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Lasting legacies: Relicts of historical plant communities in Central European grasslands amid a century of biodiversity loss☆

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ABSTRACT

Central European grasslands have undergone significant transformations due to anthropogenic pressures such as land-use change, nitrogen deposition, and climate change. The persistence of historical grassland communities in the face of environmental change offers a unique opportunity for restoration initiatives. This study evaluates the availability of such remnant grasslands in Switzerland, by identifying patches that retained species composition and richness similar to the status of grasslands a century ago, and which can thus serve as nuclei for restoration. We resurveyed 73 sites selected from historical records, previously recorded around 1900, across a range of elevations and moisture regimes. Two plot types were sampled at each site: randomly positioned plots to assess average changes in species composition and targeted plots to assess the most similar remnants of the historical community. Species richness in the current most similar plots remained remarkably comparable to historical levels across all elevations and moisture levels, whereas current average plots exhibited a decline in dry and mesic grasslands. Ecological indicator values revealed significant increases in nutrient levels in dry and wet grasslands, likely driven by nitrogen deposition and land-use intensification. These changes were accompanied by shifts in species composition and increased tolerance to grazing and mowing. The analysis of CSR strategies highlighted a growing dominance of competitive species in wet and dry grasslands, along with a notable decline in stress-tolerant specialists. Our findings demonstrate the potential of remnant grasslands for restoration while emphasizing a large influence of environmental change.

1. Introduction

Habitat restoration is an important strategy to mitigate ongoing biodiversity loss and associated declines in ecosystem services (Strassburg et al., 2019). The United Nations Decade on Ecosystem Restoration, running from 2021 to 2030, aims at strengthening global, regional, national, and local commitments to halt and reverse ecosystem degradation (UNEP, 2024). However, limited understanding of restoration processes and the failure of some restoration projects reveal significant challenges to achieving the intended outcomes (Cooke et al., 2019; Dudley et al., 2020). Ecological restoration remains an evolving field, with the scientific community yet to reconcile the gap between theory and practice (Miller et al., 2017).

Semi-natural temperate grasslands are a widespread vegetation type in Central Europe where they developed over millennia by traditional land-use practices such as mowing with scythes and low-density livestock grazing, resulting in richly structured and often rather nutrient-poor habitats (Bobbink et al., 2010; Hejcman et al., 2013; Poschlod et al., 2009; Poschlod and WallisDeVries, 2002; van Dijk et al., 2007). These conditions favor the coexistence of a large number of plant species, placing temperate grasslands among the most biodiverse European ecosystems (Dengler et al., 2014; Dierschke and Briemle, 2002; Wilson

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et al., 2012). However, over the past century, land-use change, abandonment, and land-use intensification have significantly reduced both the extent and diversity of semi-natural grasslands, so that now they are among the most threatened ecosystems in Europe (Bonari et al., 2025; Charles, 2025; Janssen et al., 2016; Török and Dengler, 2018). In the late 19th century, significant alterations in habitat composition were brought along by the Second Agricultural Revolution, marked by mechanization and the advent of artificial fertilizers. This was followed by the Third Agricultural Revolution in the mid-20th century, characterized by chemical pesticides, advanced breeding techniques applied to forage crops, further mechanization, intensified fertilizing and grazing and ultimately higher mowing frequencies (Rachoud-Schneider et al., 2007).

These land-use changes in grassland were not uniform but modulated by abiotic conditions such as elevation and soil moisture levels. In mountainous regions, the intensification process was delayed by several decades and in some areas, traditional land use still persists, particularly in alpine pastures (Kampmann et al., 2008). However, in these regions, land abandonment of marginal land in the last few decades has contributed to species declines (Elliott et al., 2023). Even where traditional low-intensity farming practices have been reinstated through conservation measures, grasslands have been impacted by eutrophication resulting from atmospheric nitrogen deposition (Bobbink et al., 2010; Payne et al., 2019; Staude et al., 2020) and habitat fragmentation (Cousins et al., 2007; Krause et al., 2011; Krause et al., 2015). Also, grasslands with different moisture levels have undergone divergent evolutionary trajectories throughout industrialization. Wet meadows, historically used for litter production, were frequently abandoned or drained to increase productivity (Lachat et al., 2010; Poschlod, 2015, and are nowadays frequently subject of restoration projects (Joyce, 2014). Mesic grasslands, which had historically already been subjected to relatively intensive use (Brockmann-Jerosch, 1925), have primarily seen intensification through increased fertilization and mowing frequency. Finally, dry grasslands have experienced either intensified agricultural practices due to increased fertilizer use, or, where hardly accessible by motorized vehicles, have been abandoned and are succumbing to shrub and tree encroachment (Bonari et al., 2025; Lachat et al., 2010; Neuenkamp et al., 2016; Pereira et al., 2012; Poschlod et al., 2005).

According to the European Environmental Agency, at least 15 % of protected (Annex I) grassland and pastoral habitats in the EU are not in a good condition and thus require restoration (EEA, 2020). Grassland restoration is a complex process that must account for local environmental conditions, land-use practices, competition-facilitation dynamics, and the availability of plant species adapted to these conditions (Buisson et al., 2022; Török et al., 2021). While seed-based restoration techniques are commonly used to establish diverse grassland habitats (Kiss et al., 2021), they are often associated with high costs and low success rates (Poschlod and Jordan, 1992). Several studies have emphasized the importance of remnant grasslands in restoration strategies, as they offer a locally adapted species pool that can serve as a reservoir of biodiversity (Kapás et al., 2024b; Prach et al., 2021a; Prach et al., 2021b; Slodowicz et al., 2023), not only for plant species but also for insects (Stöckli et al., 2021). This reservoir includes not only plant species that rely on seed dispersal but also many species utilizing vegetative dispersal mechanisms such as belowground buds and clonal growth, which are common in grassland ecosystems, and which are not usually included in seed mixtures (Ottaviani et al., 2020). Recovering species from local remnant populations is of particular importance, as it may reduce the need for costly seed propagation efforts (Johnson et al., 2018; Knight and Overbeck, 2021; Scotton, 2018).

Historical shifts in species composition of Central European grasslands have been well-documented in several studies comparing historical vegetation records with recent resurveys. However, the reference baseline data typically come only from the last five decades (Diekmann et al., 2019; Gillet et al., 2016; Jandt et al., 2011) and are often biased by preferential sampling (Michalcová et al., 2011). In a resurvey of a historical grassland dataset from Switzerland spanning over 100 years (Riedel et al., 2023), we investigated the changes in grassland communities over the last century, based on 416 historical vegetation records from diverse grassland types and 1107 present-day resampling records (Widmer et al., 2025). We found significant declines in species richness and shifts in species composition, with more pronounced changes at low than high elevations. However, our study was focused on general trends, and did not consider the occurrence of vegetation patches with a degree of conservation that might provide opportunities for restoration efforts. In fact, resurvey studies typically aim at relocating the original sampling sites spatially as closely as possible and to obtain representative average values. To our knowledge this is the first study with historical data, which specifically aimed at identifying vegetation patches in the vicinity, that best mirror the historical species composition, further on called remnant grasslands.

In the present study, we assessed the availability of remnant grasslands in Switzerland and their potential for use in grassland restoration. We surveyed a sub-sample of the sites studied by #anonymous A (under review) to locate species communities that mirror the historical ones. This would show that present-day ecological conditions still facilitate a species composition similar to the historical one, if desired and provided there is appropriate land management, but also that these remnants can serve as nuclei for restoration. Our study seeks to answer the following questions (i) Can we today find grassland patches that resemble those a century ago in terms of richness and species composition, at different elevation and moisture levels? (ii) Are there individual species that have increased or decreased in frequency, even in grassland patches that are similar to the historical ones? (iii) Can we detect shifts in ecological and land-use indicator values, reflecting directional changes in the species composition of grasslands across elevation and moisture levels, associated to either local land management or large-scale alteration such as atmospheric nitrogen deposition and climate change?

2. Material and methods

2.1. Study site

We studied temperate permanent grasslands along an elevational gradient in Switzerland, ranging from 406 m to 2504 m a.s.l. Mean annual temperature across the study sites varied from 1 °C to 12 °C, whereas mean annual precipitation ranged from 600 mm to 2000 mm (MeteoSchweiz, 2024). The study sites spanned a gradient from the lowlands, such as in the canton of Zurich, where arable land comprises 40 % of agricultural land and grassland covers approximately 55 %, to alpine regions like the canton of Grisons, where grasslands constitute 94 % of agricultural land, whereas arable land makes up just 4 % (BFS, 2023).

2.2. Sampling design

Our study was based on the Historic Square Foot dataset (Riedel et al., 2023), which includes 580 vegetation records surveyed around 1900 across Switzerland, with the main focus on generating sound knowledge on grassland vegetation to lay the foundation for improving forage production. These records cover a broad range of permanent grassland habitats, including wet to semi-dry, acidic to calcareous soils, from the lowlands to the alpine belt, species poor to species rich, with different land use and land use intensities. Each historical record corresponds to a 0.09 m^2 sample, in which aboveground dry matter of vascular plant species and the number of individuals per species were recorded. We delimited the zone of potential location of each historical record using the information provided in the original record sheets and the historical Topographic Atlas of Switzerland (“Siegfried Map,” 1870–1926, 1:25,000/1:50,000), as described by Riedel et al. (2023). To focus on monitoring changes in plant diversity in grasslands under agricultural management, we excluded areas covered by infrastructure, forests, rocks, glaciers, rivers, and lakes using the "Roads and Tracks," "Buildings," "Hydrography," and "Land Cover" layers from swissTLM3D (https://www.swisstopo.admin.ch/en/geodata/landscape/tlm3d.html), as well as arable land, using the "Agricultural Management: Utilised Areas" layer (https://www.geodienste.ch/services/lwb_nutzungsflaechen/info) from the potential area around each historical plot. The remaining area, which likely contains the location of the historical vegetation record, was termed the potential grassland area. If there was no or only marginal strips (less than 2 m wide, e.g. field margins) of grassland left, the potential area was excluded from the sampling.

From the total of 358 potential grassland areas, we selected a stratified sample of 73 areas along a transect spanning from the canton of Basle in the north of Switzerland to the canton of Grisons in the southeast. Anticipating divergent effects across different moisture regimes and elevations, to guide the selection of sites, we stratified our sampling accordingly. Based on the unweighted mean ecological indicator values (EIVs) for moisture according to Landolt et al. (2010: ranging from 1 to 5) of the historical vegetation records, we defined three moisture classes: dry (EIV < 2.75), mesic (EIV ≥ 2.75 and < 3.4), and wet (EIV ≥ 3.4) and four elevational classes: ≤ 650 m, ≤ 1350 m, ≤ 2025 m, and > 2025 m a.s.l., resulting in 12 combinations. Within each of these classes, we classified records by species richness (high, medium, low) and selected the two historical records with the smallest potential grassland areas to minimize the impact of relocation error. However, because the historical sampling was not stratified in this way, and not all sites selected by us turned out to be suitable for resampling in the field, we ended up with 5–7 sites per combination (rather than 6 as in the theoretical design), resulting in the final set of 73 sites.

At each of the 73 sites, we established two sets of resurvey plots, both of the same size of 0.09 m^2 (Fig. 1): randomly positioned plots and plots specifically selected to be similar to the historical one. The aim of this procedure was to obtain an indication of the mean changes via the randomly positioned current average plots and of the persistence of the historical grassland species pool via the specifically selected current most similar plots. The three to five current average plots, each with a size of 0.09 m^2, were selected based on randomly generated coordinates within the potential grassland area using a randomization tool in ArcGIS, accounting for the inherent inaccuracy in the original locations (#anonymous A, under review), a method also proposed by Kapfer et al. (2017). For the positioning of the current most similar plots, we intentionally searched for a grassland patch of 0.09 m^2 with the greatest species overlap relative to the historical record. This search was conducted up to a 500 m radius surrounding the above-mentioned potential area to increase the chances of finding a suitable patch. To guide our search, we utilized maps identifying grasslands under extensive agricultural management through agri-environmental measures and nature protection areas. We selected one plot that was deemed to have the greatest species overlap with the historical one. After completing the vegetation record, we continued the search for a plot that might have an even greater overlap. The time limit for this search was set to one hour and we recorded a maximum two additional plots.

2.3. Vegetation recording

We conducted fieldwork in 2021 and 2022. We placed a metal frame with inner dimensions of 30 cm × 30 cm (0.09 m^2) on the ground and, after sampling, marked its center with a magnet for future resurvey studies. We recorded the precise coordinates using a high-precision GPS (u-blox ZED-F9P-02B GNSS module with SBAS and RTK). We recorded all vascular plant species rooting inside the frame. For the plant names we followed the nomenclature of the current checklist of Switzerland (Juillerat et al., 2017). In cases where species-level identification was subject to a high degree of uncertainty, we formed an aggregate of the respective species.

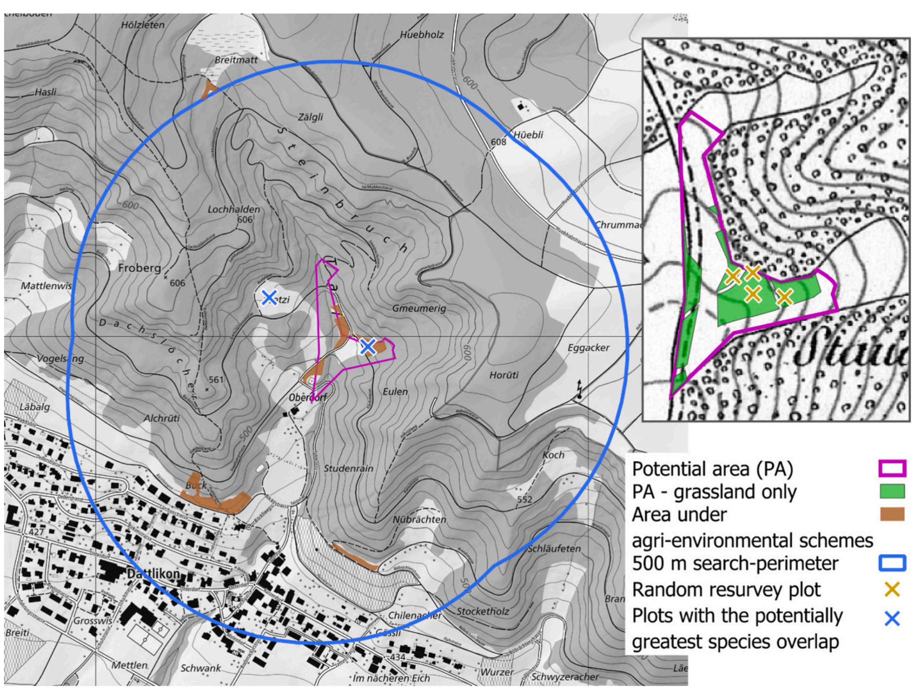

Fig. 1. Sampling design on the site level. The small inset shows the perimeter of the potential historical area, delimited according to the indications on the historical recording sheet (magenta) and the potential grassland area after subtracting forest and rivers (green). The brown crosses indicate the randomly selected coordinates for resampling, the current average plots. The large map shows the same perimeter of the potential area with the blue line marking the 500 m radius which delimits the search-perimeter for plots with the greatest species overlap to the historical plot species composition. The brown areas are land under extensive agricultural management due to agri-environmental schemes or nature conservation measures. Blue crosses indicate the plots selected in the field with the greatest species overlap to the historical record, the current most similar plots. (Background map: ©swisstopo) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Analyses

We calculated the Sørensen dissimilarity Index using the "vegdist" function from the "vegan" package (Oksanen et al., 2024), which was then transformed into a similarity measure (1 - Sørensen Index) ranging from 0 (completely different) to 1 (identical), reflecting the degree of compositional similarity. This similarity measure was used to select out of all current similar plots per site the one with the highest similarity to the historical record hereafter referred to as the current most similar plot. Our sample, forming the basis for all subsequent analyses, thus consisted of 73 historical plots, 73 current most similar plots and 73 values for the current average plots, which for each analysis had been computed as the mean of the three to five current average plots per site.

As a measure for taxonomic diversity, we calculated the species richness per plot. Due to the extraordinary small size of the sampling area and an investigation approach based on semi-permanent plots, we considered the informative value of the coverage estimate to be low and therefore refrained from calculating indicators including this measure. We further assessed species composition by calculating unweighted community means of ecological indicator values (EIVs) per plot. Specifically, we used indicators for climate (light, temperature) and soil (moisture, reaction, nutrients) variables (Landolt et al., 2010; ranging from 1 to 5), along with indicators for mowing, grazing, and trampling tolerance (Briemle et al., 2002; ranging from 1 to 9). We tested for correlations between these parameters and found that grazing and trampling were highly correlated ($r = 0.96$); therefore, we present only the results for grazing and mowing.

We determined CSR (competitor, stress-tolerant, ruderal) strategy types (Grime, 1974) for each species based on (Landolt et al., 2010) and converted these into numerical values using a linear interpolation system in three dimensions, similar to the approach by Hill et al. (2002). We assumed that the sum of all strategy types for each species equals 1: competitors (1,0,0); stress-tolerant (0,1,0); ruderal (0,0,1); stress-tolerant-ruderals (0, 0.5, 0.5); and fully intermediate types (e.g., 0.33, 0.33, 0.33). Missing values, which accounted for about 10 % of all entries, were left blank.

Mean ecological indicator values, which reflect the ecological preferences of species within a community, provide detailed insights into the underlying environmental changes driving vegetation composition (Diekmann, 2003). However, they do not provide detailed insights into species occurrence patterns. To address this, we assessed species frequencies based on their occurrence at each site, contrasting the historical and current most similar plots. We categorized observations into three groups: species that were present at a site in both the historical and current most similar plots were classified as "no change"; species found exclusively in the current most similar plot at a site were classified as "gain"; and species that were present only in the historical plot were classified as "loss."

As a measure of temporal turnover, we calculated the similarity between the current most similar and historical communities, as well as between current average and historical communities. In order to be able to test, whether the temporal effect is larger than the spatial turnover, we used mean similarity among all current average plots within a site as proxy for the spatial heterogeneity of the grassland. For the test we used paired *t*-tests. If the temporal turnover was as high or higher than the spatial turnover, we considered this as no change to the historical species composition of the site, whereas if the temporal turnover was significantly lower than the spatial turnover this was considered as change in the species composition of the site.

2.5. Statistical analyses

We performed all statistical analyses in R version 4.3.3 (R Core Team, 2024). To test for effects on species richness, we fitted linear mixed-effects models using the "glmmTMB" function from the "glmmTMB" package (Brooks et al., 2017) with Gaussian distribution. We built separate models for each moisture level, where we included survey and elevation as fixed effects and site as a random effect. We used a two-sided paired *t*-test to compare the similarity between the current most similar and historical communities, as well as between current average and historical communities, against the mean similarity among current average communities within each site. To test for effects on the community means of EIVs, we built separate models for each EIV and for each moisture level, where we included survey as fixed effects and site as a random effect. Model assumptions were validated visually with the "DHARMa" package (Hartig, 2024). We checked for collinearity with the package "performance" (Lüdecke et al., 2021).

We performed McNemar's test using the "mcnemar.test" function in R to examine changes in species frequencies from the historical to the current most similar plots (Pembury Smith and Ruxton, 2020).

3. Results

Alpha diversity at the plot level for the current most similar plots was 23.2 species, which was not significantly different from the respective historical plots at 21.5 species ($p = 0.061$) (Fig. 2, Table S1). For the current average plots, we found a significant decline to 18.2 species ($p < 0.001$). For dry grasslands, species richness did not differ significantly between the current most similar plots and historical plots (mean of 24.9 species in historical plots and 25.2 species in the current most similar plots; $p = 0.862$), but was 4.8 species lower in the current average plots ($p = 0.004$). A similar pattern appeared in historically mesic grasslands, where the historical plots and the current most similar plots both had a mean of 22.3 species ($p = 0.954$), while the current average plots had 4.7 species less ($p < 0.001$). An opposite trend was observed in historically wet grasslands, where the current most similar plots showed a significant increase of 4.7 species compared to 17.45 species in the historical plots ($p = 0.001$), but the current average plots showed no difference, with a mean of 17.1 species ($p = 0.812$). There is no significant effect of elevation on species richness in neither of the moisture levels.

Comparing species frequency between the current most similar and historical plots, we found nine significantly increased and seven significantly decreased species (Fig. 3).

The temporal variance in species composition, expressed by the mean Sørensen similarity, between the current most similar and the historical plots within sites was 0.43, whereas between current average plots and their historical counterparts, it was 0.25. The similarities in both comparisons were higher for mesic than for either dry or wet grasslands (Fig. 4). For all three moisture levels, the most similar plots did not differ significantly from the reference (p for dry = 0.257, mesic = 0.943 and wet = 0.479) whereas in all cases current average plots showed a highly significantly lower similarity ($p < 0.001$). These results show that differences between the historical and current most similar plots fall within the range of variation between current randomly placed average plots within a site, indicating that the current most similar plots are indeed suitable examples for relict vegetation patches, and thus providing the basis for all subsequent analyses.

We analyzed the effects of survey type (historical, current most similar, and current average) on mean indicator values across dry, mesic, and wet grasslands. EIV for light was significantly lower in wet grasslands for current most similar ($p = 0.004$) and in all moisture levels for current average (dry: $p = 0.001$, mesic: $p = 0.030$ and wet: $p < 0.001$) plots than in the historical plots (Fig. 5, Table S2). EIV for moisture was significantly higher for dry ($p < 0.001$) in current average plots and significantly lower for wet grasslands in current average plots ($p = 0.001$) and current most similar plots ($p = 0.019$) than in the historical plots (Fig. 5, Table S3). EIV for nutrients increased significantly in both current most similar ($p = 0.001$) and current average plots for dry ($p < 0.001$) and for current average plots for wet ($p < 0.001$) grasslands also, but no significant change was found for mesic grasslands (Fig. 5, Table S4). There were no significant effects found for EIV reaction (Fig. 5, Table S5) and for the EIV temperature, we found only a

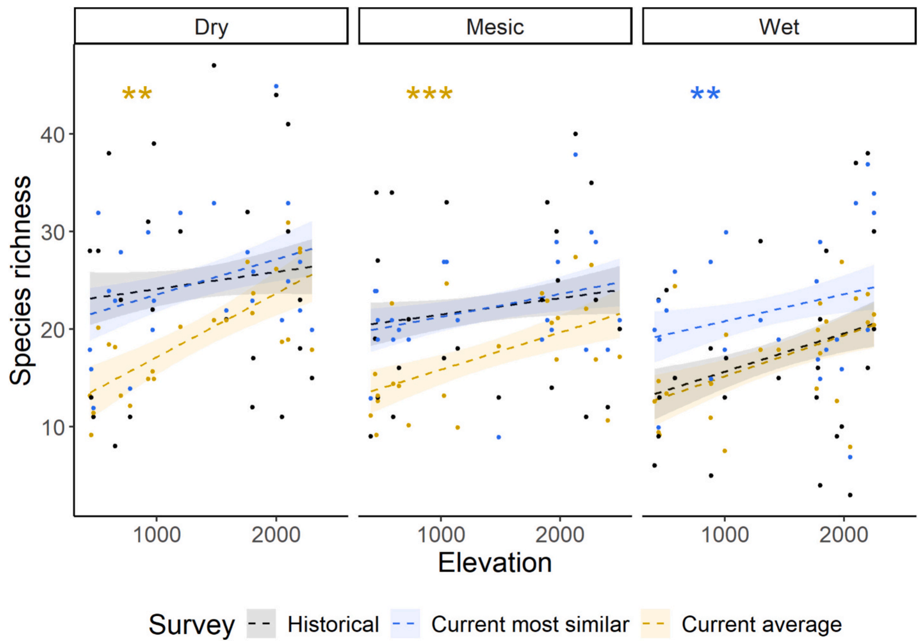

Fig. 2. Species richness along an elevational gradient divided by the three moisture classes. Statistically significant effects for the survey are indicated with an asterisk: * $p \leq 0.05$ and > 0.01, ** $p \leq 0.01$ and > 0.001, *** $p \leq 0.001$, with colours indicating which comparison is significant: blue = current most similar vs historical, brown = current average vs. historical. Statistically significant effects for elevation are indicated by solid lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

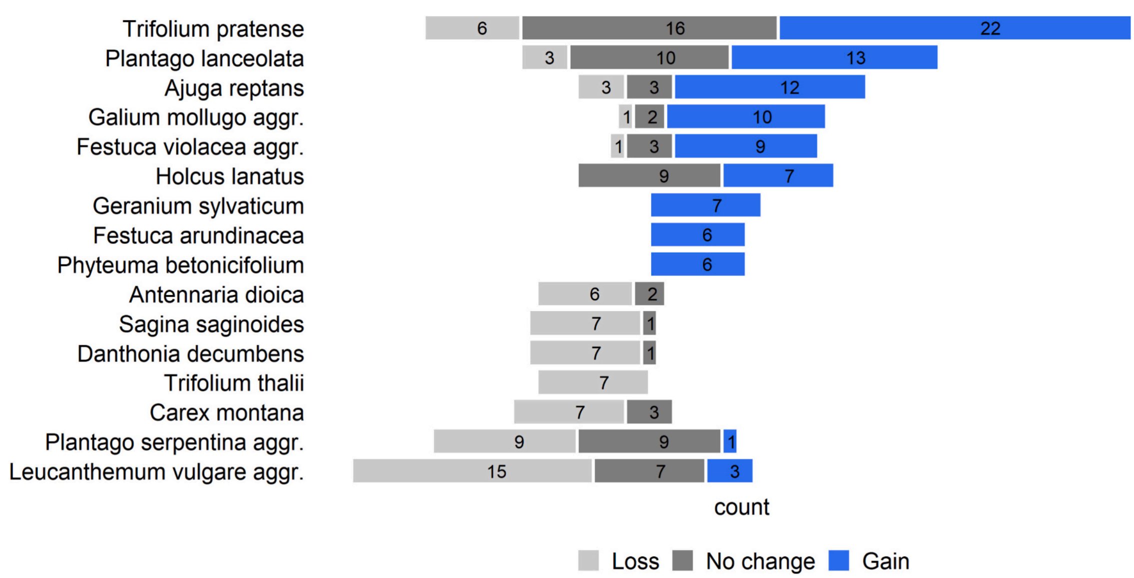

Fig. 3. Plant species with significant frequency changes between historical and current most similar surveys, with species arranged from the strongest winners on top to the strongest losers at bottom. Dark grey bars indicate the number of sites where no change was observed, light grey bars are the sites where a loss was found, and the blue colour shows sites where a gain was observed. The most significant increase appeared for *Trifolium pratense*, which occurred in 16 sites in both surveys, on 6 sites only in the historical survey, and on 22 sites only in the current most similar survey, whereas the most significant decrease was seen for *Leucanthemum vulgare* aggr., which occurred in 7 sites in both surveys, on additional 15 sites of the historical survey, but only in 3 additional sites of the current most similar survey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significantly higher value for current average plots in dry ($p = 0.025$) grasslands (Fig. 5, Table S6).

Grazing tolerance values showed significant lower values for current most similar plots in wet grassland ($p = 0.029$) (Fig. 6, Table S7). Mowing tolerance was significantly higher for current average plots in dry ($p < 0.001$) and wet ($p = 0.029$) grasslands (Fig. 6, Table S7).

In the CSR strategy analyses, there was a higher competitive ability for current most similar plots in wet ($p = 0.004$) and for random resurvey plots in all moisture levels (dry:$p < 0.001$, mesic: $p = 0.041$, wet: $p = 0.001$) (Fig. 7, Table S9). Ruderality was higher in current average plots in dry ($p = 0.001$) and in wet grasslands ($p < 0.001$, Fig. 7, Table S10). Stress tolerance was lower in current average plots for dry, mesic and wet grasslands ($p < 0.001$) and in current most similar plots for dry (p = 0.030) and wet grasslands ($p = 0.001$, Fig. 7, Table S11).

4. Discussion

In this study, we assessed the availability of remnant grasslands in

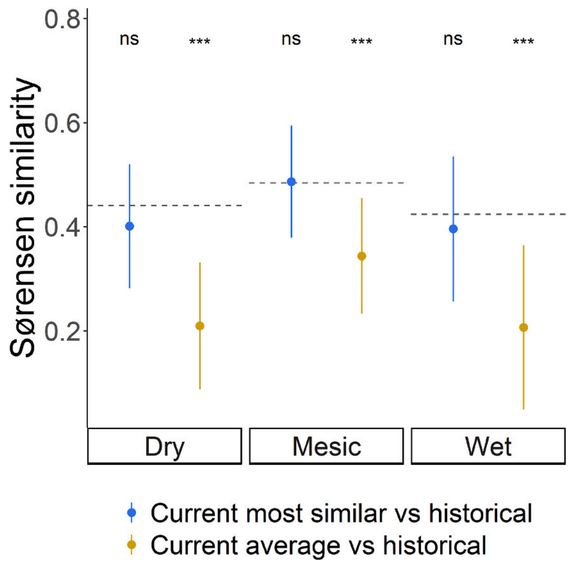

Fig. 4. Mean similarity for the species composition of the current most similar (blue) and random resurvey plots (yellow) compared to the historical plots (temporal variance). The dashed line shows the mean similarity of the current average plots within a site as a proxy for spatial heterogeneity. We tested if the effect of the temporal variance was significantly different from the spatial variance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Switzerland and their potential for grassland restoration, by analyzing the retention of species composition and richness compared to their state a century ago. Contrary to most resurvey studies, where resampling focuses on obtaining typical samples of the current vegetation, in our study we additionally set out to locate relict vegetation patches that are floristically as similar as possible to the historical plots, in order to assess whether examples of the historical vegetation still exist and to which degree these patches resemble the historical species composition. Overall, we found that these current most similar plots showed higher Sørensen similarity to historical plots than current average plots, particularly in mesic grasslands. Species richness is at the same level in the current most similar plots but declined significantly in current average plots for dry and mesic grasslands. Conversely, wet grasslands showed a higher species richness in the current most similar plots. Changes in environmental conditions were reflected in mean ecological indicator values with significant changes for mean light, moisture and nutrients values, mainly in current average plots.

4.1. Notable consistency in species richness and composition of historical and current most similar grassland communities

Our first research question was to identify the extent to which grassland communities, that occurred a century ago, are still present today. Our findings indicate that the temporal turnover shows no significant difference to the spatial turnover, which suggests that historical species composition can still be found to a substantial degree. Similarly, species richness in the current most similar plots did not differ significantly from historical plots, whereas current average plots exhibited lower richness, as previously noted by Widmer et al. (2025)).

We thus demonstrate that grassland patches exhibiting high similarity to their historical counterparts persist in Switzerland across a range of elevations and of moisture regimes. This highlights that, given the right management, current environmental conditions are suitable for the development of grasslands that, while not identical, are much more similar to those a century ago than the average grasslands found today. This highlights the opportunities for grassland restoration from relict vegetation in Central Europe as previously suggested by (Kapás et al., 2024a; Slodowicz et al., 2023). Moreover, the remnant grasslands can provide locally adapted species as well as geophytes and species with clonal growth which may both reduce the cost of restoration efforts and increase their success (Johnson et al., 2018; Knight and Overbeck, 2021; Scotton, 2018). However, our study also shows that the current relict grasslands show directional shifts in species composition that provide important insights into the drivers of plant community composition in semi-natural temperate grasslands. In the following, we explore these shifts in detail.

4.2. Species-specific changes due to land use and management intensification

Focusing on our second study question, we found that nine plant species have significantly increased in the current most similar plots compared to the historical ones, while seven have decreased. Many of these species-specific shifts mirror those found in a parallel study comparing a larger part of the historical square foot dataset with over one thousand current average plots (#anonymous A, under review) and are readily interpretable. Species decreasing in frequency comprise species from across various vegetation classes, but especially from disturbed and nutrient poor ones, while species increasing in frequency are mainly indicators of mesic grasslands. For example, the increase in *Trifolium pratense*, a species commonly associated with fertile grasslands, is expected, as it thrives in nutrient-rich conditions, provoking a vicious cycle by adding nitrogen to the system via root-nodule capturing. Since the turn of the 19th century, *T. pratense* is one of the main species included in seed mixtures for forage production (Stebler and Schröter, 1902; Suter et al., 2019). In contrast, species of low competitive ability such as *Antennaria dioica, Carex montana, Danthonia decumbens and Sagina saginoides*, have declined due to the loss of nutrient poor habitats. A decrease of species of these habitats has also been found by Hilpold et al. (2018) and Kindermann et al. (2024). *Leucanthemum vulgare* aggr. declined despite its high tolerance to mowing and its former German designation as "Wucherblume" (indicating its prolific growth), so that one might expect it to thrive in intensively managed systems. Its decrease is most probably linked to its low competitive ability in dense stands and a lack of disturbance and open soil, due to a need for good light conditions, especially for germination, as reported for other species (Landolt et al., 2010).

It should be noted that for our analyses, the small size of the study plots represents a specialty. For example, Chytrý and Otýpková (2003) suggest a plot size of 16 m^2 for grassland habitats. The small plot size in our case is due to the original data, in which small plots were extracted in the field and carried to the lab for closer study. This small size might show some shortcomings, particularly when analyzing changes in the species composition and comparing similarity. However, our previous analyses with the small plots have revealed clear patterns in richness and species composition both along elevational gradients and over time ((#anonymous A (under review, #anonymous B (under review)), which shows that the sampling strategy is informative.

4.3. Shifts in species composition due to land use and management intensification

Our third research question addressed the similarity of remnant and historical grasslands in terms of indicator values for management and ecological alterations. These indicators provide detailed insights into the underlying environmental changes driving vegetation composition, and are particularly informative as they result from the added influence of drivers over time (Diekmann, 2003). Together, in our study these indicator values paint a complex picture of changes and underlying drivers, with notable differences between grasslands of different moisture status.

Probably the most influential driver of plant community change in Central Europe has been the increase in nutrient availability, either via direct fertilization, which has massively increased since the advent of

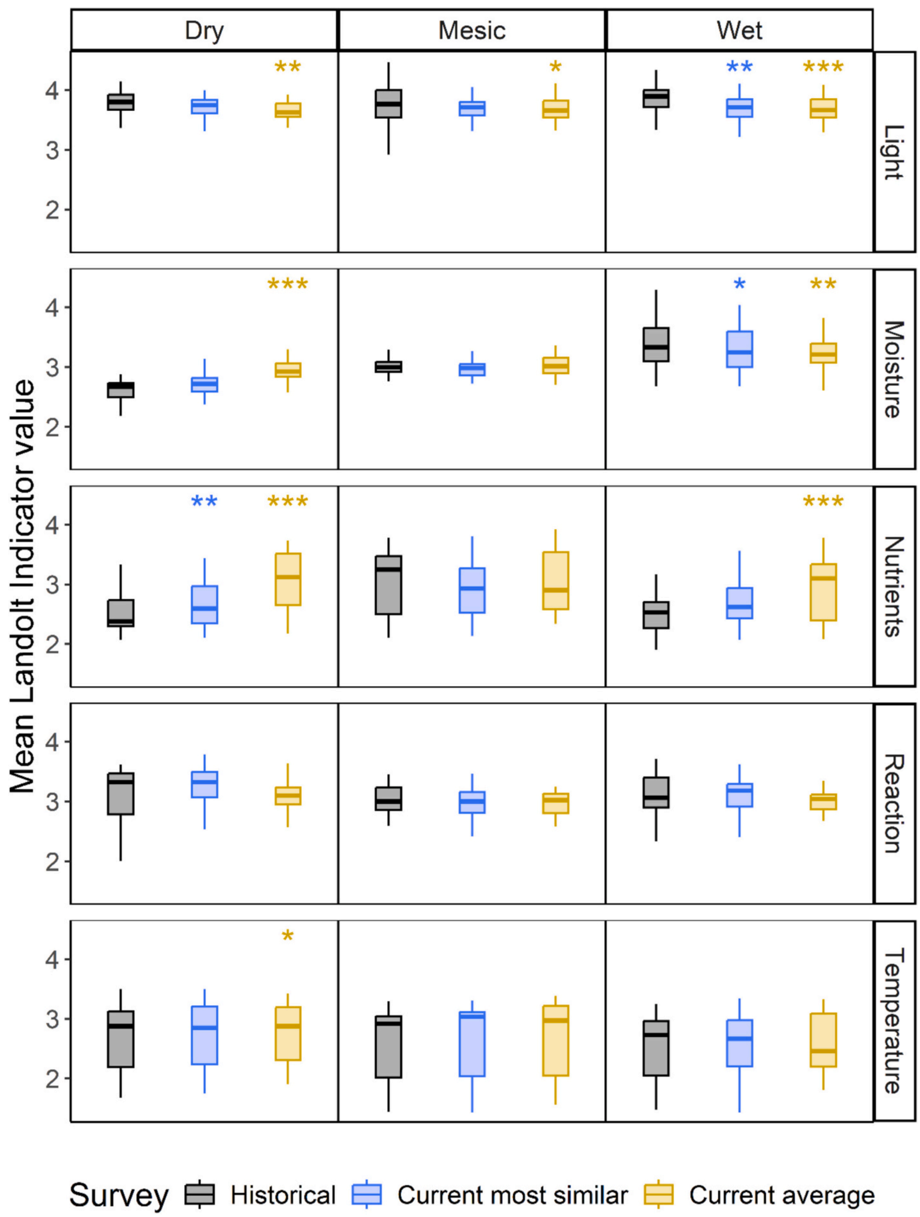

Fig. 5. Mean ecological indicator values (Landolt et al., 2010) per plot for light, moisture, nutrients, reaction, and temperature plotted per moisture class for the three surveys historical, current most similar, and current average plots. Statistically significant effects of the survey are indicated with an asterisk: * $p < 0.05$ and > 0.01, ** $p < 0.01$ and > 0.001, *** $p < 0.001$, with colours indicating which comparison is significant: brown = random vs. historical, blue = current most similar vs. historical. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

industrial nitrogen fixation at the beginning of the 20th century, or via atmospheric nitrogen deposition, which still largely exceeds critical loads for sensitive ecosystems throughout Switzerland (Bundesrat, 2018). This eutrophication has led to massive changes in vegetation composition across Europe, with declines especially of species of low competitive ability associated with open habitats (Jandt et al., 2022; Staude et al., 2020; Stevens et al., 2004), as also found in our previous analyses of the more extensive square foot dataset (#anonymous under review A, #anonymous under review B). Indeed, both dry and wet grasslands exhibited the expected significant increases in nutrient indicator values across both, current most similar and current average plots. The observed rise in species richness in the current most similar plots in wet grasslands may be related to this increase in nutrient availability, indicating a transition toward more fertile grassland communities with a mix of species from the original species pool of nutrient poor wet and species from more nutrient-rich grasslands. However, the current average plots in wet grasslands showed a marked increase in nutrient levels without a corresponding increase in species richness, pointing to a shift toward a more fertile, but species-poor community, as also observed in other studies (Francksen et al., 2022; Maskell et al., 2010). This suggests that whereas wet grasslands have generally higher nutrient conditions today, they form a mosaic of dominant areas now characterized by few highly competitive species and smaller patches that appear to be in a species-rich transitional state. This goes along with the observed increase in shade tolerance in both, the current most similar and current average plots, within wet grasslands. This shift is likely also driven by increased nutrient levels as these lead to taller and denser vegetation (Klötzli et al., 2010), where competition for light is a major driver of compositional change (Hautier et al., 2009). Interestingly, however, we detected no significant changes of nutrient indicator values in mesic grasslands between the plot types (historical, current average, current most similar). This likely reflects the long history of

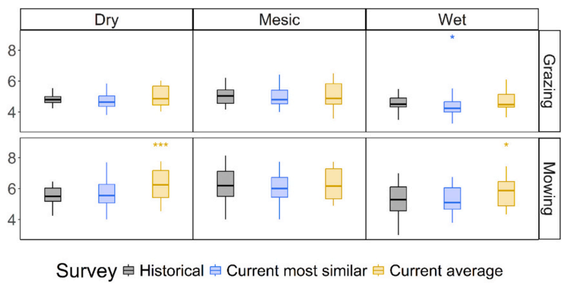

Fig. 6. Mean indicator values for mowing and grazing (Briemle et al., 2002) per plot, plotted per moisture class for the three surveys historical, current most similar, and current average plots. Statistically significant effects of the survey are indicated with an asterisk: * $p \leq 0.05$ and > 0.01, ** $p \leq 0.01$ and > 0.001, *** $p \leq 0.001$, with colors indicating which comparison is significant: blue = current most similar vs. historical, brown = current average vs. historical. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

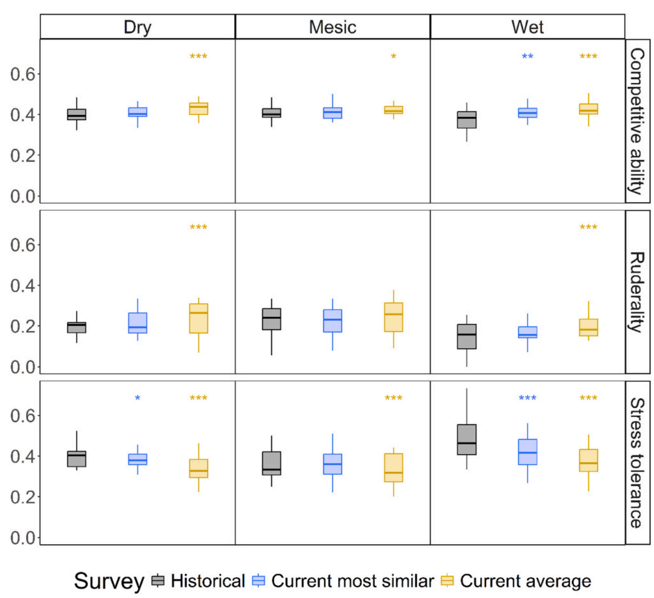

Fig. 7. Mean CSR strategies competitive ability, ruderality and stress tolerance per plot, plotted per moisture class for the three surveys historical, current most similar and current average. Statistically significant effects of the survey are indicated with an asterisk: * $p \leq 0.05$ and > 0.01, ** $p \leq 0.01$ and > 0.001, *** $p \leq 0.001$, with colors indicating which comparison is significant: blue = current most similar vs. historical, brown = current average vs. historical. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

intensive land use of mesic meadows, including pasture and hay meadow management with manure fertilization that were applied already at the time of the historical survey (Stebler and Schröter, 1887).

The analysis of moisture indicator values revealed a significant decrease in moisture indicators for the current most similar plots, which was expected, due to broad drainage activities, but stands in contrast to the study of Straubinger et al. (2023) in Germany.

While we anticipated an increase in temperature indicator values across all plot types, this trend was only observed in current average plots of dry grasslands, suggesting that the effects of climate change on plant communities of managed grasslands remain relatively minor thus far, also reported in other studies (Dengler et al., 2014; Kindermann et al., 2024; Wesche et al., 2012), unlike effects on arthropod communities (Neff et al., 2022). Moreover, active management practices, such as sowing productive species like *Lolium perenne*, may have shifted the elevational distribution of some species upwards, which would be reflected in the temperature indicator values, thereby exacerbating the appearance of climate-related changes (#anonymous B, under review). The limited importance of temperature is in accordance with previous studies on European grasslands, where the impact of land use changes so far greatly outweighs those of climate change (#anonymous B, under review (Kiebacher et al., 2023).

The increasing tolerance to mowing, mainly found in the current average plots, reflects the intensification of land use over the past century. In contrast, the current most similar plots only exhibited a slight decrease in grazing tolerance in wet grasslands, likely linked to changes in management practices, with a shift from grazing to mechanized mowing (Poschlod et al., 2005) or to abandonment of these areas. These contrasting patterns emphasize the role of land use practices in shaping community composition.

Changes in CSR strategies align with the patterns observed in ecological indicator values. In wet grasslands, the species composition of the current most similar plots shifted towards more competitive strategies, as was also the case in current average plots in dry and wet grasslands. However, no such changes were detected in mesic grasslands, suggesting that these may have already reached a certain equilibrium one century ago in terms of competitive dynamics. Stress strategists—those adapted to extreme conditions such as excessive moisture, dryness, soil alkalinity, or acidity—were notably reduced across all moisture levels in the current average plots. These shifts suggest an increase in disturbance, primarily driven by land-use practices, which has reduced the abundance of specialist species. In the current most similar plots, we noted a decline of specialists in dry and wet grasslands, which can be interpreted as an instance of ecological homogenization, with a shift toward more fertile meadow communities, which are often dominated by generalist species.

5. Conclusions

Several previous studies have resurveyed historical vegetation plots to assess temporal changes in plant community diversity and composition of grasslands in Europe. In this context our study is unique by specifically locating relict vegetation patches that might be used for restoration activities. We demonstrated that such grassland patches, exhibiting high similarity to their historical counterparts, persisted in Switzerland across a range of elevations and of moisture regimes. Although these patches on average showed no significant changes in species composition or richness when compared to the historical plots, ecological indicator values revealed detectable shifts in species composition related to ecological preferences for light, moisture, and, most notably, nutrient levels. These shifts suggested that even the least altered current grasslands have diverged from their historical states over the past century. Such changes were not unexpected, as effects such as atmospheric nutrient deposition affect landscapes universally, regardless of local management or conservation status, and as nature protection and agri-environmental schemes were initiated only a couple of decades ago. Nevertheless, many of the shifts in indicator values related to ecological conditions, land-use practices, and adaptive strategies reflect the direct impact of local land management practices such as grazing, mowing, and fertilization. Together, these results showed that, there is a high potential for restoring semi-natural grasslands to a condition close to that a century ago. Relict vegetation patches such as those documented here provide both an indication of the restoration potential and a ready source of locally adapted plant species for restoration projects. Identification of relict patches should thus be an important component of grassland restoration projects.

CRediT authorship contribution statement

Susanne Riedel: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Stefan Widmer: Writing - review & editing, Methodology, Investigation, Data curation. **Jürgen Dengler:** Writing - review & editing, Methodology, Conceptualization, Funding acquisition. **Felix Herzog:** Writing - review & editing, Methodology, Conceptualization. **Manuel K. Schneider:** Writing - review & editing, Methodology. **Thomas Wohlgemuth:** Writing - review & editing. **Michael Kessler:** Writing - original draft, Methodology, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve the readability and language of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111500.

Data availability

data will be shared in case of publication

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