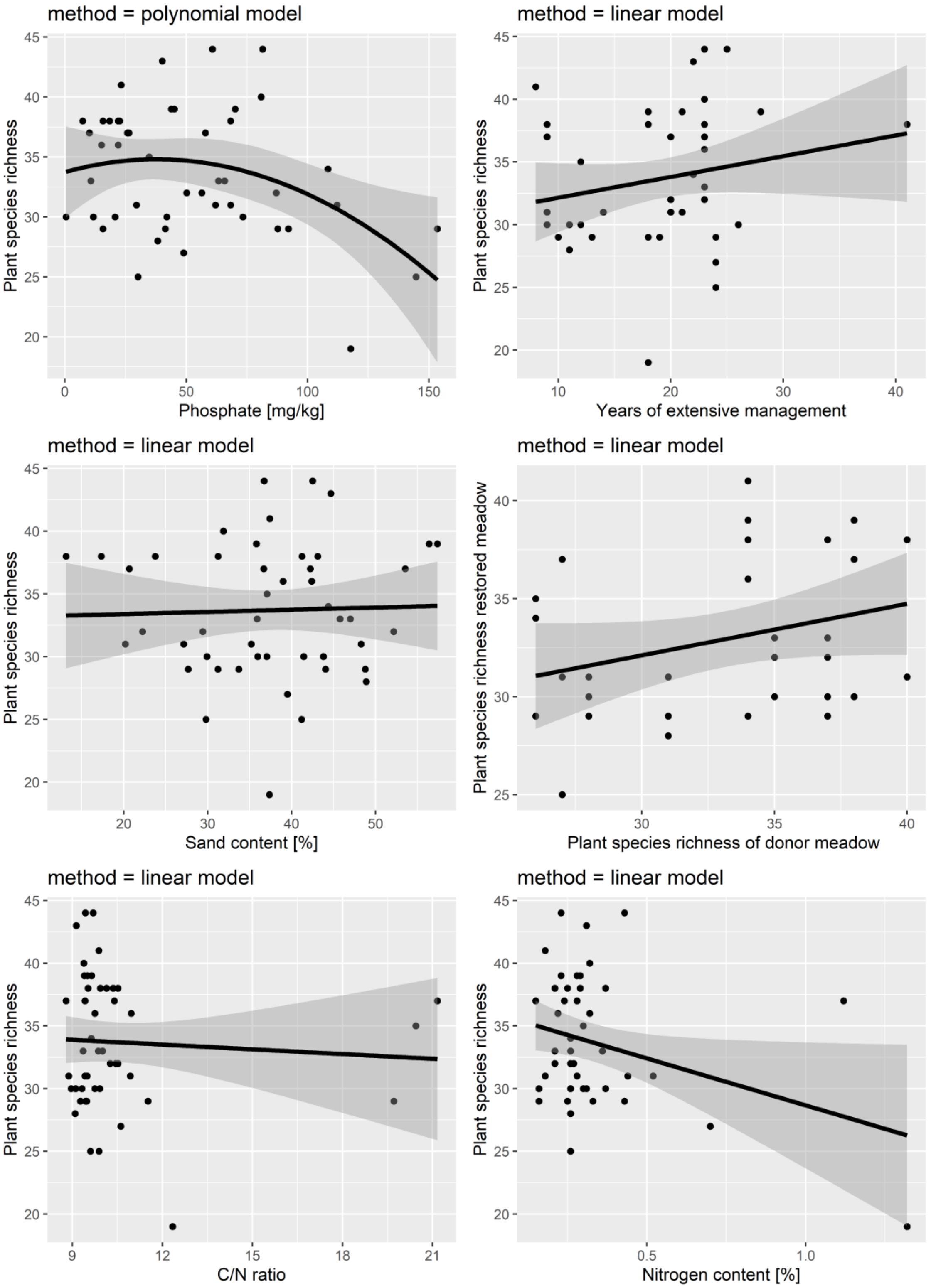
Appendix C)

Table 3: Species composition used in the seed mixture of the treatment “seed commercial” (SC). Species marked with “i” are from a Swiss ecotype. The recommended amount of seeds per area and proportion of species in the seed mixture are recorded. Species present in the official QII indicators-list are indicated.

Plant species	g/100 m^2	QII indicators
Anthoxanthum odoratum i	4.2	X
Arrhenatherum elatius i	16	
Briza media i	2.1	X
Bromus erectus i	26	X
Dactylis glomerata i	7	
Festuca pratensis i	21	
Festuca rubra rubra i	17	
Helictotrichon pubescens i	5.3	X
Poa pratensis i	5.3	
Trisetum flavescens i	1.1	
Anthyllis carpatica i	0.5	X
Campanula patula i	0.03	X
Campanula rotundifolia i	0.07	X
Carum carvi i	0.6	
Centaurea jacea i	0.15	X
Centaurea scabiosa i	0.4	X
Clinopodium vulgare i	0.1	X
Crepis biennis i	0.1	X
Daucus carota i	0.1	
Knautia arvensis i	1	X
Lathyrus pratensis i	0.4	X
Leontodon hispidus i	0.3	X
Leucanthemum vulgare i	0.3	X
Lotus corniculatus i	1	X
Medicago lupulina i	1	X
Onobrychis viciifolia i	2.7	X
Picris hieracioides i	0.2	X
Pimpinella major i	0.2	
Plantago lanceolata i	0.1	
Primula veris i	0.15	X
Salvia pratensis i	1.1	X
Sanguisorba minor i	1.6	X
Scabiosa columbaria i	0.2	X
Silene vulgaris i	0.1	X
Stachys officinalis i	0.2	X
Tragopogon orientalis i	1.6	X
Trifolium pratense i	0.4	
Vicia sepium i	0.4	

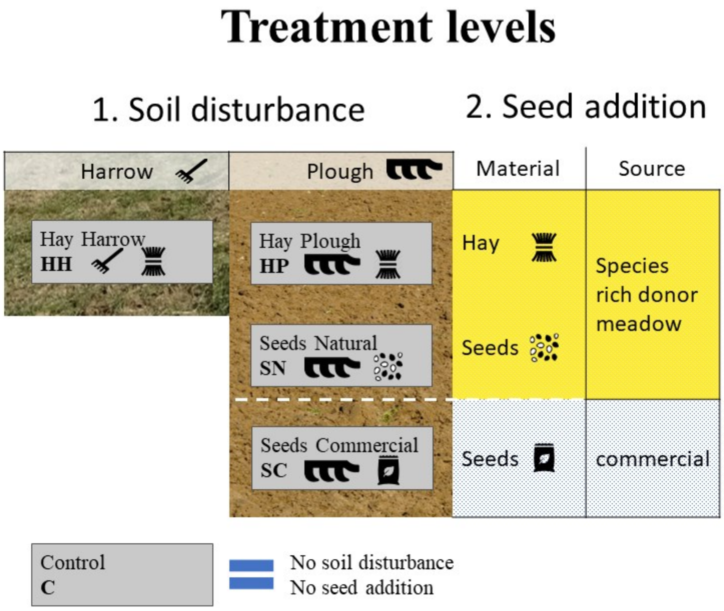
Appendix D)

Fig. 5: Linear regression models between plant species richness environmental parameters with 95% confidence intervals. Phosphate is the only parameter with significant unimodal correlation (p-value = 0.029).



Appendix E)

Fig. 6: Experimental design. The restoration treatments are classified by soil disturbance and seed addition (Author: Daniel Slodovicz).



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