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Restoring plant diversity in lowland grasslands: Efficacy of different seed addition and soil preparation methods

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ABSTRACT

The biodiversity of semi-natural grasslands has dramatically declined over the past century. We experimentally tested, at field scale, the efficacy of different assisted (active) restoration methods to enhance plant biodiversity in species-poor, extensively managed lowland meadows. Four restoration treatments, plus one control were randomly allocated to five meadows at 12 spatially-replicated study sites in the Swiss lowlands in 2019: 1) hay transfer from a species-rich donor meadow on a harrowed meadow; 2) the same as 1 but on a ploughed meadow; 3) sowing a directly harvested native seed mixture originating from a species-rich donor meadow on a ploughed meadow; 4) sowing a multiplied native seed mixture on a ploughed meadow; 5) control, i.e. with no soil disturbance and no reseeding. Vegetation surveys were performed before (2018) and after the restoration actions (2021 and 2023). After a pronounced biodiversity rise in 2021, plant species richness had stabilized by 2023 across most treatments with, on average, 29% more species compared to 2018 and 16% more species in restored compared to control meadows in 2023. Moreover, 90% of the restored meadows qualified for the result-based payment scheme in 2023. Harrowing before seeding was as effective as ploughing. While the multiplied seed mixture initially showed a stronger increase, this effect had decreased by 2023, reaching levels comparable to the other treatments. Beta diversity was higher in hay transfer treatments than in the control and other restoration treatments, indicating greater heterogeneity in community composition. Findings provide evidence-based guidance for cost-effective and practically feasible grassland restoration.

1. Introduction

Farmland biodiversity is a key component for the provision of ecosystem services on which human food production depends, such as crop pollination, pest control, nutrient cycling and soil fertility (Carvalheiro et al., 2011; Soliveres et al., 2016). Semi-natural extensively managed grasslands host a large fraction of this biodiversity, and therefore play an important eco-functional role in agricultural landscapes (Hopkins and Holz, 2005).

Unfortunately, these semi-natural grasslands have mostly disappeared (Wesche et al., 2012; Widmer et al., 2025). In Switzerland, for instance, 98% of the historical *Arrhenatherion* meadows, typical of the lowlands, have been lost (Lachat et al., 2010). This has led to a homogenisation of the landscape (Diacon-Bolli et al., 2012) with a consequential dramatic loss of biodiversity in most taxonomic groups, notably among birds, arthropods and plants (Gossner et al., 2016).

To counteract this loss of biodiversity, agri-environment schemes (AES) were established in Europe in the 1990s to promote more extensive forms of management and to compensate farmers for the loss of income due to the application of these measures (Kleijn and Sutherland, 2003). In Switzerland, the surface registered as biodiversity promotion areas (BPA, by far the main Swiss AES) has steadily increased since 2002, covering nowadays 18 −19% of the utilised agricultural area (UAA). About half of these BPAs consists of extensively managed meadows (Agrarbericht, 2024). To support this BPA type, two distinct payment schemes are offered to farmers. The first one, called "Quality I"

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(QI), is an input-based (or action-based) financial incentive, allocated to a meadow when extensive management practices are implemented, specifically no fertiliser application and a first mowing not before the 15 June. The second payment scheme, called “Quality II” (QII) is an output-based (or results-based) financial incentive for farmers, allocated to a meadow when positive effects on biodiversity are demonstrably achieved, defined as the presence of at least six indicator plant species reflecting ecological quality within a 3 m-radius circle in a representative part of the meadow (Swiss Federal Council, 2013). So far, the effects of these BPAs on biodiversity have been positive (although not always consistent across taxa), particularly compared to conventionally managed meadows (Aviron et al., 2009; Meier et al., 2024). Nevertheless, only 33% of the BPA surface reaching QI criteria also qualifies for the QII contributions (Agrarbericht, 2024). The implementation of AES measures incurs costs for farmers who are encouraged to design them carefully so as to obtain the highest biodiversity benefits that entail higher financial contributions (Batáry et al., 2015).

Natural (also known as passive) restoration, i.e. the relaxation of management intensity and the reduction of fertilizer inputs (Atkinson and Bonser, 2020), yields generally limited benefits for biodiversity in semi-natural lowland grasslands. For example, van Klink et al. (2017) showed that neither the standard Swiss AES practice nor alternative mowing regimes led to any changes in plant species richness and community composition over five years. Klaus et al. (2018) found that even if the soil seed bank is activated by mechanical sward disturbance, its contribution to the restoration of plant biodiversity is limited. This is likely because the seed bank has been impoverished by a fairly long history of intensive management of these grasslands (Hábenczyus et al., 2024). Furthermore, the fragmentation of the landscape hampers the arrival of dispersal-limited species from other sources (Bakker and Berendse, 1999; Baur, 2014; Hooftman et al., 2021). Therefore, there is a need for assisted (also known as active) restoration, i.e. reseeding, to overcome this propagule limitation (Atkinson and Bonser, 2020; Walker et al., 2004). A systematic review by Slodowicz et al. (2023) has shown that assisted restoration can effectively restore plant species richness, with its success depending mostly on the type of seed source. The most promising results were obtained by a mixture of commercially available, multiplied seeds, as well as seeds collected from a species-rich donor meadow; however, if only one seed source is used, the latter are slightly more effective. The systematic review also highlighted several shortcomings in the existing research: many of the considered studies were common garden experiments, did not have a proper control and/or were conducted over a too short period of time (often less than three years).

The aim of this study was to test the efficacy of four different assisted restoration methods to increase plant biodiversity in already extant, but species-poor, extensively managed meadows, as typically encountered in the European lowlands. The experiment was conducted at field scale using a randomised block design and spatially replicated, this to ensure generalizable results, i.e. sound management recommendations. Two different types of seed bed preparation (harrowing vs ploughing) and two different native seed sources (directly harvested in form of green hay or seeds vs farm-multiplied seeds) were tested. These restoration methods were compared to a control, where neither soil disturbance nor seed addition were performed. Regarding harrowing vs ploughing, there is a consensus that the seed bed must be prepared prior to hay transfer or sowing in order to allow seed germination, because sowing onto an existing plant community would lead to competition for resources, thereby reducing the establishment success of new species (Durbecq et al., 2021; Freitag et al., 2021). Slodowicz et al. (2023) suggest that the intensity of the seed bed preparation does not influence plant species richness in the mid-term, although this result might have been confounded by the previous land-use type (cropland vs grassland). Given the remarkable scarcity of studies comparing the impact of the intensity of seed bed preparation on restoration outcomes among mesic grasslands (but see Bischoff et al., 2018 in wet meadows), we decided to test this variable in our study. We must stress here though, that farmers are reluctant to plough permanent grasslands, while they express no reticence for harrowing (pers. comm.). There are multiple arguments against ploughing. For example, in our experiment, the soil of the harrowed sites was worked on at the beginning of June, just a week before seeding, while the soil of ploughed sites was turned in early spring, leaving the latter with open bare soil exposed to erosion hazards for up to two months. Additionally, in the restoration year, harrowed meadows still provided one grass harvest in early June before harrowing, while no harvest was possible in ploughed meadows. Concerns also arose that ploughing might be detrimental to the local invertebrate fauna. If soil preparation has been established to cause direct mortality of ground-dwelling arthropods (Thorbek and Bilde, 2004), the data collected in the year following our restoration operations (2020) showed that ground beetle and ground-dwelling spider communities had mostly recovered to a pre-disturbance state by then (Slodowicz et al., 2022). Harrowing or ploughing seem thus not to dramatically affect these two major ground-dwelling invertebrate taxa and we assume that the same applies to other epigeal arthropods.

Regarding the second factor (i.e. directly harvested green hay or seeds vs farm-multiplied seeds), there is a general concern regarding the efficacy of mixtures produced using multiplied seeds (i.e. seeds produced by propagation via culture), because even if they are defined as “local”, they might be less adapted to the specific soil conditions of the meadow to be restored; especially compared to seeds directly harvested from a species-rich donor meadow located in close proximity to the recipient meadow (Espeland et al., 2017; Török et al., 2024). On the other hand, Conrady et al. (2022) found that multiplied seeds are even more genetically diverse than natural seeds.

Our predictions were as follow. First, we predicted a higher plant species richness in the restored compared to the control meadows four years after the restoration and, consequently, a higher proportion of meadows qualifying for the QII payment scheme among restored meadows. Since grasses tend to dominate over forbs and legumes in species-poor meadows (Nerlekar et al., 2024), we assumed that the higher species richnessof restored meadows would be linked to a higher proportion of forbs and legumes compared to control meadows (Pokorny et al., 2004).

In relation to the seed bed preparation, we predicted no difference in plant species richness between harrowed and ploughed meadows, as suggested by Slodowicz et al. (2023), or a slightly higher species richness in the latter meadows, because seedling conditions (i.e. reduced competition) are likely to be more favourable when the soil is ploughed (Bischoff et al., 2018; Freitag et al., 2021). We also expected seed bed preparation to have an effect on the soil availability of nutrients and moisture conditions, since ploughing is known not only to favour nitrogen mineralisation, a process that makes nitrogen available for plants (Sainju et al., 2012), but also to promote water evaporation (Mielke et al., 1986). Therefore, we expected ploughing to promote plant species associated with drier and nutrient-rich soils.

Concerning the seed addition method, we hypothesised that in the meadows seeded through hay transfer there would be fewer late-flowering species, since these seeds may not all have been ripe at the time of the hay harvest (Willems et al., 2026). Moreover, we predicted plant species producing many seeds, which are often the species producing small seeds, to be abundant in the meadows restored with hay or seeds from the donor meadows, because of a higher probability for these seeds to be transferred and to germinate in the recipient meadow (Wagner et al., 2021).

Additionally, we predicted that, at the landscape scale, the plant community of meadows sown with the multiplied seed mixture would be less diverse (i.e. would have a lower beta diversity) compared to the other treatments because the same seed mixture was sown in all sites.

2. Materials and methods

2.1. Study sites

The study was conducted on the Swiss Plateau, a lowland region situated between the Alps and the Jura mountain ranges. It is characterized by an Atlantic climate with mean annual temperatures ranging from 8 to 12°C and average precipitation from 900 to 1300 mm (MeteoSwiss, 2025). Farmland typically accounts for 60–70% of the study region, which is dominated by intensive agriculture, while semi-natural habitats such as forest stands and hedgerows cover about 20% of the landscape, with the remaining proportion consisting mostly of settlements (Zingg et al., 2019). In 2018, 60 extensively managed meadows regularly distributed in 12 study sites (with 5 meadows each) were selected across the region (Fig. 1, Appendix A). The five meadows of a given study site were located within a 5 × 5 km square, with a minimal distance of 340 m between two nearby meadows, while the 12 study sites themselves were at least 10 km apart to ensure data independence. The average size of the meadows was 0.5 ha (range: 0.2–1 ha) and their elevation varied between 420 and 760 m. While all meadows were registered as biodiversity promotion areas (BPA) since at least 2013, we purposely selected BPA meadows that did not qualify for the Quality II (QII) payments, i.e. had fewer than 6 plant species indicators of botanical quality (range: 0–5). In Switzerland, extensively managed meadows registered as BPA must follow several management guidelines, including at least one annual cut (not before 15 June), fertilisers are not allowed and pasture is possible only in autumn. In addition, 12 ancient, extensively managed grasslands (one per site) were chosen as donor meadows. At the onset of the study, these donor meadows harboured a richer plant species community (mean ± SD = 34.5 ± 6 species per 16 m^2) than the 60 selected meadows to be restored (24.8 ± 4.5), reflected by ≥ 10 QII-indicator plant species at meadow scale and ≥ 7 at a 3 m-radius scale. Depending on the site, donor meadows consisted of mesic hay meadows predominantly belonging to the *Arrhenatherion* community, with varying degrees of influence from the *Mesobromion* community.

2.2. Experimental design

A randomized block design was adopted, where four different assisted restoration treatments and a control were randomly allocated to the five meadows in each of the sites, the latter representing the blocks (Fig. 2). The restoration treatments (and control) consisted of:

- Seed addition via hay transfer: spreading the hay harvested from a donor meadow on the surface of the recipient meadow where the soil has previously been harrowed (Hay Transfer on a Harrowed meadow, HT-H).
- Seed addition via hay transfer: similar to HT-H, but the recipient meadow has been previously ploughed instead of harrowed (Hay Transfer on a Ploughed meadow, HT-P).
- Seed addition via direct sowing: directly harvested native seeds from a donor meadow were sown onto the surface of a ploughed recipient meadow at a seeding density of 1.2 g/m^2 (Directly harvested native Seeds on a Ploughed meadow, DS-P).
- Seed addition via direct sowing: a multiplied native seed mixture adapted to the local context (UFA Salvia CH-G, a commercial mix) was sown onto the surface of a ploughed recipient meadow at a seeding density of 1.2 g/m^2 (Multiplied native Seeds on a Ploughed meadow, MS-P).
- No soil disturbance nor seed addition were performed (Control, C).

The restoration operations were performed in May and June 2019 at the field scale, i.e. a given, randomly pre-selected restoration treatment was assigned to the entire area of a meadow. The HT-H treatment was harrowed a few days before seeding and again on the same day of seeding. HT-P, DS-P and MS-P were ploughed 2–3 months before seeding and subsequently harrowed every 4–6 weeks until seeding (Fig. B.1.). This approach follows standard agricultural practice for crop fields (Carter and McKyes, 2005). Ploughing brings seeds to the soil surface, where they germinate during the 2–3 months before seed addition and are then removed by harrowing. The seeds for the DS-P treatment were harvested on the donor meadows with a seed

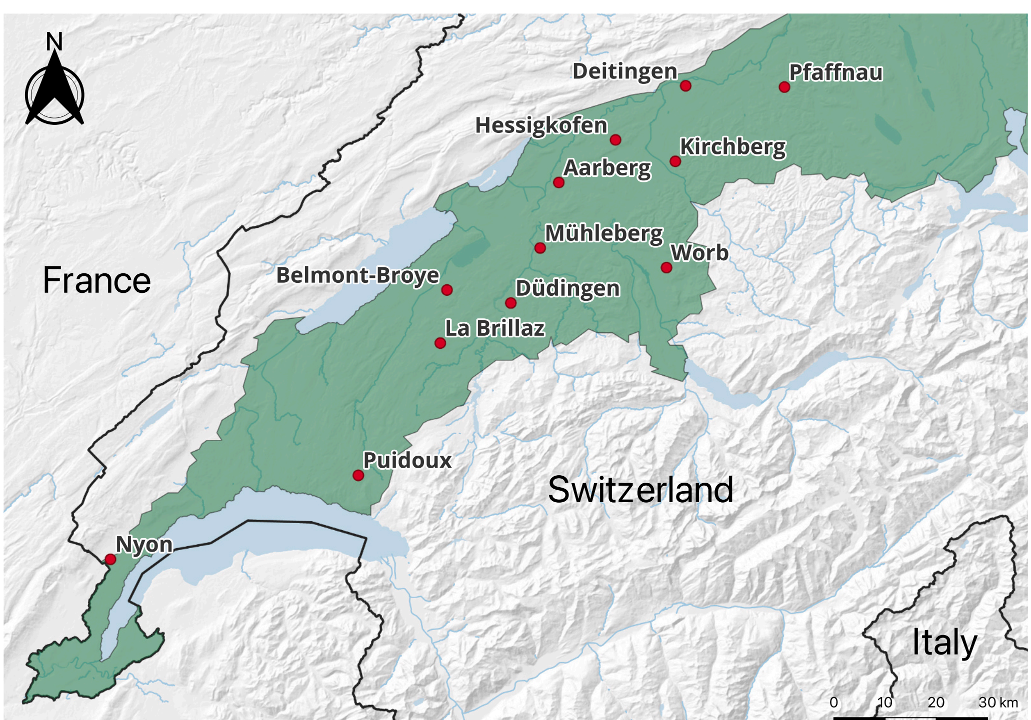

Fig. 1. Map of the Swiss Plateau (in green) with the 12 study regions. Each region consists of five meadows (4 different treatments and a control; see Materials and methods for more details). See Appendix A for a list of the study meadows.

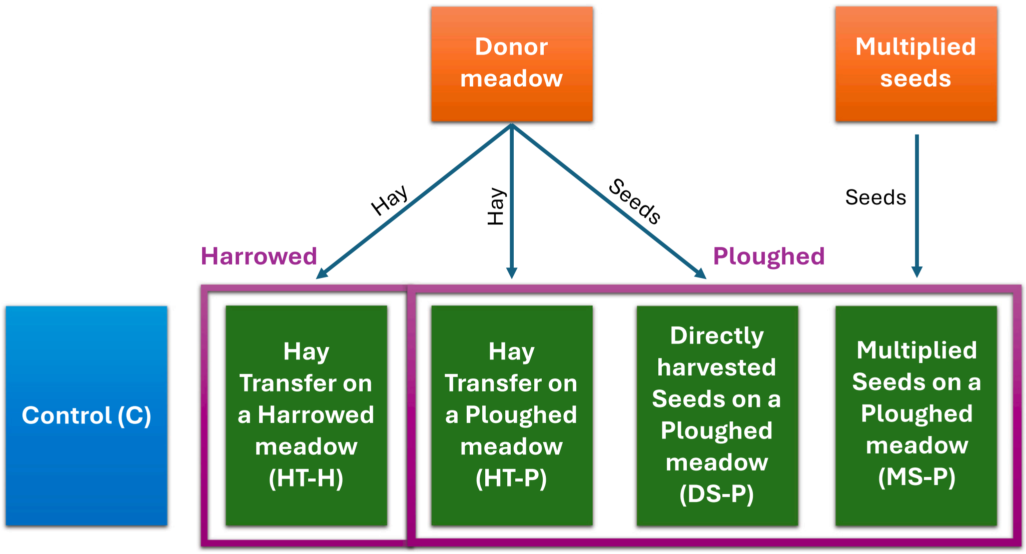

Fig. 2. Overview of the grassland restoration treatments. The treatments differed in both the soil preparation and type of seed addition deployed: Control (C), no soil disturbance or seed addition; Hay Transfer on a Harrowed meadow (HT-H), the receiver meadow was harrowed and hay transferred from a donor meadow was spread over it; Hay Transfer on a Ploughed meadow (HT-P), the receiver meadow was ploughed and hay transferred from a donor meadow was spread over it; Directly harvested native Seeds on a Ploughed meadow (DS-P), the receiver meadow was ploughed and seeds directly harvested from a donor meadow were sown; Multiplied native Seeds on a Ploughed meadow (MS-P), the receiver meadow was ploughed and a mixture of multiplied seeds was sown.

harvester (eBeetle, HoloSem) in June 2018 with additional hand collections before and after the cut, while the green hay for the HT-H and HT-P treatments was collected in 2019 and transferred the same day onto the recipient meadows (Fig. B.2.). For a detailed description of the restoration process see Appendix B. One of the DS-P meadows was discarded from the experiment because the restoration failed due to an extreme rainfall that occurred after seeding, washing the seeds away.

2.3. Vegetation surveys

Vegetation surveys were conducted before the restoration (in 2018), two years and four years afterwards (in 2021 and 2023), between May and June, in two rectangular plots of 8 m^2 each. The plots were permanently marked with two nails placed deep in the ground, so that the surveys could always be conducted at the same location over the years. The first point was randomly set in the meadow, with the second one placed at 14 m of distance in a random direction (North, South, East or West). The plots were orthogonal, so that they could capture the vegetation heterogeneity of the meadow as much as possible. We listed all the plant species present in the two plots and estimated their absolute cover percentage. Because cover was estimated independently for each species, overlapping vegetation layers could result in total plot cover exceeding 100%. Between the two rectangular plots, a circular plot of 3 m-radius was placed in order to evaluate the botanical quality according to the official QII assessment key for BPA meadows (Fig. 3; Swiss Federal Council, 2013). In 2023, vegetation assessment in one DS-P meadow could not be carried out because the meadow was mowed prior the scheduled survey. This meadow was therefore excluded from the analysis.

2.4. Statistical analyses

All the statistical analyses were performed in R 4.5.0 (R Core Team, 2025). The vegetation data from the two rectangular plots were merged to obtain a single measure per meadow. The effect of the restoration treatment was then analysed with linear mixed-effect models using the package *lme4* (Bates et al., 2015) and assuming a Gaussian distribution. Response variables were plant species richness (either total or per functional group, i.e. grasses, forbs and legumes), percentage cover of each functional group, number of quality II indicator species, beta

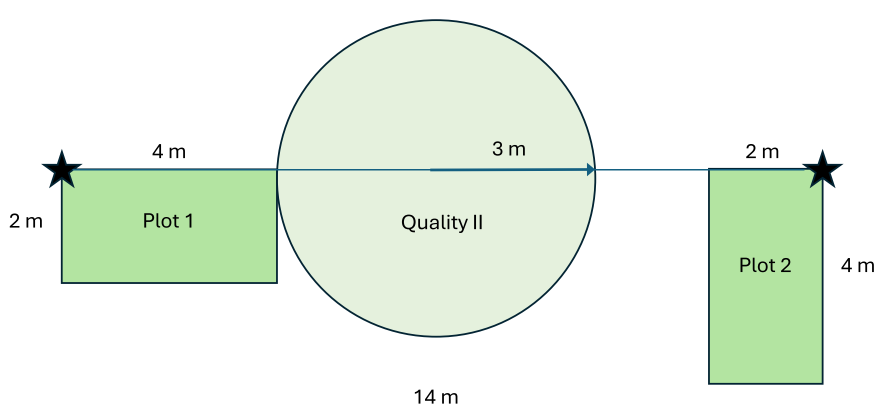

Fig. 3. Design applied in the vegetation surveys. The black stars depict the permanent nails enabling plot location over time. An exhaustive vegetation survey (i.e. listing all the plant species and estimating their cover) was conducted in the two rectangular plots (8 m^2 each) while a vegetation quality II survey (number of indicator plant species present) was conducted in the 3 m-radius circular plot.

diversity (additive partitioning of diversity) and community weighted means (CWM) of different functional traits (i.e. month of first flowering; seed mass, in mg; number of seeds) and of the Landolt values for nutrients and moisture. The information about seed mass and number were retrieved from the LEDA trait database (Kleyer et al., 2008), while the information regarding the month of the first flowering and the Landolt values for nutrients and moisture were extracted from the Flora Helvetica (Lauber et al., 2018).

The effect of the year, entered as a categorical factor, was also analysed with linear mixed effect models assuming a Gaussian distribution, with plant species richness and number of QII indicator species by treatment as response variables. The site was included in all the models as a random effect to account for site-specific variability.

Beta diversity between treatments, or their difference in terms of species composition, was also investigated. Firstly, considering the additive partitioning of diversity (Lande, 1996) and taking into account only the species richness (i.e. presence or absence of a species), but not species abundance: $\beta = \gamma - \alpha$. Where α represents the species richness of a single meadow, γ represents the species richness of all the meadows within the respective treatment and β represents the difference between meadows belonging to that treatment.

Secondly, still considering only species richness (i.e. whether the species were present or absent) but not abundance, the Sørensen index for pairwise dissimilarities was calculated (Koleff et al., 2003; Baselga, 2010):

$$\beta_{sor} = \frac{b + c}{2a + b + c}$$

Where *a* represents the number of species common to meadows 1 and 2, *b* represents the number of species that are present only in meadow 1 and *c* represents the number of species present only in meadow 2. To calculate this index, we used the *betapart* package (Baselga and Orme, 2012). Note that conventional linear models (without random effect) were fitted to test the effect of the treatment on this beta diversity index.

Lastly, beta diversity was calculated considering both species richness and abundance, using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). We checked with a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations if the difference between treatments was significant. If that was the case, we tested if the difference was due to location (i.e. the mean values) or dispersion (i.e. the variation around the mean values) with a permutational test for homogeneity of multivariate dispersion (BETADISPER) and an ANOVA test. For the multivariate analyses we used the *vegan* package (Oksanen et al., 2020).

The CWMs were used to weigh community trait values by species abundance. For this purpose, the mean cover of each species in the two vegetation survey plots was considered with the following formula:

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

Where c_i represents the cover for the plant species *i*, c_{tot} the cover of all species in a particular meadow and F_i the median functional trait value.

To check if there was a statistically significant difference among treatments, we changed the intercept running the relevel function, which reorders the levels of a factor. Model assumptions were visually checked by inspecting the respective residual plot (residuals against fitted values) and quantile-quantile plot.

3. Results

3.1. Total species richness and number of QII indicator species

In 2023, the total number of plant species was higher in all the experimental treatments compared to the controls, but the difference was significant only for HT-P and MS-P (Appendix C). The restored meadows had on average (± SD) 32 ± 4.9 species, while the control meadows harboured 27 ± 5.4 species (HT-H: 30 ± 5.3; HT-P: 32 ± 4.7; DS-P: 31 ± 4.9; MS-P: 33 ± 4.9). Regarding the number of QII indicator plant species in 2023, all the restored treatments had significantly more (106% more on average) QII indicators than the controls (C: 4 ± 1.6; HT-H: 8 ± 2.7; HT-P: 8 ± 2.5; DS-P: 9 ± 2.4; MS-P: 9 ± 2.7). As a result, 90% of the restored meadows reached QII (≥ 6 indicator species), while only 25% of the control meadows qualified for it.

For each treatment, when comparing the total species richness and the number of QII indicator species in each survey year with those in other years, the control was not significantly different across years, while almost all the treatments increased significantly from 2018 to 2021 and remained stable between 2021 and 2023. MS-P was an exception, with an increase in 2021 followed by a decline in 2023 of −5.3 ± 1.5 plant species (mean ± SD, P = 0.002) and −2.33 ± 0.71 QII indicator species (P = 0.003) (Figs. 4 and 5, Appendix D).

3.2. Functional groups

The species richness and cover were evaluated also according to the functional groups, i.e. grasses, forbs and legumes (Fig. E.1. and E.2, Appendix C for statistical analyses). Regarding species richness, the only significant difference between a treatment and the control that emerged was HT-P for the grasses (HT-P vs C: 1.67 ± 0.81, $P = 0.047$) and MS-P for the forbs (MS-P vs C: 3.17 ± 1.41, $P = 0.028$). Concerning the legumes, none of the treatments were significantly different from the control, but HT-P and MS-P always performed slightly better than the other treatments. The most remarkable difference regarding cover was observed for the legumes, where HT-P had a significantly higher cover than all other treatments and the control (HT-P vs C: 15.8 ± 4.0, $P < 0.001$). This still holds true after removing an extreme outlier (HT-P vs C: 12.4 ± 3.5, $P < 0.001$).

3.3. Beta diversity

The additive partitioning of diversity was found to be higher than the control only for HT-H (HT-H vs C: 5.1 ± 2.1, $P = 0.018$) and HT-P (HT-P vs C: 6.17 ± 2.06, $P = 0.005$) (Fig. 6A, Appendix C for statistical analyses). The Sørensen index for pairwise dissimilarities was slightly higher in HT-P (HT-P vs C: 0.02 ± 0.01, $P = 0.019$) and lower in MS-P (MS-P vs C: −0.04 ± 0.01, $P < 0.001$) than in the controls, respectively (Fig. 6B, Appendix C). Regarding the beta diversity calculated with the Bray-Curtis dissimilarity index (Fig. E.3.), the PERMANOVA was significant ($F = 1.83$, $P = 0.004$), but not the ANOVA calculated on the BETADISPER distances ($F = 0.91$, $P = 0.467$), indicating a difference among the treatments given by location but not by dispersion. Pairwise PERMANOVA tests were conducted to see among which treatments there was a statistically significant difference: MS-P was the only one found to be different compared to both the control (MS-P vs C: $F = 2.97$, $P = 0.006$) and all the other treatments (MS-P vs HT-H: $F = 1.97$, $P = 0.035$; MS-P vs HT-P: $F = 2.03$, $P = 0.015$; MS-P vs DS-P: $F = 2.33$, $P = 0.009$). The treatment explained 12% of the variation of the plant community composition ($R^2 = 0.12$).

3.4. Functional traits and Landolt values

The analysis of the traits comparing the treatments with the control, gave a significant result for the month of first flowering and the moisture (Appendix C). HT-H (HT-H vs C: 0.16 ± 0.07, $P = 0.028$) and, especially, DS-P (DS-P vs C: 0.2 ± 0.07, $P = 0.009$), had a later flowering compared to the control. Furthermore, DS-P had more plant species adapted to drier soils compared to the control and the other treatments (DS-P vs C: −0.20 ± 0.05, $P < 0.001$; DS-P vs HT-H: −0.18 ± 0.05, $P = 0.001$; DS-P vs HT-P: −0.13 ± 0.05, $P = 0.022$; DS-P vs MS-P: −0.11 ± 0.05, $P = 0.041$).

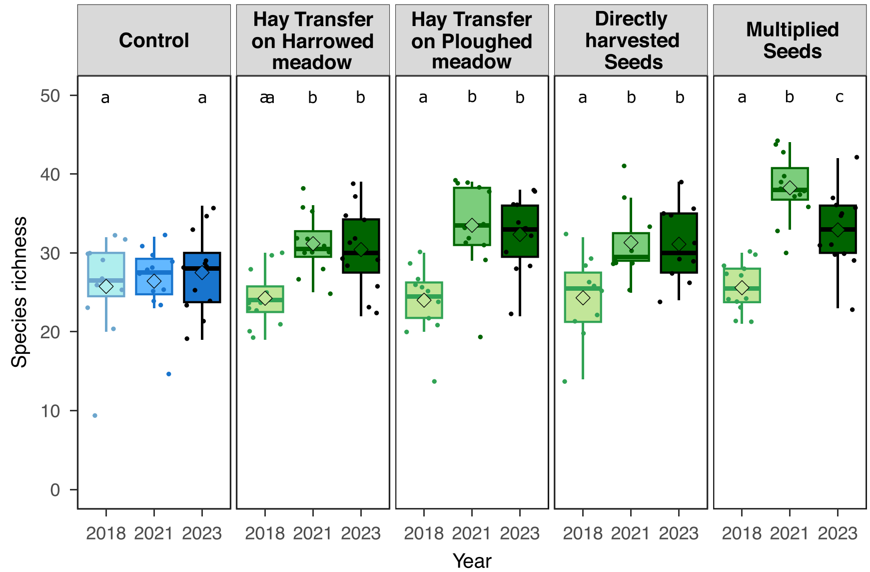

Fig. 4. Plant species richness by restoration treatment in 2018, 2021, and 2023. Plant species richness with respect to restoration treatment in 2018 (before restoration), in 2021 and 2023, i.e. two and four years after restoration, respectively. Horizontal bars indicate the median, diamond shapes the mean and dots the outliers. Different letters indicate whether there is a statistically significant difference at $P < 0.05$ within treatment with respect to year. See Appendix D for statistical analyses.

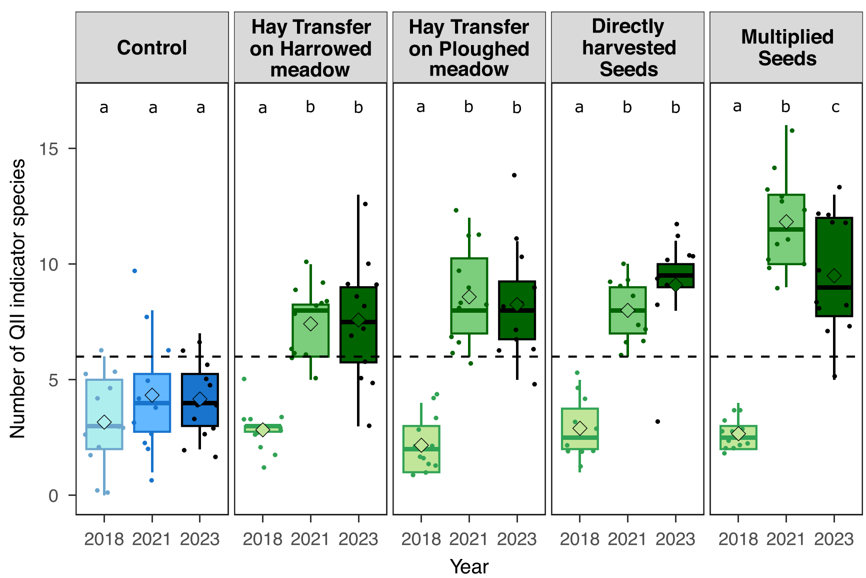

Fig. 5. Number of QII indicator plant species by restoration treatment in 2018, 2021, and 2023**.** The black dashed line represents the threshold of 6 indicator plant species, i.e. the minimum required to be eligible for the QII payment scheme. Boxplot features and statistical symbols as in Fig. 4. See Appendix D for statistical analyses.

4. Discussion

This study evaluated the efficacy of assisted restoration techniques combining soil preparation intensity (harrowing or ploughing) with different seed addition strategies to overcome propagule limitation in species-poor lowland grasslands. Seed addition involved either hay transfer, seeds directly harvested from a donor meadow, or multiplied seed mixtures. Findings indicate that all restoration methods successfully enhanced plant biodiversity, with 16% more species in restored meadows compared to control meadows. This outcome is promising not only for biodiversity conservation but also for farmers, as 90% of the restored meadows reached the BPA quality level II and thus qualified for the additional output-based payment schemes. The study also demonstrates that plant biodiversity restoration in intensively managed landscapes, such as the Swiss lowland Plateau, can be achieved in a much shorter timeframe than those observed in natural restoration processes, i.e. under passive relaxation of farming intensity (Marriott et al., 2004). To better understand the mechanisms underlying these patterns, we further investigated how functional group composition, community-weighted means of selected ecological traits, and beta diversity responded to restoration treatments.

A key strength of the study certainly lies in its experimental approach, which used a fully spatially replicated randomized block design, including a control, the latter being meadows undergoing natural (passive) regeneration without any soil disturbance or seed addition. Additionally, the fact that the study was carried out at real field

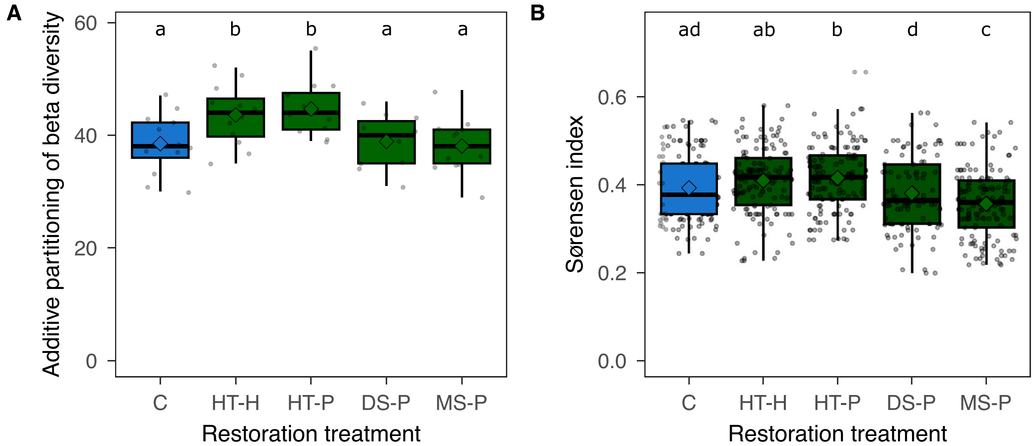

Fig. 6. Two measures of beta diversity in 2023. A) additive partitioning of diversity; and B) Sørensen index for pairwise dissimilarities. Abbreviations for the restoration treatments are: C = Control; HT-H = Hay Transfer on a Harrowed meadow; HT-P = Hay Transfer on a Ploughed meadow; DS-P = Directly harvested native Seeds on a Ploughed meadow; MS-P = Multiplied native Seeds on a Ploughed meadow. Boxplot features and statistical symbols as in Fig. 4. See Appendix C for statistical analyses.

scale renders its outcome much more convincing in the eyes of the stakeholders; this will boost the uptake of these various grassland restoration methods by farmers (Jones et al., 2018; Slodowicz et al., 2023). Finally, restoring plant diversity is likely to promote invertebrate recovery, triggering cascading effects throughout the whole ecosystem (Arnold et al., 2025; Borer et al., 2012; Britschgi et al., 2006).

4.1. Species richness and QII indicator species

The species richness and the number of QII indicator species experienced a striking increase in all the treatments in 2021 (by 37% and 242%, respectively) with a slight decline and stabilization in 2023 (increase of 29% and 226%, respectively, comparing to 2018). As a result, 90% of the restored meadows achieved QII and qualified for the output-based (or results-based) payments, whereas no meadows qualified for it before restoration in 2018. While species richness and number of QII species did not significantly increase in control meadows, three (25%) of them also reached QII by 2023. These meadows harboured 6 or 7 indicators plant species (just reaching the threshold for QII payment, which is set at $\geq$ 6). This shows that the ecological quality of the meadows can also naturally improve a little bit with time (Iberl et al., 2023).

In 2023, restored meadows had 16% more plant species compared to the controls. This result is in line with what was found by Slodowicz et al. (2023), that reported a mean increase in plant species of 17.4% for the studies analysed. In the same year, the treatments Hay Transfer on a Ploughed meadow (HT-P) and, in particular Multiplied native Seeds on a Ploughed meadow (MS-P), were found to be the ones with the highest species richness, with 32 ± 4.7 and 33 ± 4.9 species per 16 m^2, respectively. Moreover, Hay Transfer on a Ploughed meadow was found to have a significantly higher legume cover compared to all the other treatments. The hay transfer method has apparently succeeded in effectively transferring legumes when their seeds were ripe (Bischoff et al., 2018). Since this difference was found only in the Hay Transfer on a Ploughed meadow but not in the Hay Transfer on a Harrowed meadow (HT-H) treatment, the ploughing of the soil may have further helped the establishment of legumes. It is known that N (nitrogen) is released following ploughing, decreasing N concentration in the soil, which may have favoured legume species in the mid-term (Davies et al., 2001; Lambers et al., 2004). Furthermore, by turning the soil, ploughing can bury the topsoil rich in P and K as well as the seeds of weedy grasses, reducing the concentration of those nutrients and the competition from grasses (Pywell et al., 2002).

In relation to the seed source, the Multiplied Seeds treatment was the only one declining in 2023, compared to 2021. One possible explanation is that, even if the employed multiplied seed mixture contains Swiss ecotypes, some of the plants in the mix may have been maladapted to site conditions, resulting in their progressive disappearance (Bucharova et al., 2017), as expected with commercially available seed mixtures designed for broad environmental conditions. Interestingly, this phenomenon was not evidenced in the treatments involving hay transfer and natural seeds collected from species-rich donor meadows. This may be due to donor meadows being located within 10 km of each of our 12 study sites, i.e. presenting a higher likelihood of converging environmental conditions with the recipient site than general commercial seed mixes. This notwithstanding, the Multiplied Seeds treatment remains one of the most successful restoration tactics due to the high diversity of the initial commercial seed mixture, which contained 38 plant species. While the donor meadows harboured a similarly rich plant community based on our vegetation surveys, with 34.5 ± 6 species per 16 m^2 (and 48 ± 5 species at the field scale, unpublished data), a fraction of the plant species could probably not be transferred into the recipient meadows due to natural variation in plant phenology and maturation (Wagner et al., 2021).

The community weighted mean of the month of first flowering, a key functional trait, as expected, was not higher in the hay transfer treatments, but it was in the meadows having received the directly harvested seeds, indicating that plant species with a later phenology were more abundant in that treatment. This may be explained by the seed collection method as, in addition to the main seed harvest in June, seeds were also hand-collected later in the season from uncut grass strips. Moreover, the treatment Directly harvested native Seeds on a ploughed meadow (DS-P) had a higher proportion of plant species adapted to drier soils compared to the control meadows and, but to a lesser extent, the other treatments. Ploughed soils are known to lose water easily and this may have favoured the establishment of more dry-tolerant species the year of seeding (Mielke et al., 1986).

4.2. Beta diversity

Additive partitioning of beta diversity was found to be higher in Hay Transfer on a Harrowed meadow and Hay Transfer on a Ploughed meadow compared to Control, Directly harvested Seeds and Multiplied Seeds, meaning that at the landscape scale Hay Transfer on a Harrowed meadow and Hay Transfer on a Ploughed meadow were more distinct compared to the meadows within the other treatments. The Sørensen index for pairwise dissimilarities gave a similar result, but according to this index the differences between Hay Transfer on a Harrowed meadow and Hay Transfer on a Ploughed meadow, on the one hand, and the other treatments, on the other hand, were less evident. The two indices focus on presence/absence of a species but, while the additive partitioning of beta diversity focuses more on the quantitative aspect, the Sørensen index is more qualitative. The former measures the difference in species richness between a meadow and all the others grouped together, within a given treatment category, i.e. across study sites (Lande, 1996), while the latter compares a given meadow with each of the other 11 meadows belonging to a given treatment, providing a measure of the community composition dissimilarity (Koleff et al., 2003; Baselga, 2010). Therefore, Hay Transfer on a Harrowed meadow and Hay Transfer on a Ploughed meadow are more different among them in terms of species richness but less so in terms of community composition compared to the other treatments (Scotton and Ševčíková, 2017). Based on the Sørensen index, Multiplied Seeds exhibited lower beta diversity than the other treatments and the Control. The additive partitioning index, however, showed a slightly different result, with Multiplied Seeds being lower than the hay transfer treatments, but similar to Directly harvested Seeds and Control. Combined with the results on alpha diversity, this suggests that while Multiplied Seeds meadows are as species-rich, as the other restored meadows, they are more homogeneous in terms of community composition. This is in line with our predictions given that Hay Transfer on a Harrowed meadow and Hay Transfer on a Ploughed meadow received hay from different donor meadows in each study site, whereas all Multiplied Seeds meadows were sown with the same seed mixture. As for Control meadows, regional differences in management histories likely contribute to their somewhat greater diversity in community composition compared to Multiplied Seeds meadows. Directly harvested Seeds meadows exhibited an intermediate pattern. However, it was unexpected that its additive partitioning index was lower than that of Hay Transfer on a Harrowed meadow and Hay Transfer on a Ploughed meadow, since Directly harvested Seeds meadows received seeds from the same donor meadows as the hay transfer treatments. This could be due to the different seed collection methods: the hay transfer method is less selective and more efficient in terms of seed number, as it gathers and transfers the entire aboveground plant material to the recipient meadow, whereas the directly harvesting seed method loses some seeds during collection and processing, a loss that might be unequal among species and could probably not be fully compensated by our targeted, hand-picked seeds later in the season for that treatment (Scotton and Ševčíková, 2017).

Consistent with the Sørensen index, the Bray-Curtis dissimilarity index (which incorporates both species presence/absence and abundance) showed that the Multiplied Seeds treatment differed in community composition from the control and the other treatments (Anderson et al., 2011).

4.3. Conclusion and management implications

All the experimental treatments successfully increased the ecological quality of the meadows with, four years after restoration, 90% of the restored meadows qualifying for the output-based QII payments. Our results indicate that any farmer implementing the restoration methods tested in this study will likely succeed and be financially rewarded for their commitment to biodiversity promotion. As for the efficacy of harrowing vs ploughing, the latter performed slightly better. However, since both soil preparation methods are effective, we recommend leaving the choice to the farmer. As mentioned in the introduction, farmers are often reluctant to plough their semi-natural meadows. Nonetheless, Hay Transfer on a Ploughed meadow was one of the most effective treatments, probably because the deep soil disturbance it involves annihilates the previous plant community, providing better growing opportunities for the new seedlings (Pywell et al., 2002; Vymyslický et al., 2024).

Multiplied seeds was one of the best performing treatments in terms of local species richness (alpha diversity), even if some of the species were lost over time, but the least diverse in terms of community composition (beta diversity). Indeed, the decline in alpha diversity may continue beyond five years, which was the duration of our experiment, calling for further monitoring of the plant community development into the future. Meadows restored with the seeds from donor meadows (either in form of hay or directly harvested) demonstrated a higher stability over time, probably because they benefit from local ecotypes that are better adapted to the site-specific environmental conditions (Bucharova et al., 2019). Future research should investigate whether mixing seeds from different donor meadows in the same site may further boost biodiversity, as proposed by Bucharova et al. (2019). Finally, it would be interesting to document how the micro-fauna responds to these different restoration methods. Altogether our results pave the way towards more efficient strategies for restoring farmland biodiversity.

CRediT authorship contribution statement

Raphaël Arlettaz: Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Jean-Yves Humbert:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Laura Forgione:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Daniel Slodowicz:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Miro Bergauer:** Investigation. **Richard Arthur Dupont:** Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110369.

Data Availability

Restoring plant diversity in lowland grasslands: efficacy of different seed addition and soil preparation methods (dataset) (Mendeley Data)

References

Agrarbericht, 2024. Rapport agricole. 〈https://www.agrarbericht.ch/fr/politique/paiements-directs/contributions-a-la-biodiversite〉 (accessed 2 April 2025).

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x.

Arnold, I., Marchand, G., Hayoz-Andrey, A., Serres-Hänni, A., Arlettaz, R., Humbert, J.-Y., 2025. Relaxation of management intensity promotes butterfly communities in

mountain grasslands. Biol. Conserv 304, 111027. https://doi.org/10.1016/j.biocon.2025.111027.
Atkinson, J., Bonser, S.P., 2020. Active" and "passive" ecological restoration strategies in meta-analysis. Restor. Ecol. 28, 1032–1035. https://doi.org/10.1111/rec.13229.
Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schüpbach, B., Walter, T., Herzog, F., 2009. Ecological cross compliance promotes farmland biodiversity in Switzerland. Front. Ecol. Environ. 7, 247–252. https://doi.org/10.1890/070197.
Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends Ecol. Evol. 14, 63–68. https://doi.org/10.1016/S0169-5347(98)01544-4.
Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.
Baselga, A., Orme, C.D.L., 2012. Betapart: An R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.
Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. https://doi.org/10.1111/cobi.12536.
Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01.
Baur, B., 2014. Dispersal-limited species - a challenge for ecological restoration. Basic Appl. Ecol. 15, 559–564. https://doi.org/10.1016/j.baae.2014.06.004.
Bischoff, A., Hoboy, S., Winter, N., Warthemann, G., 2018. Hay and seed transfer to re-establish rare grassland species and communities: how important are date and soil preparation? Biol. Conserv 221, 182–189. https://doi.org/10.1016/j.biocon.2018.02.033.
Borer, E.T., Seabloom, E.W., Tilman, D., 2012. Plant diversity controls arthropod biomass and temporal stability. Ecol. Lett. 15, 1457–1464. https://doi.org/10.1111/ele.12006.
Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349. https://doi.org/10.2307/1942268.
Britschgi, A., Spaar, R., Arlettaz, R., 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat Saxicola rubetra: Lessons for overall Alpine meadowland management. Biol. Conserv 130, 193–205. https://doi.org/10.1016/j.biocon.2005.12.013.
Bucharova, A., Michalski, S., Hermann, J.M., Heveling, K., Durka, W., Hölzel, N., Kollmann, J., Bossdorf, O., 2017. Genetic differentiation and regional adaptation among seed origins used for grassland restoration: lessons from a multispecies transplant experiment. J. Appl. Ecol. 54, 127–136. https://doi.org/10.1111/1365-2664.12645.
Bucharova, A., Bossdorf, O., Hölzel, N., Kollmann, J., Prasse, R., Durka, W., 2019. Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. Conserv. Genet 20, 7–17. https://doi.org/10.1007/s10592-018-1067-6.
Carter, M.R., McKyes, E., 2005. Cultivation and tillage. in: Encyclopedia of Soils in the Environment. Elsevier, pp. 356–361. https://doi.org/10.1016/B0-12-348530-4/00514-2.
Carvalheiro, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. Ecol. Lett. 14, 251–259. https://doi.org/10.1111/j.1461-0248.2010.01579.x.
Conrady, M., Lampei, C., Bossdorf, O., Durka, W., Bucharova, A., 2022. Evolution during seed production for ecological restoration? a molecular analysis of 19 species finds only minor genomic changes. J. Appl. Ecol. 59, 1383–1393. https://doi.org/10.1111/1365-2664.14155.
R. Core Team, 2025. R: A Language and Environment for Statistical Computing, Version 4.5.0. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.
Davies, M.G., Smith, K.A., Vinten, A.J.A., 2001. The mineralisation and fate of nitrogen following ploughing of grass and grass-clover swards. Biol. Fertil. Soils 33, 423–434. https://doi.org/10.1007/s003740100348.
Diacon-Bolli, J., Dalang, T., Holderegger, R., Bürgi, M., 2012. Heterogeneity fosters biodiversity: Linking history and ecology of dry calcareous grasslands. Basic Appl. Ecol. 13, 641–653. https://doi.org/10.1016/j.baae.2012.10.004.
Durbecq, A., d'Ambly, M., Buisson, E., Jaunatre, R., Cluchier, A., Bischoff, A., 2021. Seedling recruitment in mountain grassland restoration: Effects of soil preparation and grazing. Appl. Veg. Sci. 24, 1–11. https://doi.org/10.1111/avsc.12564.
Espeland, E.K., Emery, N.C., Mercer, K.L., Woolbright, S.A., Kettenring, K.M., Gepts, P., Etterson, J.R., 2017. Evolution of plant materials for ecological restoration: insights from the applied and basic literature. J. Appl. Ecol. 54, 102–115. https://doi.org/10.1111/1365-2664.12739.
Freitag, M., Klaus, V.H., Bolliger, R., Hamer, U., Kleinebecker, T., Prati, D., Schäfer, D., Hölzel, N., 2021. Restoration of plant diversity in permanent grassland by seeding: assessing the limiting factors along land-use gradients. J. Appl. Ecol. 58, 1681–1692. https://doi.org/10.1111/1365-2664.13883.
Gossner, M., Lewinsohn, T., Kahl, T., Grassein, F., Boch, S., Prati, D., Birkhofer, K., Renner, S., Sikorski, J., Wubet, T., Arndt, H., Baumgartner, V., Blaser, S., Blüthgen, N., Börschig, C., Buscot, F., DIekötter, T., Jorge, L., Jung, K., Keyel, A., Klein, A., Klemmer, S., Krauss, J., Lange, M., Müller, J., Overmann, J., Pašali, E., Penone, C., Perovic, D., Purschke, O., Schall, P., Socher, S., Sonnemann, I., Tschapka, M., Tscharntke, T., Türke, M., Venter, P., Weiner, C., Werner, M., Wolters, V., Wurst, S., Westphal, C., Fischer, M., Weisser, W., Allan, E., 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540, 266–269. https://doi.org/10.1038/nature20575.
Hábenczyus, A.A., Weiterová, I., Foremnik, K., Jakob, A., Khopkar, S., Kumar, A., Lazăr, A., Paganeli, B., Samraoui, K.R., Sidwell, J., Hrček, J., Lepš, J., Segrestin, J., 2024. Long-term effects of meadow management on seed bank diversity and composition. J. Veg. Sci. 35. https://doi.org/10.1111/jvs.13282.
Hooftman, D., Kimberley, A., Cousins, S.A.O., Escribano-Avila, G., Honnay, O., Krickl, P., Plue, J., Poschlod, P., Traveset, A., Bullock, J.M., 2021. Dispersal limitation, eutrophication and propagule pressure constrain the conservation value of Grassland Green Infrastructure. Biol. Conserv 258, 109152. https://doi.org/10.1016/j.biocon.2021.109152.
Hopkins, A., Holz, B., 2005. Grassland for agriculture and nature conservation: production, quality and multifunctionality. in: 13th International Occasional Symposium of the European Grassland Federation, Grassland Science in Europe. European Grassland Federation, Tartu.
Iberl, K., Poschlod, P., Reisch, C., 2023. Restoration of calcareous grasslands by natural recolonization after forest clearing and its impact on the genetic variation of three common herb species. Biodivers. Conserv 32, 671–690. https://doi.org/10.1007/s10531-022-02518-2.
Jones, H.P., Jones, P.C., Barbier, E.B., Blackburn, R.C., Rey Benayas, J.M., Holl, K.D., McCrackin, M., Meli, P., Montoya, D., Mateos, D.M., 2018. Restoration and repair of Earth's damaged ecosystems. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2017.2577.
Klaus, V.H., Hoever, C.J., Fischer, M., Hamer, U., Kleinebecker, T., Mertens, D., Schäfer, D., Prati, D., Hölzel, N., 2018. Contribution of the soil seed bank to the restoration of temperate grasslands by mechanical sward disturbance. Restor. Ecol. 26, S114–S122. https://doi.org/10.1111/rec.12626.
Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40, 947–969. https://doi.org/10.1111/j.1365-2664.2003.00868.x.
Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: A database of life-history traits of Northwest European flora. J. Ecol. 96, 1266–1274.
van Klink, R., Boch, S., Buri, P., Rieder, N.S., Humbert, J.Y., Arlettaz, R., 2017. No detrimental effects of delayed mowing or uncut grass refuges on plant and bryophyte community structure and phytomass production in low-intensity hay meadows. Basic Appl. Ecol. 20, 1–9. https://doi.org/10.1016/j.baae.2017.02.003.
Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. J. Anim. Ecol. 72, 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x.
Lachat, T., Pauli, D., Gonseth, Y., Klaus, G., Scheidegger, C., Vittoz, P., Walter, T., 2010. Evol. De. la biodiversité En. Suisse depuis 1900 avonsnous Touché Le. Fond. ? Haupt Bern.
Lambers, J.H.R., Harpole, W.S., Tilman, D., Knops, J., Reich, P.B., 2004. Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands. Ecol. Lett. 7, 661–668. https://doi.org/10.1111/j.1461-0248.2004.00623.x.
Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76, 5–13.
Lauber, K., Wagner, G., Gygax, A., 2018. Flora Helvetica: Flore illustrée de Suisse, 5th ed. Haupt Verlag.
Marriott, C., Fothergill, M., Jeangros, B., Scotton, M., Louault, F., 2004. Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. Agronomie 447, 462. https://doi.org/10.1051/agro.
Meier, E.S., Lüscher, G., Herzog, F., Knop, E., 2024. Collaborative approaches at the landscape scale increase the benefits of agri-environmental measures for farmland biodiversity. –108948 Agric. Ecosyst. Environ. 367, 108948. https://doi.org/10.1016/j.agee.2024.108948.
MeteoSwiss, 2025. Clim. Switz. ⟨https://www.meteoswiss.admin.ch/climate/the-climate-of-switzerland.html⟩ (accessed 1 April 2025).
Mielke, L.N., Doran, J.W., Richards, K.A., 1986. Physical environment near the surface of plowed and no-tilled soils. Soil Tillage Res 7, 355–366.
Nerlekar, A.N., Sullivan, L.L., Brudvig, L.A., 2024. Grassland restorations must better foster forbs to facilitate high biodiversity. Restor. Ecol. 1–6. https://doi.org/10.1111/rec.14214.
Oksanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., 2020. vegan Community Ecol. Package.
Pokorny, M.L., Sheley, R.L., Svejear, T.J., Engel, R.E., 2004. Plant species diversity in a grassland plant community: evidence for forbs as a critical management consideration. West. North Am. Nat. 64, 219–230.
Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., Peel, S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. J. Appl. Ecol. 39, 294–309. https://doi.org/10.1046/j.1365-2664.2002.00718.x.
Sainju, U.M., Lenssen, A.W., Caesar-TonThat, T., Jabro, J.D., Lartey, R.T., Evans, R.G., Allen, B.L., 2012. Dryland soil nitrogen cycling influenced by tillage, crop rotation, and cultural practice. Nutr. Cycl. Agroecosyst 93, 309–322. https://doi.org/10.1007/s10705-012-9518-9.
Scotton, M., Ševčíková, M., 2017. Efficiency of mechanical seed harvesting for grassland restoration. Agric. Ecosyst. Environ. 247, 195–204. https://doi.org/10.1016/J.AGEE.2017.06.040.

Slodowicz, D., Auberson, C., de Carvalho, E.F., Angeleri, R., Stańska, M., Hajdamowicz, I., Kurtogullari, Y., Roth, R., Rossier, L., Enz, G., Humbert, J.Y., Arlettaz, R., 2022. No detrimental effects of soil disturbance resulting from grassland restoration operations on aboveground-dwelling invertebrate communities. Restor. Ecol. 1–11. https://doi.org/10.1111/rec.13860.

Slodowicz, D., Durbecq, A., Ladouceur, E., Eschen, R., Humbert, J.Y., Arlettaz, R., 2023. The relative effectiveness of different grassland restoration methods: a systematic literature search and meta-analysis. Ecol. Solut. Evid. 4. https://doi.org/10.1002/2688-8319.12221.

Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Hölzel, N., Jung, K., Klaus, V.H., Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E. K., Müller, J., Oelmann, Y., Overmann, J., Pašalić, E., Rillig, M.C., Schaefer, H.M., Schloter, M., Schmitt, B., Schöning, I., Schrumpf, M., Sikorski, J., Socher, S.A., Solly, E.F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Türke, M., Venter, P.C., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M., Allan, E., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536, 456–459. https://doi.org/10.1038/nature19092.

Swiss Federal Council, 2013. Ordonnance sur Les. Paiem. Directs Vers. éS. dans l'Agric. 1998, 1–54.

Thorbek, P., Bilde, T., 2004. Reduced numbers of generalist arthropod predators after crop management. J. Appl. Ecol. 41, 526–538. https://doi.org/10.1111/j.0021-8901.2004.00913.x.

Török, K., Valkó, O., Deák, B., 2024. Ecosystem restoration with local or broad seed provenancing: debates and perceptions in science and practice. Biol. Conserv 293, 110535. https://doi.org/10.1016/j.biocon.2024.110535.

Vymyslický, T., Jiroušek, M., Frei, I., Smetanová, S., Winkler, J., Zdražílková, M., Fabšičová, M., 2024. Will small-scale ploughing increase the plant diversity of species-poor grasslands? Folia Geobot. 59, 1–16. https://doi.org/10.1007/s12224-024-09448-7.

Wagner, M., Hulmes, S., Hulmes, L., Redhead, J.W., Nowakowski, M., Pywell, R.F., 2021. Green hay transfer for grassland restoration: species capture and establishment. Restor. Ecol. 29, 1–11. https://doi.org/10.1111/rec.13259.

Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., Pywell, R.F., 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biol. Conserv 119, 1–18. https://doi.org/10.1016/j.biocon.2003.10.020.

Wesche, K., Krause, B., Culmsee, H., Leuschner, C., 2012. Fifty years of change in Central European grassland vegetation: large losses in species richness and animal-pollinated plants. Biol. Conserv 150, 76–85. https://doi.org/10.1016/j.biocon.2012.02.015.

Widmer, S., Riedel, S., Babbi, M., Herzog, F., Wohlgemuth, T., Kessler, M., Dengler, J., 2025. One century of change: stronger diversity decline in lowland than in mountain grasslands in central Europe. Glob. Chang. Biol. 31, e70529. https://doi.org/10.1111/gcb.70529.

Willems, F.M., Bantin, J., Hölzel, N., Bucharova, A., 2026. Earlier reproductive phenology of restored grasslands. Restor. Ecol., e70298 https://doi.org/10.1111/rec.70298.

Zingg, S., Ritschard, E., Arlettaz, R., Humbert, J.Y., 2019. Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale. Biol. Conserv 231, 39–48. https://doi.org/10.1016/j.biocon.2018.12.022.