

The effects of sprinkler irrigation on semi-natural grasslands in Valais (Switzerland)

Die Auswirkungen der Sprinklerbewässerung auf halbnatürliches Grasland im Wallis (Schweiz)

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Abstract

In the inneralpine dry valleys of Valais (Switzerland), irrigation is a centuries-old practice to increase productivity in semi-natural grasslands. In recent decades, the traditional irrigation by so-called Suonen (small water channels) has been replaced increasingly by irrigation with sprinklers. To investigate the long-term effects of sprinkler irrigation on semi-natural grasslands in Valais, we carried out a resurvey of eight sprinkler-irrigated permanent plots in the municipality of Bettmeralp, complementing this data by sampling 20 comparable pairs of irrigated/unirrigated plots in a nearby area. Our aim was to detect and quantify changes in biodiversity, site conditions as represented by mean ecological indicator values, and adaptive strategies after over 30 years of irrigation, and compare these results to differences between currently irrigated and unirrigated grasslands. We used paired *t*-tests or analysis of covariance with slope of the study site as covariate to test for differences in these parameters and carried out a sign test to evaluate changes in the frequency of individual species. For the permanent plots, a strong decline in plant species richness was found. However, this study was unable to elucidate drivers for the decline in species richness over time, despite the clear and intuitive signals observed for the paired plots. Only one species each was found to have increased or decreased significantly in frequency, while rarer and specialist species appeared to have generally decreased. The permanent plots showed unexpected and significant increases in mean indicator values of light availability and soil reaction over time. Within the plot pairs, irrigated plots showed much lower species richness than unirrigated ones. According to their mean indicator values, the irrigated plots within the plot pairs were significantly cooler and more humid, with more acidic, nutrient-rich, and humus-rich soils. We theorize that the lower species richness observed for the irrigated plots may be the result of nutrient enrichment and the exclusion of specialist dry grassland species, but there are possible confounding factors which make our results inconclusive. Since the need for irrigation in the inneralpine valleys of the Swiss Alps is expected to increase due to climate change, and irrigation has been shown in some cases to trivialize grassland vegetation, further long-term studies should be carried out in order to forestall potential risks to grassland biodiversity.

Keywords: biodiversity, CSR strategy, ecological indicator value, inneralpine dry valley, resurvey, semi-natural grasslands, sprinkler irrigation, Switzerland, vegetation change

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Throughout the Palaearctic realm, semi-natural grasslands host exceptional biodiversity (e.g. Dengler et al. 2014, Biurrun et al. 2021) and provide a broad range of essential ecosystem services (Manning et al. 2018). However, these diverse habitats are increasingly threatened by global change (IPBES 2018). In Switzerland, semi-natural grasslands were long shaped by traditional management practices (Boch et al. 2020), but are now threatened by land-use intensification, abandonment, and indirect nutrient inputs (Bornand et al. 2016, Kosonen et al. 2019, Dengler et al. 2020). An estimated 95% of dry grasslands were lost between 1900 and 1990 (Lachat et al. 2010), and about 35% of the typical species of dry grasslands are threatened (Bornand et al. 2016). On the Swiss plateau, typical mesic meadows are estimated to have declined to 2–5% of their original area (Lachat et al. 2010), also suffering strong decreases in species richness (Gattlen & Klaus 2023).

For grasslands of the dry central valleys of the Swiss Alps, irrigation is often a basic requirement for securing yields and improving fodder quality (Dipner-Gerber et al. 2010). In the canton of Valais, about 60% of its agricultural land is irrigated, of which about 64% consists of grassland (Zurwerra 2010). For centuries, elaborately constructed channel systems – so-called Suonen (DE) or bisses (FR) – have carried glacial meltwater to the valleys. There, they are dammed in varying cycles according to regional contracts, flooding the parcels below for set time periods (Volkart 2008). Since the 1980s, sprinkler systems have increasingly replaced this traditional irrigation practice (Crook & Jones 1999), although flooding irrigation still continues in many localities. Modern sprinkler irrigation is more efficient (Crook & Jones 1999, Zurwerra 2010) since it distributes the water much more homogeneously than traditional water-channel systems.

A range of studies have analyzed the effects of traditional and modern irrigation on the plant diversity of semi-natural grasslands, often yielding conflicting results which seem to strongly depend on grassland type. A synthesis by DeMalach et al. (2017) found no significant effect of irrigation on plant biodiversity in grasslands worldwide, although the individual experiments included showed great heterogeneity in the direction and magnitude of species richness responses. On traditional flood-irrigated hay meadows in Germany, Müller et al. (2016) found that irrigation is associated with higher alpha and beta diversity. In mountain hay meadows in Valais, it has been observed that irrigation has no effect on Shannon index (sprinkler irrigation; Lessard-Therrien et al. 2017), phylogenetic diversity (Lessard-Therrien et al. 2017), and species richness (Riedener et al. 2013 for both flooding and sprinkler irrigation; Lessard-Therrien et al. 2017 for sprinkler irrigation; Boch et al. 2021 for sprinkler irrigation). In xeric grasslands, irrigation is thought to decrease biodiversity by causing the loss of specialized plant species (Volkart 2008). Thus, the long-term effects of irrigation on grassland biodiversity remain unclear (Müller et al. 2016, Boch et al. 2021).

In light of this knowledge gap, we revisited a local study in Martisberg in Valais (see Section 2.1) with the aim of detecting general long-term changes in the grassland vegetation brought about by over 30 years of sprinkler irrigation and associating these changes with possible drivers. We resurveyed the 8 irrigated permanent plots of the Martisberg study and tested for changes in plant diversity, species composition, ecological site conditions, and

adaptive strategy types. To complement the small sample size of the permanent plots, we sampled 20 pairs of unirrigated and irrigated paired plots in close proximity and with otherwise similar conditions. In this way, we aimed to contrast any discerned temporal changes after decades of sprinkler irrigation with differences observed between contemporary irrigated and unirrigated grasslands.

2. Study system

2.1 The Martisberg study

To investigate the long-term effects of sprinkler irrigation on semi-natural grassland vegetation in Valais, the Swiss federal center for agricultural research, Agroscope Changins, took advantage of the situation presented by land melioration in the municipality of Bettmeralp in 1988. Around the village of Martisberg, flooding irrigation had been abandoned in the 1960s due to the high effort involved in maintaining its infrastructure (Volkart & Godat 2007). Between 1988 and 1989, the municipality installed sprinkler systems during a land melioration (Jeangros & Bertola 2001). Agroscope Changins established a total of 12 permanent plots in grasslands within reach of the newly installed sprinklers which were then monitored over 18 years (see Methods section).

Unfortunately, the monitoring in Martisberg encountered numerous difficulties: i) Irrigation was not enforced, and some farmers opted not to irrigate certain plots; ii) For various reasons, sampling was inconsistent between the surveys. Data from two intervals of the monitoring were analyzed by Jeangros & Bertola (2001) and Volkart & Godat (2007), using different methodologies and often demonstrating only slight trends to which no statistical significance could be ascribed. After the first stage of the monitoring, Jeangros & Bertola (2001) observed that the species composition of the study plots did not change substantially between 1988–1996. Often, results deviated between grassland types: in plots located in initially nutrient-rich grasslands, the number of species in 25 m² decreased slightly, and the forage value increased. In plots which farmers chose not to irrigate (i.e. the driest, least productive ones), the vegetation scarcely changed. Grasslands with an “intermediate botanical composition” (semidry grasslands) developed under the influence of irrigation into more nutrient-rich stands with increased forage value. Overall, Volkart & Godat (2007) found that the range of values for species richness on 25 m² decreased from 37–56 to 23–45 species (1988–2006). The authors observed that regularly irrigated grasslands appeared to transform into more nutrient-rich habitats, with characteristic dry meadow species decreasing and rare species disappearing. They noted that soils which were watered moderately (but not too intensively so as to cause runoff) show an increase in potassium and phosphorus, thus increasing their fertility. Grassland vegetation which was sprinkler-irrigated one to three times a year and fertilized once a year maintained its overall quality, but a change in species composition was observed.

2.2 Study area

The study sites are located in the upper part of the Rhône valley in the canton of Valais (Fig. 1), on southeast-facing slopes. The permanent plots lie within an area of ca. 1 km² around the settlement of Martisberg (Fig. 2), while the additional paired plots are located in a roughly equivalent area near the neighboring village of Betten Egga (Fig. 3). According to

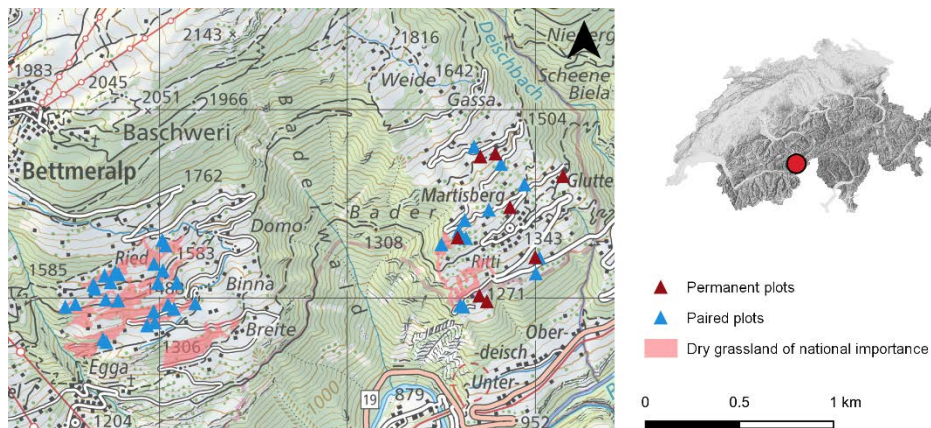


Fig. 1. Map of the study site within Switzerland (geodata: © Swisstopo).

Abb. 1. Lage der Untersuchungsflächen in der Schweiz (Geodaten: © Swisstopo).

the cantonal inventory of Suonen (Office for Land-Use Planning Canton Valais 2023) and our observations in the field, none of the grasslands in Betten Egga are irrigated by means of flooding irrigation.

Two by law protected dry grasslands (dry meadows and pastures of national importance no. 7414 and 7424; FOEN 2017a and 2017b, respectively) are located in the area, enclosing some of the plots of this study (the unirrigated counterparts to Martisberg 3 and 4, as well as all unirrigated plots in Betten Egga). The studied grasslands range from mesic (*Arrhenatherion elatioris*, *Polygono-Trisetion*), via meso-xeric (*Cirsio-Brachypodion*) to dry (*Stipo-Poion xerophilae*; typology according to Delarze et al. 2015) and are grazed and/or mown (land-use details in Supplement E4).

The study site lies over glacial moraine and Variscan / pre-Variscan siliceous bedrock (gneiss, amphibolite), with some over Permian-Carboniferous sedimentary rock at lower elevations. The soils are sandy and slightly acidic, with low skeleton content, mostly consisting of phaeozem and brown earth (Nievergelt 1985, Jeangros & Bertola 2001).

The elevation ranges from 1240 to 1660 m a.s.l., placing the sites within the montane belt (Fig. 1). The region is characterized by a continental climate with high daily and seasonal temperature contrasts, and intense solar radiation (Baltisberger et al. 2013). Measurements taken nearby give the mean annual precipitation from 1990–2020 as 1077 mm (Fieschertal, 1175 m a.s.l.) and the mean annual temperature as 4.2 °C (Ulrichen, 1348 m a.s.l.) (MeteoSwiss 2023).

3. Methods

3.1 Field sampling

In 1988, 12 permanent plots of 25 m² were placed by Agroscope Changins in collaboration with the University of Bern, the Nature and Cultural Heritage Commission of the Canton of Valais, and the Melioration Office of Upper Valais (Meier 1990). The selected study sites were similar in terms of local topography and site conditions. The original study included 12 permanent plots, which were sampled from 1988–1996 and again in 2006; however, sampling was inconsistent between the seven



Fig. 2. Photographic impressions of the irrigated permanent plots in Martisberg. **a)** plot 6; **b)** plot 8 (Photos: M. Schindler, 2021).

Abb. 2. Impressionen der bewässerten Dauerflächen in Martisberg. **a)** Fläche 6; **b)** Fläche 8 (Fotos: M. Schindler, 2021).



Fig. 3. Photographic impressions of the paired plots in Betten Egga. Top row: **a)** irrigated and **b)** unirrigated plots of pair 4; bottom row: **c)** irrigated and **d)** unirrigated plots of pair 12 (Photos: M. Schindler, 2021).

Abb. 3. Impressionen der Flächenpaare in Betten Egga. Obere Reihe: **a)** bewässerte und **b)** unbewässerte Flächen von Paar 4; untere Reihe: **c)** bewässerte und **d)** unbewässerte Flächen von Paar 12 (Fotos: M. Schindler, 2021).

completed surveys (Supplement E5). Three plots (no. 5, 6, and 11) were moved in 1989 after they had been damaged due to small construction projects and rodent activity. In 2006, vascular plant species coverage was recorded using a 7-step Braun-Blanquet scale, then scaled according to frequency analysis (method from Daget & Poissonet 1969, Volkart & Godat 2007). In the vegetation table from Volkart & Godat (2007), plots 1 and 10 from 1988 and 1989 were not included. These were taken from Meier (1990), where they were recorded on the Braun-Blanquet scale. Soil samples were collected in 1988, 1996, and 2006, and their pH as well as P₂O₅, K₂O, and Mg content were measured (Volkart & Godat 2007).

In June 2021, the *permanent plots* were relocated using coordinates and maps from Meier (1990). Given the topography, we estimate the relocation error to be around 10 m. We completed a resurvey using the same method as the historical vegetation surveys but supplementing the 25-m² grain size with a 10-m² plot nested around the center of each permanent plot. We chose the additional 10 m² grain size to match the standards of the Swiss national biodiversity monitoring programs (e.g. Bergamini et al. 2019) and GrassPlot (Biurrun et al. 2021) and allow comparisons with their data. Additionally, for each of the permanent plots which had been irrigated since 1988, we surveyed a complementary unirrigated 10-m² plot nearby, selecting grasslands with comparable site conditions, especially regarding slope and aspect. We supplemented these eight pairs with twelve additional pairs of 10-m² plots (irrigated/unirrigated) in the neighboring community of Betten Egga, again selecting comparable sites, for a total of 20 pairs of plots. All plots had a square shape.

We recorded the cover of all vascular plants, vegetation layers (bryophyte, lichen, herb, shrub, and tree), litter, and rock / stones in percent. Standard vegetation height, soil depth, and microrelief were measured according to the methods of Dengler et al. (2016). The species were determined with Binz and Heitz (1991), Lauber et al. (2018), Graf (2019) and Eggenberg & Möhl (2020). Vascular plant

nomenclature corresponds to Juillerat et al. (2017). All plots were aligned along the North-South axis and permanently marked with a magnet buried in the NW corner to allow future relocation. Land-use details (mowing and/or grazing, fertilizer application, frequency of sprinkler irrigation) were gathered by means of interviews with the farmers.

The header data of the surveys are provided in Supplement E1, the species cover data in Supplements E2 and E3 and land-use details in Supplement E4.

3.2 Data analyses

Since the surveys of the previous monitoring were repeated over varying time intervals, and the number of plots sampled in a given year varied considerably (Supplement E5), we opted to simply compare the data from the beginning of the monitoring with that of our resurvey in 2021. We omitted from the temporal comparison those permanent plots which had not been consistently irrigated since 1988 (no. 1, 7, 9, and 10). Since some plots were moved in 1989, we opted to take the second survey in 1989 as point of comparison for 2021.

We used VEGEDAZ (Küchler 2023) to calculate the Shannon index, Shannon evenness, and mean square-root cover-weighted ecological indicator values (EIVs) and CSR (competition-stress-ruderality) adaptive strategies (Grime 2001). The EIVs (scale 1–5) and CSR strategies of the species were taken from Landolt et al. (2010). Instead of analyzing the individual CSR strategies distinguished in this system (ccc, ccr, ccs, crr, ...), we relied on the numerical implementation in VEGEDAZ, where these categories are translated for each species into ordinal scores from 0 to 3 for each of the three strategy dimensions, with the three individual scores always adding up to 3. This coding allowed us to treat the strategy dimensions mathematically in the same way as the EIVs. The CSR strategy types are defined by Landolt et al. (2010) as follows:

- C, competitive strategists – highly competitive species; often long-lived, woody taxa adapted to low light conditions.
- S, stress strategists – specialists adapted to conditions which are unfavorable to most species; frequently smaller, less lush plants with evergreen leaves. In comparison to Grime, Landolt et al. also focus on anaerobic conditions in the soil as a stress factor.
- R, ruderal strategists – species with pioneer character; often small and short-lived plants, rarely woody, with high light requirements, producing large amounts of seeds and able to rapidly disperse.

We converted the aspect in degrees to the south component suitable for statistical analysis (Leyer & Wesche 2007).

All statistical analyses were performed using the R program (R Core Team 2023), with a significance threshold of $\alpha = 0.05$ or of $\alpha = 0.025$ in cases where the residual distribution did not meet parametric criteria and transformations did not improve it (in two cases: total vegetation cover and litter cover). To analyze the effects of sprinkler irrigation, two separate comparisons were made: for the permanent 25-m² plots of between the years 1989 and 2021, and for the paired plots between the irrigated and unirrigated 10-m² plots of 2021. To check for test parameters, we performed a visual inspection of the distribution of the data and residuals using boxplots and the command *plot()* in R. In cases where the Central Limit Theorem applies (Quinn & Keough 2002) – e.g. mean indicator values – we focused on homoscedasticity. Data showing unsuitable distributions were transformed as specified in the results.

For the permanent plots, we used paired *t*-tests to analyze differences in biodiversity metrics, EIVs, and CSR strategies. As a basis for the analyses, we took species cover data from previous surveys which had been recorded in the Braun-Blanquet scale and modified according to frequency analysis. We assume that such data will represent the proportions of the covers in a fashion comparable to our preferred method of recording species cover directly in percent, which is the method we applied in 2021 (for methods comparison, see Dengler & Dembicz 2023). Since the test parameters derived from species data do not rely on values for total vegetation cover, the scaling of the species cover values to 100% does not present a problem for our analyses.

Paired t -tests and covariance analysis were used to test whether the abiotic parameters of the paired plots differed from one another. Preliminary tests showed that the irrigated and unirrigated plots differed significantly with respect to slope ($p = 0.006$; higher in unirrigated plots) but did not in their south component ($p = 0.933$), mean soil depth ($p = 0.706$), or maximum microrelief ($p = 0.065$). Hence, for each test variable we first fit a covariance analysis (ANCOVA) with slope as covariate, and plot pair as error term. If slope was found to be insignificant in the ANCOVA, the model was simplified to a paired t -test. Again, we tested for differences in biodiversity metrics, EIVs, and CSR strategies, as well as descriptors of vegetation structure. To preserve degrees of freedom for the analysis of this small dataset, possible interactions between slope and irrigation effects were not considered. To check whether individual species had significantly increased or decreased in frequency since 1988, we carried out a sign test (binomial test).

4. Results

4.1 Biodiversity

4.1.1 Permanent plots

The paired plots were generally more species-rich than the historical or resurveyed permanent plots proportional to their grain size. The permanent plots significantly decreased in species richness since 1989 (Fig. 4a; mean of 42.3 vs. 33.8 species in 25 m²). Viewing the complete time series (Supplement E6), many plots seemed to experience a precipitous drop in species richness during the first few years of sprinkler irrigation which then leveled off in later years.

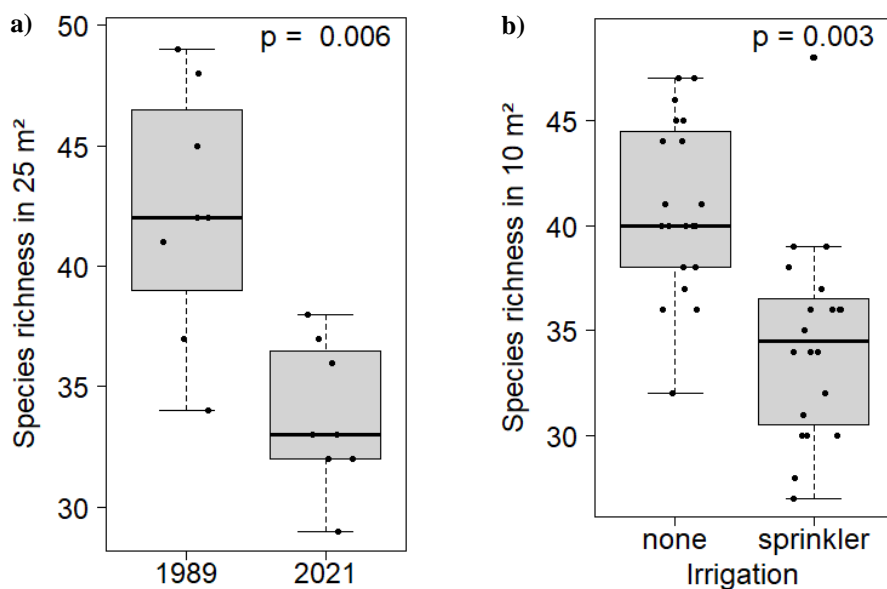


Fig. 4. Boxplots of species richness for the permanent plots in 25 m² (a); $n = 8$ time series) and paired plots in 10 m² (b); $n = 20$ pairs), with data points superimposed.

Abb. 4. Boxplots der Artenzahlen für die Dauerflächen auf 25 m² (a); $n = 8$ Zeitreihen) und die Flächenpaare auf 10 m² (b); $n = 20$ Paare), mit überlagerten Datenpunkten.

4.1.2 Paired plots

Similarly, among the paired plots, irrigated plots harbored significantly fewer species than unirrigated ones (Fig. 4b; mean of 46.5 vs. 33.8 species in 10 m²). Neither the Shannon index or Shannon evenness differed significantly between the time steps or between the paired plots. Slope showed no significant effect on any of the tested biodiversity metrics of the paired plots.

4.2 Site conditions

4.2.1 Permanent plots

From 1989–2021, the permanent plots experienced significant increases in mean EIVs for light ($p = 0.025$) and soil reaction ($p = 0.038$) (Tab. 1, Fig. 5). No other significant differences between the two time steps could be observed. A moderate increase in temperature EIVs was observed, although this trend was not statistically significant ($p = 0.155$; Tab. 2). In certain cases (e.g. soil moisture EIV, soil reaction EIV), the complete time series suggests that the development of site conditions over time differed strongly between plots (Supplement E6).

4.2.2 Paired plots

The paired plots showed highly significant differences in most of the mean EIVs tested (Tab. 2). The largest effect sizes were seen for soil moisture, continentality, soil nutrient content, and soil humus content; in each of these cases, the difference was extremely significant ($p < 0.001$) (Fig. 6). Only mean light EIVs showed no significant difference between the irrigated and unirrigated plots.

Table 1. Tested differences in mean square-root cover-weighted ecological indicator values (EIVs, range 1–5) and CSR strategy values (range 0–3) for the eight permanent plots between the two time steps. Asterisks (*) denote significant results.

Tabelle 1. Getestete Unterschiede bei den quadratwurzelgewichteten mittleren ökologischen Zeigerwerten (EIVs, Bereich 1–5) und CSR-Werten (Bereich 0–3) für die Dauerflächen zwischen den beiden Zeitschritten. Sternchen (*) kennzeichnen signifikante Ergebnisse.

EIV / CSR value	Mean 1989	Mean 2021	<i>t</i> -statistic	<i>p</i> -value
Temperature	3.13	3.37	3.871	0.155
Continentality	3.33	3.35	1.589	0.888
Light*	3.68	3.79	0.263	0.025
Soil moisture	2.66	2.53	-1.594	0.327
Soil reaction*	3.07	3.25	-0.146	0.038
Soil nutrient content	2.94	2.90	-2.838	0.745
Soil humus content	3.27	3.37	1.055	0.369
Soil aeration	2.46	2.60	-2.547	0.421
Competition	1.20	1.12	0.339	0.266
Ruderality	0.78	0.80	-0.960	0.833
Stress	1.02	1.08	-0.855	0.357

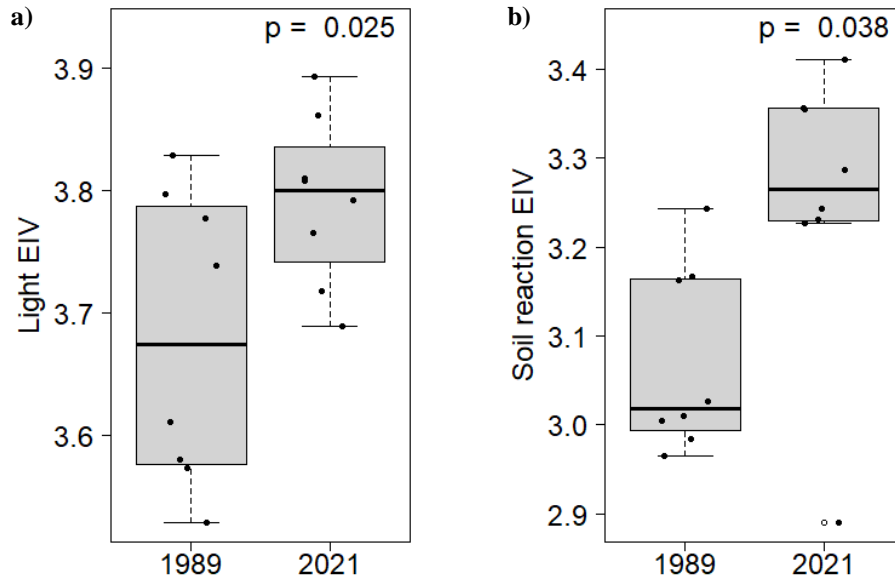


Fig. 5. Boxplots of significantly differing square-root cover-weighted mean ecological indicator values (EIVs, range 1–5) for the permanent plots between the two time steps, with data points superimposed ($n = 8$ time series).

Abb. 5. Boxplots der signifikant unterschiedlichen quadratwurzelgewichteten mittleren ökologischen Zeigerwerte (EIVs, Bereich 1–5) für die Dauerflächen zwischen den beiden Zeitschritten, mit überlagerten Datenpunkten ($n = 8$ Zeitreihen).

Table 2. Tested differences in square-root cover-weighted ecological indicator values (EIVs, range 1–5) and CSR strategy values (range 0–3) between unirrigated and irrigated plots within the 20 plot pairs. Asterisks (*) denote significant results, (**) highly significant, and (***) extremely significant.

Tabelle 2. Getestete Unterschiede in den quadratwurzelgewichteten mittleren ökologischen Zeigerwerten (EIVs, Bereich 1–5) und CSR-Werten (Bereich 0–3) zwischen unbewässerten und bewässerten Flächen der 20 Flächenpaare. Sternchen (*) kennzeichnen signifikante Ergebnisse, (**) hoch signifikant und (***) extrem signifikant.

EIV / CSR value	Mean unirrigated	Mean irrigated	Test	Statistic	p -value	Effect of slope
Temperature***	3.6	3.3	t -test	$t = 7.575$	< 0.001	none
Continentality***	3.8	3.3	t -test	$t = 10.342$	< 0.001	none
Light	3.8	3.8	t -test	$t = 1.4678$	0.159	none
Soil moisture***	2.0	2.6	t -test	$t = -14.171$	< 0.001	none
Soil reaction**	3.4	3.3	t -test	$t = 3.685$	0.002	none
Soil nutrient content***	2.4	2.9	t -test	$t = -7.799$	< 0.001	none
Soil humus content***	2.8	3.3	t -test	$t = -7.470$	< 0.001	none
Soil aeration***	2.9	2.6	t -test	$t = 4.776$	< 0.001	none
Competition**	1.3	1.2	ANCOVA	$F = 15.14$	0.001	$p = 0.003$
Ruderality**	0.6	0.7	ANCOVA	$F = 11.667$	0.003	$p = 0.019$
Stress	1.1	1.1	t -test	$t = 0.794$	0.437	none

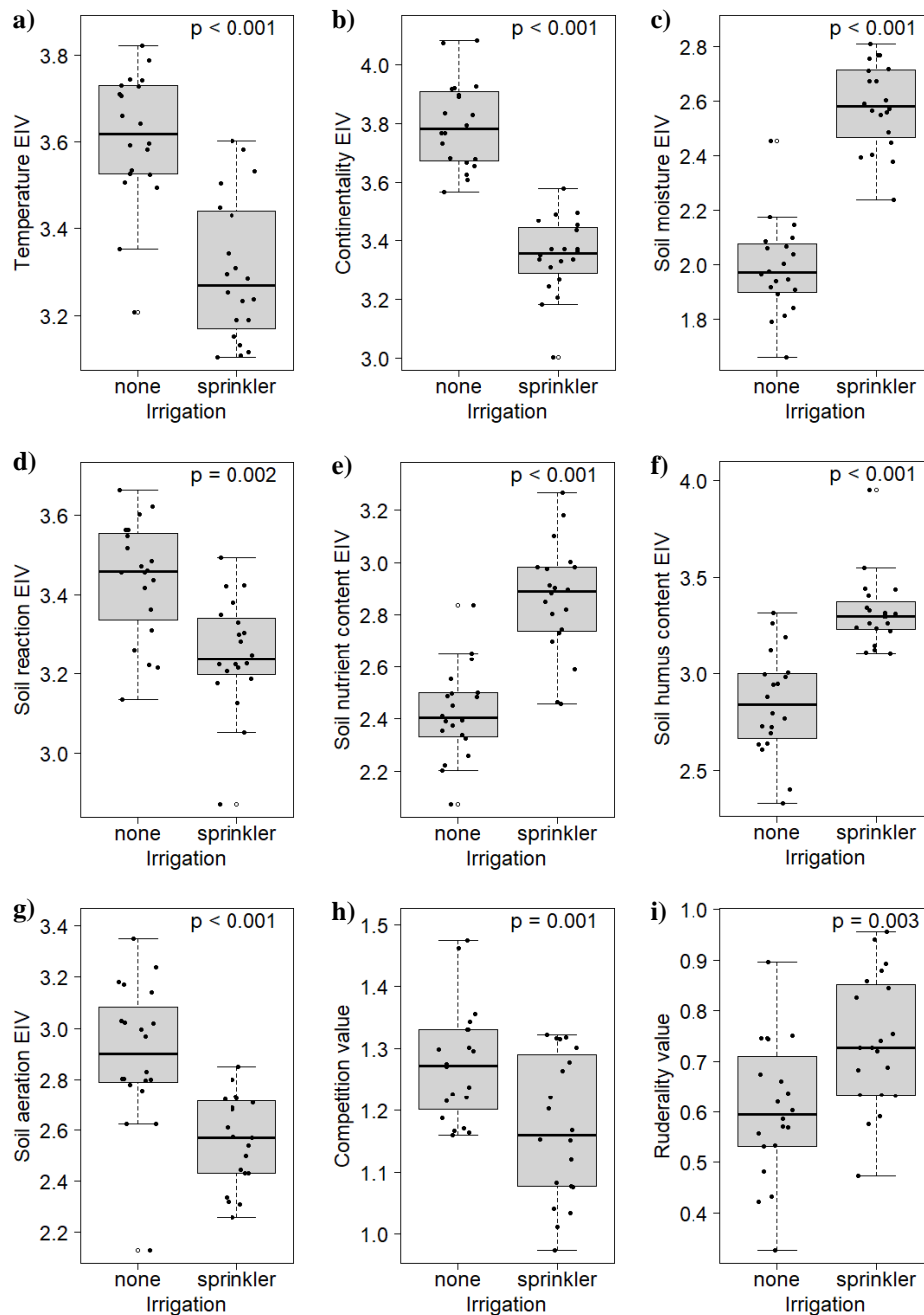


Fig. 6. Boxplots of significantly differing square-root cover-weighted ecological indicator values (EIVs, range 1–5) and CSR strategy values (range 0–3) between unirrigated and irrigated plots within the plot pairs, with data points superimposed ($n = 20$ pairs).

Abb. 6. Boxplots der signifikant unterschiedlichen quadratzurzelgewichteten mittleren ökologischen Zeigerwerten (EIVs, Bereich 1–5) und CSR-Werten (Bereich 0–3) zwischen unbewässerten und bewässerten Flächen der Flächenpaare, mit überlagerten Datenpunkten ($n = 20$ Paare).

4.3 CSR strategies

Mean CSR values did not differ significantly between the two time steps of the permanent plots. By contrast, irrigated plots in the paired plots showed significantly lower competition values ($p = 0.001$) and higher ruderality values ($p = 0.003$) (Table 2, Fig. 6h and I). Both showed a significant effect of slope, with steeper slopes showing higher competition values and lower ruderality values.

4.4 Species composition

Comparing the species composition of irrigated permanent plots from 1989–2021, the binomial test revealed no significant increases in the frequency of individual species, and only one significant decrease: *Poa chaixii* ($p = 0.016$), a species of open woodland and heathland found over acidic soils in mountainous regions of Switzerland. Other species which disappeared are associated in large part with dry grasslands (*Geum montanum*, *Cirsium acaule*), including some protected species which were already infrequent in the plots in 1988 (*Dactylorhiza sambucina*, *Orchis ustulata*). By contrast, the few species experiencing at least moderate increases in frequency after 1988 are often associated with mesic conditions (*Arrhenatherum elatius*, *Festuca nigrescans*, *Rhinanthus alectorolophus*). In all, 42 species disappeared from the plots, while only 27 new species appeared.

4.5 Vegetation structure

Although vegetation structure was not recorded in the historical surveys, it could be analyzed for the paired plots. Sprinkler-irrigated plots within the plot pairs tended to have denser vegetation, although this effect was not statistically significant ($p = 0.071$; $\alpha = 0.025$ due to poor residual distribution). Slope was found to have a significant effect on total vegetation cover ($p = 0.047$; $F = 4.564$), with plots over steeper slopes harboring less dense vegetation. On average, the herb layer was significantly taller in irrigated plots ($p < 0.001$; $t = -5.056$). Litter cover was generally higher in unirrigated plots, although this was not statistically significant ($p = 0.003$; $F = 11.819$; $\alpha = 0.025$ due to poor residual distribution). Slope had a significant effect on litter cover ($p < 0.001$; $F = 17.86$). The covers of shrubs, bryophytes, and lichens were not significantly affected by irrigation or by slope.

5. Discussion

5.1 Declines in biodiversity

We observed a strong and significant decrease in species richness with time and associated with sprinkler irrigation for the permanent and paired plots, respectively. The clear decline of species richness within the *permanent plots* over time tracks with the overall decline in habitat quality observed in Swiss grasslands over the past decades (e.g. Boch et al. 2019), contributing to the general biodiversity crisis in Switzerland (see e.g. Lachat et al. 2010, Gattlen & Klaus 2023). However, differences in ecological site conditions as described by mean EIVs demonstrate no clear pattern which could represent a driver of this change.

5.2 Changes in site conditions (permanent plots)

Surprisingly, mean light EIVs increased significantly in the permanent plots over time, although the effect size was small (0.11 on the 1–5 scale, a difference which is in our experience not recognizable in the field). The reason for this increase is unclear. According to information from the local farmers, there was no general increase in land-use intensity. Sprinkler irrigation may have created gaps in the vegetation through increased erosion, but this is not reflected in the ruderality values. Similarly, the increase of soil reaction EIVs in the permanent plots over time defies the general pattern of soil development observed in irrigated grasslands of the region. Meier (1990) classified the soils of the study site as typical phaeozems, gleysol / phaeozems, brown earth / phaeozems, and brown earths (Meier 1990). Liniger (1983) found that traditional flooding irrigation generally transformed the typical phaeozem of the region into humus-rich brown earth. This would correspond to a drop in pH resulting from carbonate leaching. The lack of significant changes in nutrient EIVs and ruderality values stands in contrast to results from Boch et al. (2019), who found increases in both values indicative of an overall decline in habitat quality in the dry grasslands of Valais.

The seemingly counterintuitive visual trend toward increasing temperature in the permanent plots with time after establishing sprinkler irrigation may be a signal of climate change: Switzerland experienced its hottest summers on record in 2003, 2015, and 2018 (FOEN 2019).

5.3 Differences in site conditions with irrigation (paired plots)

By contrast, irrigated plots in the *plot pairs* were cooler and more humid, as would be intuitively expected. This may prevent dry grassland species from developing on these plots. The unirrigated plots had higher continentality EIVs ($p < 0.001$), indicating a dearth of steppe specialists which are adapted to drastic shifts in temperature. This may be due to the development of better-insulating vegetation cover with irrigation. However, a corresponding increase in stress values which one could expect with such shifts in species assemblages could not be observed. Both soil nutrient content and soil humus content were much higher in the irrigated plots, pointing to higher productivity and fodder quality as qualitatively observed for the permanent plots by Jeangros & Bertola (2001). The increased nutrient availability may be due to edaphic processes supported by sprinkler irrigation or may simply be the result of selection bias. It is important to note that farmers in the region do not irrigate indiscriminately, instead choosing grasslands which show potential to produce high-quality fodder. Additionally, results may be confounded by differences in fertilization or other land-use parameters. Land-use details are not known for the paired plots, but it is possible that the irrigated plots are also fertilized.

In irrigated plots of the plot pairs, higher ruderality could be observed, even after correcting for the effect of slope. This could stem from the effects of sprinkler irrigation on the soil surface, leading to erosion and the formation of puddles. The lower competition values in the irrigated plots seem to contradict the high soil moisture, nutrient, and humus content suggested by the mean EIVs. However, since CSR values according to Landolt complement one another to add up to 3 for each species, the difference may simply be driven by the higher ruderality EIVs which must somehow be compensated for in the overall balance. Mean EIVs for soil aeration were lower in the irrigated plots. This aligns with results from Liniger (1983), who found that irrigation in the Aletsch region is associated with slight soil compaction attributable to accelerated weathering of mica, leading to increased clay formation.

5.4 Changes in species assemblages (permanent plots)

Although only one species changed significantly in frequency over time in the *permanent plots*, the overall pattern appears to confirm the impression of Volkart & Godat (2007) that the species composition shifted from more specialist dry grassland communities to mesic ones. Other studies on sprinkler irrigation in Valais also found an increase in generalist species (Riedener et al. 2015). However, Riedener et al. (2013) found that species composition on plots in Valais irrigated via sprinkler system or flooding did not change significantly in 25 m². In hay meadows in Valais, the number of specialists has been observed to remain similar, but the number of generalists to increase due to modern sprinkler irrigation (Riedener et al. 2015). In Valais, Boch et al. (2021) observed a significant increase in nitrophilous grasses and forbs such as *Arrhenatherum elatius* and *Heracleum sphondylium* due to high intensity irrigation or fertilization, while species associated with nutrient-poorer conditions (e.g. *Briza media*) decreased in cover. This pattern could be seen only in a general sense in our data, with no statistically significant shift in the frequency of most species.

5.5 Limitations of the study

Given the overall findings in the literature that the irrigation either increases or has no significant effect on the biodiversity of semi-natural grasslands (see Introduction), it is somewhat surprising that in our case sprinkler irrigation was associated with lower species richness for both the permanent and paired plots of this study. Since no detailed land-use information could be gathered for the paired plots, it is possible that the irrigation effect is confounded with another dimension of land use such as fertilization type or frequency, as can be deduced from the differences in nutrient EIVs. Indeed, in the inneralpine dry valleys of Switzerland, irrigated grasslands are often also fertilized (Boch et al. 2021). The link between nutrient enrichment and decreased species richness is well-established.

This study was unable to elucidate drivers for the decline in species richness of the permanent plots, despite the clear and intuitive signals observed for the paired plots. Overall, no clear trend in changes in ecological conditions could be found after 33 years of sprinkler irrigation. Additionally, the few significant changes that could be observed in the permanent plots often contradict the differences between the paired plots, so that a possible irrigation effect may be called into question. Various reasons may be considered, alone or acting in combination:

- The small sample size ($n = 8$) has prevented the true pattern from being recognized (increased Type II error rate).
- Omitting the unirrigated permanent plots from the temporal analyses eliminated the driest vegetation (i.e. vegetation of the *Stipo-Poion xerophilae*). However, such vegetation was included to a certain degree within the analyses of the paired plots (4 plots out of 40).
- Land-use intensity and fertilizer application on the permanent plots appears to have not changed significantly since 1988 (Volkart & Godat 2007; Supplement E4), but compared to the previous period for which we have no data, it is likely that a land-use intensification did occur once irrigation was reestablished (see Graf et al. 2014). This would likely strongly confound irrigation effects. Still, we would have expected such an intensification to affect a host of EIVs (e.g. nutrient content, competition value).

- Traditional flooding irrigation may have had a long-lasting impact on the experimental site which persisted even 20 years after its cessation, so that no substantial change in edaphic conditions took place. According to Zurwerra (2010), the oldest *Suonen* date approximately to the 12th century; the age of the now-defunct *Suone* in Martisberg is unknown to us.
- Interaction effects between slope and sprinkler irrigation were not considered (see Methods section). Such effects could obscure patterns in the data as analyzed by our simple tests. For example, irrigation could cause humus accumulation which is negated for grasslands on steep slopes due to greater erosion, leading to diverging trends.
- Although the local farmers could offer information about land use which generally exceeds the quality of what is most often available, in certain cases they could not remember exactly what was done in a given year.

6. Conclusions

Although both the permanent and paired plots of this study demonstrated reduced species richness associated with sprinkler irrigation, the nature of this relationship is unclear. The permanent plots of this study show only a few, contradictory changes in ecological conditions over time, so that no driver can be attributed to their strong decline in biodiversity. However, the paired plots differed strongly in a broad range of ecological conditions. Based on differences in mean EIVs, we suspect that the main reason for the lower species richness found in the irrigated plots is nutrient enrichment, followed by a possible exclusion of specialist (dry grassland, steppe) species due to greater soil moisture and lower temperatures resulting from more efficiently insulating vegetation cover. However, these factors may also be caused by fertilization, which due to lack of information could not be directly included as an explanatory variable in our analyses.

The future need for irrigation will be strongly influenced by climatic patterns. Climate scenarios predicted for the Alps show a decrease in summer precipitation and an increase in winter precipitation by 2050, as well as an increase in mean annual temperature of 0.7 to 3.9 °C, depending on which climate protection measures can be implemented (MeteoSwiss 2018). The need for irrigation in the dry inneralpine valleys may therefore increase in the future. Hence, researchers should continue to investigate the effect of sprinkler irrigation on semi-natural grassland vegetation in order to head off potential risks to grassland biodiversity.

Erweiterte deutsche Zusammenfassung

Einleitung – In den inneralpinen Trockentälern des Wallis (Schweiz) ist die Bewässerung eine jahrhundertalte Praxis, um die Produktivität von halbnatürlichem Grasland zu steigern. Ab ca. 1980 wurde begonnen, die traditionelle Flutbewässerung mittels Suonen durch Beregnungsanlagen zu ersetzen. Verschiedene Studien haben die Auswirkungen der traditionellen und modernen Bewässerung auf halbnatürliches Grünland untersucht und dabei oft widersprüchliche Ergebnisse festgestellt, welche die Frage der langfristigen Auswirkungen auf die Biodiversität nicht klären konnten. Deshalb führten wir Wiederholungsaufnahmen auf 8 Dauerflächen in der Gemeinde Bettmeralp durch. Die Gemeinde installierte zwischen 1988 und 1989 Beregnungsanlagen auf Wiesen und Weiden, deren Zustand anschließend durch Vegetationsaufnahmen auf Dauerflächen verfolgt wurde. Das Ziel der Wiederholungsaufnahmen nach über 30 Jahren Bewässerung war, Veränderungen der Artenvielfalt, der Stand-

ortbedingungen (ökologische Zeigerwerte), und der adaptiven ökologischen Strategien (CSR-Werte) zu ermitteln. Zur Ergänzung der Dauerflächen haben wir insgesamt 20 Flächenpaare (bewässert/unbewässert) in der Nähe untersucht.

Untersuchungsgebiet – Die Untersuchungsstandorte befinden sich in der Gemeinde Bettmeralp in den Siedlungen Martisberg (Dauerflächen) und Betten Egga (Flächenpaare) (Abb. 1). Sie werden beweidet und/oder gemäht (Anhang E4). Die Höhenlage reicht von 1240 bis 1660 m ü.M. Die Region ist durch ein kontinentales Klima gekennzeichnet. Messungen in der Nähe zeigen einen mittleren Jahresniederschlag mit 1077 mm und die mittlere Jahrestemperatur mit 4,2 °C.

Methoden – Im Jahr 1988 wurden von der Eidgenössische Forschungsanstalt Agroscope Changins Dauerflächen von 25 m² angelegt, welche von 1988 bis 1996 und im Jahr 2006 untersucht wurden. Die Vegetationsaufnahmen wurden jedoch in unterschiedlichen Zeitabständen wiederholt und die Anzahl der untersuchten Flächen variierte stark (Anhang E5). Im Jahr 2021 haben wir die Vegetationsaufnahmen auf einer Fläche von 25 m² wiederholt, mit einer darin eingemitteten 10 m² großen Fläche ergänzt. Zusätzlich haben wir 20 Flächenpaare (bewässert/unbewässert) von 10 m² in benachbartem Gebiet untersucht. Die Kopfdaten der Erhebungen finden sich in Anhang E1, die Daten zur Artenvielfalt in Anhang E2 und die Angaben zur Landnutzung in Anhang E4.

Die Dauerflächen analysierten wir mit gepaarten *t*-Tests. Bei den Flächenpaare haben wir gepaarten *t*-Tests oder Co-Varianzanalysen mit der Hangneigung als Covariate verwendet, um auf Unterschiede in diesen Parametern zu testen. Zudem haben wir den Binomialtest durchgeführt, um Veränderungen in der Häufigkeit der einzelnen Arten zu bewerten.

Ergebnisse – Auf den Dauerflächen hat der Artenreichtum seit 1989 deutlich abgenommen (Abb. 4a). Auch bei den Flächenpaaren wiesen die bewässerten Flächen signifikant weniger Arten auf als die unbewässerten (Abb. 4b). Die gewichtete Lichtzahl und Reaktionszahl zwischen 1989 und 2021 nahmen signifikant zu (Tab. 1, Abb. 5); sonst gab es keine signifikanten Entwicklungen der Zeigerwerte. In einigen Fällen (z.B. bei den Feuchtigkeits- und Reaktionszahlen) deuten die vollständigen Zeitreihen darauf hin, dass die Entwicklungsrichtungen der Standortbedingungen im Laufe der Zeit zwischen den Flächen stark variierte (Anhang E6). Bei den Flächenpaaren waren, außer der Lichtzahl, alle gewichteten Zeigerwerte signifikant unterschiedlich (Tab. 3). Die größten Unterschiede wurden bei der Feuchtezahl, der Kontinentalitätszahl, der Nährstoffzahl und der Humuszahl festgestellt (Abb. 6). Die gewichteten CSR-Strategien unterschieden sich bei den Dauerflächen nicht signifikant. Im Gegensatz dazu wiesen die bewässerten Flächenpaare eine signifikant niedrigere Konkurrenzzahl und eine höhere Ruderalzahl auf (Tab. 2, Abb. 6h und I). In beiden Fällen zeigte sich ein signifikanter Einfluss der Hangneigung. Beim Vergleich der Artenzusammensetzung der bewässerten Dauerflächen zwischen 1989 und 2021 gab es nur eine signifikante Abnahme einer Art. Die Analyse der Vegetationsstruktur der Flächenpaare zeigte, dass die Hangneigung einen Einfluss auf die Gesamtvegetationsdeckung hat, wobei Flächen mit steileren Hängen eine weniger dichte Vegetation aufwiesen. Die Krautschicht war in bewässerten Flächen signifikant höher und die Deckung der Streu tendenziell tiefer, obwohl letztere nicht signifikant war.

Diskussion – Der deutliche Rückgang der Artenzahlen auf den Dauerflächen steht im Einklang mit dem allgemeinen Rückgang der Lebensraumqualität, der in den letzten Jahrzehnten im Schweizer Grünland beobachtet wurde. Obwohl bei den Flächenpaaren klare und intuitive Treiber festgestellt wurden, konnten wir in dieser Studie die Ursachen für den Rückgang des Artenreichtums im Laufe der Zeit nicht klären. Wir haben festgestellt, dass nur eine Art in ihrer Häufigkeit signifikant abnahm; generell scheinen seltener und auf Trockenheit spezialisierte Arten jedoch abzunehmen. Bei den Zeigerwerten stehen die wenigen signifikanten Veränderungen, die in den Dauerflächen beobachtet werden konnten, oft im Widerspruch zu den Unterschieden zwischen den gepaarten Flächen, so dass ein möglicher Bewässerungseffekt in Frage gestellt werden kann. Dafür kommen verschiedene Gründe in Frage, wie die kleine Stichprobengröße und mögliche Störeffekte durch Nutzungsintensivierung. Gemäß den mittleren Zeigerwerten waren die bewässerten Flächen der Flächenpaare deutlich kühler und feuchter,

und verfügten über saurere, nährstoffreichere und humusreichere Böden. Wir vermuten, dass der geringere Artenreichtum in den bewässerten Parzellen auf Eutrophierung und den Ausschluss spezialisierter Trockenrasenarten zurückzuführen ist.

Da der Bewässerungsbedarf in den inneralpinen Tälern der Schweizer Alpen aufgrund des Klimawandels voraussichtlich zunehmen wird und die Bewässerung in einigen Fällen nachweislich zu einer Verarmung der Grünlandvegetation führt, sollten weitere Langzeitstudien durchgeführt werden, um potenziell negative Auswirkungen auf die Artenvielfalt im Grünland vorzubeugen.


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Author contributions

M.S. carried out the fieldwork and initial analyses for her Bachelor thesis under the supervision of J.D. H.S. revised and expanded the statistical analyses. The manuscript was drafted by H.S. with major contributions by M.S. and J.D.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Header data for the permanent (1989 vs. 2021) and paired plots.

Anhang E1. Kopfdaten für die Dauerflächen (Aufnahmen 1989 und 2021) und gepaarten Flächen.

Supplement E2. Species cover data for the permanent plots in Martisberg.

Anhang E2. Artendeckungen der Dauerflächen in Martisberg.

Supplement E3. Species cover data for the paired plots in Martisberg and Betten Egga.

Anhang E3. Artendeckungen der gepaarten Flächen in Martisberg und Betten Egga.

Supplement E4. Land-use details for the permanent plots in Martisberg over time.

Anhang E4. Details zur Landnutzung der Dauerflächen in Martisberg im Laufe der Zeit.

Supplement E5. Studies carried out in Martisberg from 1988 to 2020.

Anhang E5. In Martisberg durchgeführte Studien von 1988 bis 2020.

Supplement E6. Individual development of the eight permanent plots from 1988–2021 with regards to species richness and a selection of important site parameters.

Anhang E6. Individuelle Entwicklung der acht Dauerflächen von 1988–2021 hinsichtlich des Artenreichtums und einer Auswahl wichtiger Standortparameter.

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Supplement E1: Header data of the plots included in our analyses. In each case, the header data of the 10-m² plot was recorded. Coordinates were taken using the Swiss national coordinate system CH1903 / LV03.

Beilage E1. Kopfdaten der Flächen, die in unsere Analysen einbezogen wurden. In jedem Fall wurden die Kopfdaten der 10 m² großen Flächen erfasst. Koordinaten entsprechen derjenigen des nationalen Schweizer Koordinatensystems CH1903 / LV03.

Plot-ID	Number	Location	Year	Irrigation	Dataset	Use	Coordinate	Coordinate	Imprecision	Date	Area	Aspect	Southing	Slope	Total	Maximum	Soil	Soil	Soil	Soil	Soil	Average	Vegetation	Vegetation	Vegetation	Vegetation	Vegetation	Average vege-	Maximum	Herb	Shrub	Moss	Lichen	Litter	Stones	
							Y	X							GNSS	vegetation	microrelief	depth 1	depth 2	depth 3	depth 4	depth 5	soil depth	height 1	height 2	height 3	height 4	height 5	tation height	vegetation	layer	layer	layer	layer	layer	layer
B-1-I	1	Betten Egga	2021	sprinkler	paired	pasture	649016	137308	8	09.06.2021	10	133	-0.68	39	55	12	33	39.5	50	39.5	45.5	41.5	11.5	14.5	17	9.5	17.5	14	65	55	0	0	0	0	20	0
B-2-I	2	Betten Egga	2021	sprinkler	paired	meadow	649019	137148	6	15.06.2021	10	98	-0.14	36	92	6	39.5	31	36.5	35.5	33	35.1	16	23.5	31	25.5	37.5	26.7	117	92	0	0	0	0	5	0
B-3-I	3	Betten Egga	2021	sprinkler	paired	meadow, autumn pasture	648784	137128	8	13.06.2021	10	160	-0.94	36	92	4	40	55	66.5	37	22	44.1	18	20	10	17.5	15	16.1	124	92	0	0	0	0	5	0
B-4-I	4	Betten Egga	2021	sprinkler	paired	meadow, autumn pasture	648741	137084	9	10.06.2021	10	174	-0.99	36	90	10	47.5	39	31	54	38.5	42	17	34	18	22	23.5	22.9	100	90	0.001	0	0	0	20	0
B-5-I	5	Betten Egga	2021	sprinkler	paired	meadow, autumn pasture	648657	137051	8	11.06.2021	10	162	-0.95	36	97	8	38.5	28.5	28	42	31	33.6	7	13.5	13.5	20	11.5	13.1	102	97	0	0	0	0	5	0
B-6-I	6	Betten Egga	2021	sprinkler	paired	meadow	649094	137082	6	15.06.2021	10	155	-0.91	28	75	22	27.5	32	29.5	35.5	26.5	30.2	3	8	8.5	11.5	13	8.8	114	75	0	0	0	0	5	0
B-7-I	7	Betten Egga	2021	sprinkler	paired	meadow, autumn pasture	648715	136993	9	11.06.2021	10	180	-1	34	90	11	33.5	52	33.5	42	38.5	39.9	21	26	19	13	27	21.2	59	90	0.2	0	0	0	20	0
B-8-I	8	Betten Egga	2021	sprinkler	paired	meadow, autumn pasture	648553	136969	8	11.06.2021	10	190	-0.98	31	97	6	34.5	37	20	37	42.5	34.2	13	34	18	11.5	19	19.1	122	95	0	0	0	0	5	0
B-9-I	9	Betten Egga	2021	sprinkler	paired	meadow	649109	136895	16	09.06.2021	10	127	-0.6	23	95	8	43	34	34	37	35	36.6	15.5	20	27.5	22.5	30	23.1	80	95	0	0	0	0	5	0
B-10-I	10	Betten Egga	2021	sprinkler	paired	meadow, autumn pasture	649046	136967	9	10.06.2021	10	175	-1	30	85	9	34	35.5	36.5	38.5	41.5	37.2	13	19.5	24	23.5	10	18	110	85	0.7	0	0	0	25	0
B-11-I	11	Betten Egga	2021	sprinkler	paired	meadow	648935	136856	13	10.06.2021	10	174	-0.99	41	90	7	34	37.5	48	41	35.5	39.2	13	17	21	17	20	17.6	98	90	0	0	0	0	5	0
B-12-I	12	Betten Egga	2021	sprinkler	paired	meadow	648718	136768	8	13.06.2021	10	175	-1	38	97	6	36	44.5	32.5	39	42	38.8	34	24	27	25	14	24.8	85	97	0.01	0	0	0	5	0
M21-2-I	2	Martisberg	2021	sprinkler	paired, permanent	pasture	650999	137218	9	08.06.2021	10 (25)	125	-0.57	30	80	7	47	24.5	18	18	20.5	25.6	10	5.5	5	6.5	6	6.6	58	80	0	0	0	0	30	0
M21-3-I	3	Martisberg	2021	sprinkler	paired, permanent	meadow	650742	136983	6	08.06.2021	10 (25)	135	-0.71	20	97	3.5	25.5	26.5	26	19	20.5	23.5	18.5	16	14	17.5	16	16.4	90	97	0	0	0	0	5	0
M21-4-I	4	Martisberg	2021	sprinkler	paired, permanent	meadow	650702	137014	8	12.06.2021	10 (25)	170	-0.98	19	97	4	30	25	32.5	26.5	28	28.4	10	15.5	18	23.5	13	16	94	97	0	0	0	0	5	0
M21-5-I	5	Martisberg	2021	sprinkler	paired, permanent	meadow	650865	137483	8	12.06.2021	10 (25)	125	-0.57	18	97	5	21	27.5	33	19.5	36.5	27.5	25.5	18.5	33	28.5	17	24.5	107	97	0	0	0	0	5	0
M21-6-I	6	Martisberg	2021	sprinkler	paired, permanent	meadow	651148	137654	8	12.06.2021	10 (25)	126	-0.59	20	97	4	23.5	28	31	26	27	27.1	14	19	17	14.5	15	15.9	92	97	0	0	0	0	5	0
M21-8-I	8	Martisberg	2021	sprinkler	paired, permanent	pasture	650585	137322	8	17.06.2021	10 (25)	142	-0.79	25	65	6	35.5	40	46	33.5	43.5	39.7	4	5.5	5	6.5	4	5	45	65	0	0	0	0	15	0
M21-11-I	11	Martisberg	2021	sprinkler	paired, permanent	meadow, autumn pasture	650787	137767	6	14.06.2021	10 (25)	125	-0.57	26	88	4	30.5	29.5	32.5	29	39	32.1	29.5	19.5	8.5	21	17.5	19.2	101	88	0	0	0	0	5	0
M21-12-I	12	Martisberg	2021	sprinkler	paired, permanent	meadow, autumn pasture	650707	137752	6	14.06.2021	10 (25)	134	-0.69	23	95	3	30	29	10	47	27	28.6	36	32	16	28	10	24.4	106	95	0	0	0	0	5	0
B-1-U	1	Betten Egga	2021	none	paired	pasture	649033	137280	16	09.06.2021	10	158	-0.93	43	85	10.5	12	23	50.5	23.5	34.5	28.7	7	6	7	12	8	8	60	85	0	0	0	0	35	0
B-2-U	2	Betten Egga	2021	none	paired	pasture	648972	137181	6	15.06.2021	10	125	-0.57	44	75	17	26	19.5	24.5	13.5	41	24.9	9	10	5.5	9.5	5.5	7.9	71	75	0	0	0.001	0	25	0
B-3-U	3	Betten Egga	2021	none	paired	meadow	648766	137139	6	13.06.2021	10	134	-0.69	39	80	9	18	30	32	28.5	29.5	27.6	19.5	7	5	5.5	8	9	60	77	0.3	0	0	0	41	0.05
B-4-U	4	Betten Egga	2021	none	paired	none	648709	137120	12	10.06.2021	10	175	-1	40	75	16	25.5	30	38	27	30.5	30.2	11	18.5	8	8	10	11.1	82	75	0	0	0	0	30	0
B-5-U	5	Betten Egga	2021	none	paired	pasture	648650	137072	11	11.06.2021	10	155	-0.91	49	75	8	33	62	23.5	53	29	40.1	6.5	8.5	11.5	12	7	9.1	73	80	0.2	0.2	0	0	35	2
B-6-U	6	Betten Egga	2021	none	paired	pasture	648992	137081	6	15.06.2021	10	170	-0.98	40	75	15	38.5	25	25	20	11.5	24	9.5	10.5	12	8	7.5	9.5	80	75	0.3	0	0	0	30	0
B-7-U	7	Betten Egga	2021	none	paired	pasture	648781	136989	6	07.06.2021	10	178	-1	32	70	9	20	18	20	22.5	46.5	25.4	19	15	6	7	6	10.6	76	70	0	0	0	0	15	0
B-8-U	8	Betten Egga	2021	none	paired	pasture	648500	136954	6	17.06.2021	10	170	-0.98	41	80	13	36	10.5	22.5	52	35	31.2	12	18	7.5	9	15	12.3	88	85	0.1	10	0	0	70	0.3
B-9-U	9	Betten Egga	2021	none	paired	none	649191	136973	12	09.06.2021	10	120	-0.5	38	80	7.5	40	58	65	36.5	31	46.1	8	11.5	15.5	8	9.5	10.5	84	80	0.1	0	0	0	20	0
B-10-U	10	Betten Egga	2021	none	paired	meadow	648970	136930	8	07.06.2021	10	173	-0.99	43	95	7	35	20	26.5	26.5	16	24.8	10	5	13.5	16.5	8.5	10.7	104	95	0.2	0	0	0	20	0
B-11-U	11	Betten Egga	2021	none	paired	meadow	648980	136859	8	10.06.2021	10	165	-0.97	28	90	8	21.5	27.5	23.5	37.5	20	26	5.5	6.5	6	7	7.5	6.5	90	90	0	0	0	0	50	0
B-12-U	12	Betten Egga	2021	none	paired	meadow	648701	136782	8	13.06.2021	10	160	-0.94	39	70	15	43.5	27	25.5	28	45.5	33.9	13.5	7	8	8.5	9	9.2	86	70	0	0.001	0	0	30	1
M21-2-U	2	Martisberg	2021	none	paired	pasture	651021	137215	13	08.06.2021	10	140	-0.77	26	75	6	66	34	42	51	50	48.6	15	12	10	9.5	9.5	11.2	74	75	0	0.1	0	0	20	0
M21-3-U	3	Martisberg	2021	none	paired	pasture	650616	136955	12	12.06.2021	10	111	-0.36	33	80	7	44	25	32.5	31.5	38	34.2	14	15	12.5	14.5	12.5	13.7	86	80	0.1	0	0	0	20	0
M21-4-U	4	Martisberg	2021	none	paired	pasture	650599	136963	6	17.06.2021	10	140	-0.77	24	90	6	40	12.5	19	24	33	25.7	6	8	5.5	9.5	11	8	86	90	0	0	0	0	10	0
M21-5-U	5	Martisberg	2021	none	paired	pasture	650752	137469	6	02.07.2021	10	128	-0.62	23	78	5	45	30.5	65	9.5	16	33.2	10	9.5	12	16	14.5	12.4	120	78	0	0	0	0	12	0
M21-6-U	6	Martisberg	2021	none	paired	meadow	650941	137603	6	17.06.2021	10	125	-0.57	23	97	4	19.5	37	27.5	26.5	19	25.9	8	8	8.5	6	12	8.5	84	95	0	0	0	0	7	0.1
M21-8-U	8	Martisberg	2021	none	paired	pasture	650624	137414	6	14.06.2021	10	138	-0.74	29	85	6	31.5	54.5	53	53	43	47	13	17.5	11	17	11.5	14	85	85	0.3	0	0	0	10	0
M21-11-U	11	Martisberg	2021	none	paired	meadow, autumn pasture	650817	137712	8	14.06.2021	10	118	-0.47	22	97	5	32	40.5	32	36.5	29.5	34.1	5	10	12.5	7.5	10	9	80	97	0	0	0	0	5	0
M21-12-U	12	Martisberg	2021	none	paired	pasture	650674	137804	6	14.06.2021																										

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Supplement E4. Land-use details for the permanent plots in Martisberg over time. Plots in gray were excluded from our analyses.

Beilage E4. Details zur Landnutzung der Dauerflächen in Martisberg im Laufe der Zeit. Die grau hinterlegten Flächen wurden von unseren Analysen ausgeschlossen.

Plots in analysis	Number	Irrigation frequency per year			Number of uses per year			Use type			Fertilizer applications per year			Fertilizer type		
		1988–1996	1997–2006	2021	1988–1996	1997–2006	2021	1988–1996	2006	2021	1988–1996	1997–2006	2021	1988–1996	1997–2006	2021
-	1	5	2	0	2	2	2	pasture, mowing in autumn	pasture	pasture	0–1	1	1	manure	slurry	slurry
M89-2-I, M21-2-I	2	4	3–5	4–5	2	3	2	pasture, mowing in autumn	pasture	pasture	1	1	1	slurry	slurry	manure
M89-3-I, M21-3-I	3	7	4–5	4–5	3	3	2	meadow, autumn pasture	meadow	meadow	1–2	1	2–3	slurry / manure	slurry / manure	slurry, manure
M89-4-I, M21-4-I	4	7	4–5	4–5	3	3	2	meadow, autumn pasture	meadow	meadow	1–2	1	2–3	slurry / manure	slurry / manure	slurry, manure
M89-5-I, M21-5-I	5	6–7	5–6	4–5	3	3	2	meadow, autumn pasture	meadow	meadow	1	1–2	1	slurry / manure	slurry / manure	manure
M89-6-I, M21-6-I	6	ND	ND	4–5	3	ND	2	meadow, autumn pasture	ND	meadow	ND	ND	1	slurry / manure	ND	manure
-	7	0	(0–1)*	0	1–2	2	2	meadow, autumn pasture	pasture	pasture	0	0–1	0			slurry
M89-8-I, M21-8-I	8	2–3	2–4	2–3	1–2	2	2	meadow, autumn pasture	pasture	pasture	0–1	1	0	manure	slurry	
-	9	0	(0–1)*	0	0–2	2	2	meadow, autumn pasture	pasture	pasture	0	0–1	0			slurry
-	10	ND	ND	0	1	ND	2	meadow	ND	pasture	0	ND	0			
M89-11-I, M21-11-I	11	4	6–7	2–3	2	2	3	meadow, autumn pasture	meadow	ow, autumn pa	1–2	0–2**	1	slurry / manure	slurry	manure
M89-12-I, M21-12-I	12	5	3–5	2–3	2–3	3	2	meadow, autumn pasture	meadow	ow, autumn pa	1	1	1	slurry / manure	manure	manure

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Supplement E5. Studies carried out in Martisberg from 1988 to 2020 (modified from Volkart & Godat 2007).

Beilage E5. In Martisberg durchgeführte Studien von 1988 bis 2020 (aus Volkart & Godat 2007, adaptiert).

Year	Study subject	Author(s)	Comment
1985	Soil	Nievergelt (1985)	
1988	Fodder value	Carlen (1988)	
1988	Vegetation	Agroscope Changins*	
1989	Vegetation, soil, land use	Agroscope Changins*	Plots 5, 6, and 11 moved
1990	Vegetation	Meier (1990)	Plot 10 excluded
1991–1995	Land use	Agroscope Changins*	
1994	Vegetation	Agroscope Changins*	Plots 1, 2, and 10 excluded
1995	Vegetation	Agroscope Changins*	Plots 6 and 10 excluded
1996	Vegetation, soil, land use	Agroscope Changins*	Plots 1 and 10 excluded
2006	Vegetation, soil, land use	Volkart & Godat (2007)	Plots 5, 6, 8, 11, and 12 excluded (or presence / absence data only)
2020	Vegetation of federally protected dry grassland, land use	Valeco GmbH, Visp	Plot 10 only

*Results discussed in Meier (1990) and Jeangros & Bertola (2001).

Supplement E6. Individual development of the eight permanent plots from 1988–2021 with regards to species richness and a selection of important site parameters (as mean ecological indicator values according to Landolt et al. 2010).

Beilage E6. Individuelle Entwicklung der acht Dauerflächen von 1988–2021 hinsichtlich des Artenreichtums und einer Auswahl wichtiger Standortparameter (als mittlere ökologische Zeigerwerte nach Landolt et al. 2010).

