

## REPORT

# The Historic Square Foot Dataset – Outstanding small-scale richness in Swiss grasslands around the year 1900

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## Abstract

Grasslands host a significant share of Europe's species diversity but are among the most threatened vegetation types of the continent. Resurvey studies can help to understand patterns and drivers of changes in grassland diversity and species composition. However, most resurveys are based on local or regional data, and hardly reach back more than eight decades. Here, we publish and describe the Historic Square Foot Dataset, comprising 580 0.09-m<sup>2</sup> and 43 1-m<sup>2</sup> vegetation plots carefully sampled between 1884 and 1931, covering a wide range of grassland types across Switzerland. We provide the plots as an open-access data set with coordinates, relocation accuracy and fractional aboveground biomass per vascular plant species. We assigned EUNIS habitat types to most plots. Mean vascular plant species richness in 0.09 m<sup>2</sup> was 19.7, with a maximum of 47. This is considerably more than the present-day world record of 43 species for this plot size. Historically, species richness did not vary with elevation, differing from the unimodal relationship found today. The data set provides unique insight into how grasslands in Central Europe looked more than 100 years ago, thus offering manifold options for studies on the development of grassland biodiversity and productivity.

## KEYWORDS

elevational gradient, grassland, historic data set, long-term vegetation dynamics, quasi-permanent plot, species richness, Switzerland, vascular plant, vegetation plot, world record

## 1 | THE IMPORTANCE AND DISCOVERY OF THE DATA SET

Semi-natural grasslands are among the most threatened habitat types in Europe (Janssen et al., 2016) and specifically within Switzerland (Delarze et al., 2016). Their plant diversity is generally assumed to be declining (Janssen et al., 2016; Dengler et al., 2020). However, it is hard to quantify the amount of biodiversity loss and the direction of compositional change over longer periods, as there

are few quantitative data sets on historical species richness and composition that have been collected in a standardised manner to allow for comparisons with today's biodiversity. Some of the oldest known permanent vegetation plots in the world are located in Switzerland, for example on the Schynige Platte (Lüdi, 1936, 1940; Hegg & Schaffner, 2012) and in the Swiss National Park (Schütz et al., 1998). However, they come from very narrow geographic areas, making it difficult to derive results of general validity. More recently, in Switzerland, several country-wide systems of thousands of

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stratified-systematic vegetation monitoring plots were established, but the earliest of these schemes started only after the year 2000 (Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2009). Thus, so far, we have no standard approach to describe and quantify biodiversity change in Swiss grasslands during the 20th century, during which the largest alterations are assumed to have occurred (Lachat et al., 2010).

During a building renovation in 2003, a historic data set covering larger geographic and environmental gradients, reaching back more than 100 years and having been sampled with a uniform method was found at Agroscope. It seemed unlikely that such a data set would exist, since phytosociology as a discipline began in the 1910s and 1920s (Braun-Blanquet, 1921), in its infancy mostly dealing with local studies and using variable methods. The data set comprises the original records (Figure 1) for several hundred vegetation plots conducted between 1884 and 1931 in grassland habitats all over Switzerland. We termed it the “Historic Square Foot Dataset” because most of the records relate to squares of 30 cm × 30 cm, with 30 cm being the length unit foot which was commonly used in Switzerland at the time. These data are unique in providing precise descriptions of how grasslands in Central

Europe were composed more than a century ago, making them an important source of information for vegetation science, macroecology, conservation biology and global-change studies. We have digitised and relocated the data and wish to make them publicly accessible through this publication.

## 2 | BACKGROUND OF THE ORIGINAL SURVEY

In the late 19th century, the researchers Dr Friedrich Gottlieb Stebler of the Swiss Federal Seed Control Station Zurich and Prof. Dr Carl Schröter of the Swiss Federal Institute of Technology Zurich (ETH Zurich) (Figure 2) perceived a need to increase the productivity of Swiss meadows and pastures. As a prerequisite, they considered it necessary to characterise the composition of Swiss grasslands (Stebler & Schröter, 1887a).

The researchers published most of their studies in the *Landwirtschaftliches Jahrbuch der Schweiz* (Agricultural Yearbook of Switzerland) as a 15-piece series on “Contributions to the knowledge of the meadows and pastures of Switzerland” from 1887 to 1905 (Stebler & Schröter, 1887a, 1887b, 1887c, 1887d, 1888a, 1888b, 1889, 1891, 1892; Stebler & Volkart, 1888, 1905; Stebler, 1897, 1898b, 1898c, 1899). The cornerstone of this series is Volume X, where Stebler and Schröter proposed the first-ever classification of the meadows and pastures in Switzerland. In addition, they wrote thematic publications, for example on litter meadows (Stebler, 1898a). Together, the publications contain the data of 218 square-foot plots (30 cm × 30 cm) recorded until 1903. Several records aimed at investigating effects of drivers such as shading (36 plots), irrigation (10 plots), grazing (4 plots) and fertilisation (20 plots) on grassland vegetation (see Appendix S1). There are further 362 square-foot plots, which, to the best of our knowledge, have not been published yet. Finally, the researchers also sampled 43 plots of 1 m<sup>2</sup>.

Judging from the publishing activities (Stebler & Schröter, 1887a, 1887b, 1887c, 1887d, 1888a, 1888b, 1889, 1891, 1892, 1902; Stebler & Volkart, 1888, 1905; Stebler, 1897, 1898a, 1898b, 1898c, 1899), we assume that Stebler, as head of the Swiss Federal Seed Control Station, was the initiator and main data collector of the grassland studies. From 1884 to 1903, he and Schröter carried out most of these activities. After publication of Volume X of the series (Stebler & Schröter, 1892), Schröter was no longer involved as co-author. Later, Prof. Dr Albert Volkart (Figure 2), who succeeded Stebler as the head of the Swiss Federal Seed Control Station in 1917 (Lehmann, 2003), aided the fieldwork and analyses. In this context, he co-authored the extensive Volume XV, “The influence of shading on the sod,” together with Stebler (Stebler & Volkart, 1905). The citation of several square-foot analyses by Grisch (1907) lead us to assume that Dr Andreas Grisch, who was head of the Seed Control Department at the Swiss Federal Seed Control Station from 1920 until 1944, continued the studies with Volkart in the later years.

Bestandesaufnahme  
N 2153 Lengen

Nutzungsart: Melwiese  
Ort: Lengen  
Höhe über Meer: Ca 1240m  
Datum der Aufnahme: 22.10.19  
Boden: sandiger Lehmboden  
Düngung: Natürlicher (Kalkmilch)  
Allgemeine Bemerkungen: Weidung (Frühjahr, Herbst); Diese Stelle würde den ganzen Winter hindurch schneefrei gehalten.

1 Quadratfuß (900 □ Cm.) enthält:

Zahl der Stiele	Gewicht der Stiele in Gramm	Name der Pflanze	Gewicht der			Prozentatz der			Prozent süd der Faszi
			Stiele Trocken	Stiele Grün	Stiele Grün	Stiele Trocken	Stiele Grün	Stiele Grün	
<i>Gewinnlose Grün</i>									
11	472	7	<i>Bromus tectorum</i>	1000	1000	1000	1000	1000	1000
2	24	24	<i>Festuca ovina</i>	250	250	250	250	250	250
21	21	21	<i>Lolium perenne</i>	210	210	210	210	210	210
24	10	10	<i>Trisetum flavescens</i>	100	100	100	100	100	100
32			<i>Stylosanthes triflorata</i>	320	320	320	320	320	320
1	18	18	<i>Leucaena carnea</i>	180	180	180	180	180	180
15	50	50	<i>Trisetum flavescens</i>	500	500	500	500	500	500
2			<i>Stylosanthes triflorata</i>	200	200	200	200	200	200
3			<i>Stylosanthes triflorata</i>	300	300	300	300	300	300
2	1	1	<i>Stylosanthes triflorata</i>	200	200	200	200	200	200
55	742	17		5500	5500	5500	5500	5500	5500

FIGURE 1 Partial reproduction of an original recording sheet. Header data of the illustrated record sheet: Nutzungsart (Land use), Ort (Municipality and/or Toponym\_TA and or Additional\_location), Höhe über Meer (Metres above sea level), Datum der Aufnahme (Date of record), Boden (Soil), Düngung (Fertil\_treatment), Allgemeine Bemerkungen (General remarks).



**FIGURE 2** Researchers who sampled the Historic Square Foot Dataset. From left to right: F.G. Stebler (1852–1935) and C. Schröter (1855–1939) (<http://doi.org/10.3932/ethz-a-000068526>), A. Volkart [Peter Moser, Volkart, Albert (1873–1951)--DB3669, Portal ARH People and institutions, November 2022 version, [https://www.histoierurale.ch/pers/personnes/Volkart,\\_Albert\\_\(1873\\_1951\)\\_DB3669.html](https://www.histoierurale.ch/pers/personnes/Volkart,_Albert_(1873_1951)_DB3669.html) consulted on 9 January 2023] and A. Grisch [Peter Moser, Grisch, Andreas (1879–1952)--DB1342, Portal ARH People and institutions, November 2022 version, [https://www.histoierurale.ch/pers/personnes/Grisch,\\_Andreas\\_%281879\\_1952%29\\_DB1342.html](https://www.histoierurale.ch/pers/personnes/Grisch,_Andreas_%281879_1952%29_DB1342.html) consulted on 9 January 2023].

### 3 | ORIGINAL SAMPLING DESIGN

The site selection method for the plots is not explicitly explained, either in the publications, the original records themselves or the diaries that we consulted in the Swiss Federal Archives. There is no indication of a systematic sampling design, but, with regard to the above-mentioned objective, the authors wanted to provide an overview of the grassland types in Switzerland. We thus can assume that the authors tried to select representative stands for most grassland habitats (Stebler & Schröter, 1892). Additionally, at lower elevation, particular plots were selected to investigate the influence of certain environmental factors. For example, one unfertilised plot was selected next to a fertilised one, with otherwise identical site factors. According to the available descriptions, the general sampling approach was as follows: once a grassland stand had been chosen, the researchers noted parameters such as name of the village, toponyms, elevation, aspect, soil conditions, type of use, fertilisation, water management and phenological state of the plants. Then the grassland stand was characterised by listing the scientific name of all vascular plant species and their relative abundance. Within a homogeneous part of the respective stand, the researchers dug out a piece of sod measuring one Swiss square foot, that is, 30 cm × 30 cm or 0.09 m<sup>2</sup>, including the uppermost 2–3 cm of soil. These pieces of sod were transported to the laboratory, where the researchers harvested the aboveground biomass of vascular plants, sorted it by species and for each species, counted the number of seedlings as well as sterile and fertile shoots. After air-drying to constant weight, the dry matter of each species was weighed on an analytical balance. By contrast, the 1-m<sup>2</sup> plots were not dug out, but their biomass was harvested and sorted by species in the field (Stebler & Schröter, 1887a).

### 4 | RELOCATING PROCEDURE

We located each plot geographically based on the information on the record sheets. At a minimum, the notes contain the name of the village and the elevation. Often, additional information such as toponyms, aspect and/or distance and direction from a certain landmark or farm are given. We translated this information into one or several polygons corresponding to the area in which the original plot could have been located, the so-called potential areas (PAs), using a geographic information system (GIS) (ArcGIS Pro 2.6.3, ESRI). Historic vegetation-plot records that contained identical or very similar location information were assigned to the same PA.

For the creation of the PAs, we used a digital version of the Topographic Atlas of Switzerland (“Siegfried Map,” 1870–1926, 1:25,000/1:50,000) (swisstopo, 2022a, 2022b) as background map, in the edition that was available at the time of the plot recording (reference level of elevation “Repère du Niton,” which was the “old horizon”: −3.26 m of the current Swiss height system LN02) (swisstopo, 2022c). For localising toponyms, we also used Swiss Map Raster 10 (swisstopo, 2022d), an online database (<https://www.ortsnamen.ch>), and we searched for hints in local historical documents. Where the description of the original record indicated wet grassland, the PA was restricted to the wetland signatures in the Topographic Atlas. To ensure consistent relocation, all PAs defined by a single person were evaluated and discussed among Susanne Riedel, Stefan Widmer and Manuel Babbi. We excluded built-up areas and forests from the PAs, based on the signatures in the Topographic Atlas, except for those plots explicitly located in open forests. It was not possible to exclude arable land from the PAs, as the Topographic Atlas does not differentiate this land use from grassland. We assumed that the elevational accuracy of the historical recording had been ±50 m.

If the verbal descriptions, for example the direct connection to a landmark with known elevation, allowed higher precision, we documented and applied this. In a second step, we included the effect of the horizontal accuracy on the elevation accuracy of the Siegfried Map, which accounts for 12.5m for the 1: 25,000 scale and 35m for the 1: 50,000 scale (swisstopo, 2022c). We multiplied the average slope of the preliminary perimeter with the above-mentioned horizontal accuracy divided by 100, resulting in an additional elevation inaccuracy not exceeding 12.5m or 35m, respectively. We used the elevation model swissALTI3D (swisstopo, 2022e) for delimiting the PA elevation-wise. This model itself typically has a precision of  $\pm 0.5$ m, although it reaches  $\pm 3$ m in rare cases. The preliminary polygon was thus adjusted by taking these correction values into account. For this publication, we derived the minimum spanning circle of the resulting polygon (FME Workbench 2021.1, Safe Software), defined as the smallest circle that encloses all vertices of the PA, using its radius to define the imprecision in metres as well as its centroid as the coordinate.

The 580 0.09-m<sup>2</sup> plots are distributed all over Switzerland, with the highest numbers in the canton of Zurich (157 plots), where the researchers were based at the Swiss Federal Control Station and at ETH, and the canton of Grisons (156 plots), especially at Fürstenalp (67 plots) (Figure 3). The 43 1-m<sup>2</sup> plots cover a narrower area, with 72% being from the canton of Zurich. In general, the western and southern regions of Switzerland are less represented in the data set.

The sampling was conducted from 1884 until 1931, but mainly until 1902 (400 plots). From 1903 onwards, sampling activities declined, with only up to 15 plots per year, except in 1910 (30 plots, mainly from a two-day excursion in four grassland municipalities in the canton of Lucerne) and 1924 (36 plots situated around the former alpine experimental research station Fürstenalp, canton of Grisons) (Stebler & Schröter, 1989; Lehmann, 2003) (Figure 4).

The 0.09-m<sup>2</sup> plots cover a wide elevational range, from 212 to 2547m a.s.l., with higher concentration in the lowlands than in the regions of higher elevation (Figure 3). The 1-m<sup>2</sup> plots are mainly distributed at an altitude around 400m a.s.l. (63% of the plots), the highest plot being located at an elevation of 1278m a.s.l. The size of the retrieved PAs ranges from 286 m<sup>2</sup> to 11.19 km<sup>2</sup> (mean: 0.3814 km<sup>2</sup>, median: 0.1224 km<sup>2</sup>). This translates into geographic

imprecision of the assigned centroid coordinates from 14m to 3813m (mean: 524m, median: 374m).

## 5 | VEGETATION AND HEADER DATA

The original plant names were translated to the nomenclature of the current checklist of Switzerland (Juillerat et al., 2017). The correct assignment was supported by the Euro+Med PlantBase (Euro+Med, 2022), various literature sources (for example Schinz & Keller, 1900; Marzell, 2000) and the herbarium of Agroscope. We specifically considered that taxa thought of as species at the time of original recording might have meanwhile been split into multiple species, becoming aggregates. If no suitable aggregate could be found in Juillerat et al. (2017), we defined one to reflect the historic species circumscription (for example "*Festuca ovina* aggr. s.l." = *F. ovina* aggr. + *F. valesiaca* aggr. sensu Juillerat et al., 2017).

Once digitised, the original data sheets were systematically cross-checked for digitising errors. While the original records, except those from Chapter XV (Stebler & Volkart, 1905), contained absolute dry mass per species in a plot, we translated this into fractional biomass per plot (in %), and added the total biomass of all species (in g) to the header data.

## 6 | ADDITION OF EUNIS HABITAT TYPES AND MEAN ECOLOGICAL INDICATOR VALUES

We classified the plots according to the refined EUNIS Habitat Classification (Chytrý et al., 2020) using the software JUICE (Tichý, 2002). This resulted in the automatic classification of 396 0.09-m<sup>2</sup> and 38 1-m<sup>2</sup> plots. For the plots that could not be automatically classified, we applied Section 2 of the EUNIS Expert System (EUNIS-ESy), which enumerates species belonging to individual species groups. This allowed the assignment of another 55 0.09-m<sup>2</sup> plots and three 1-m<sup>2</sup> plots to the habitat whose species group clearly prevailed, based on presence/absence data. Another 55 0.09-m<sup>2</sup> and two 1-m<sup>2</sup> plots without clear prevalence of one

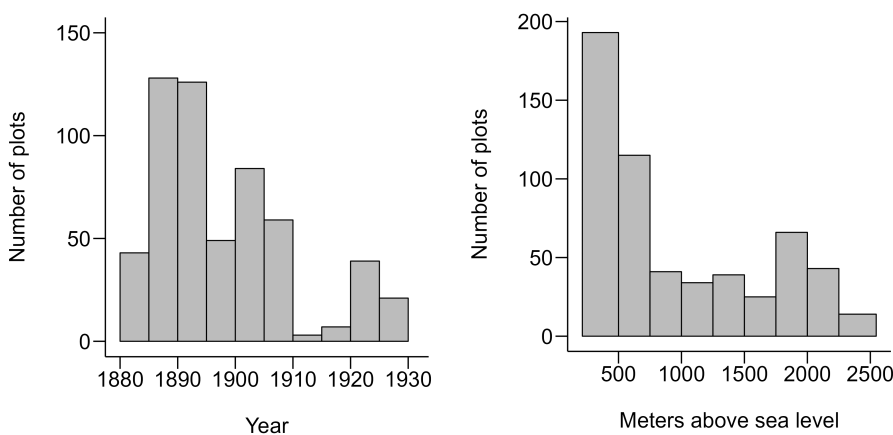
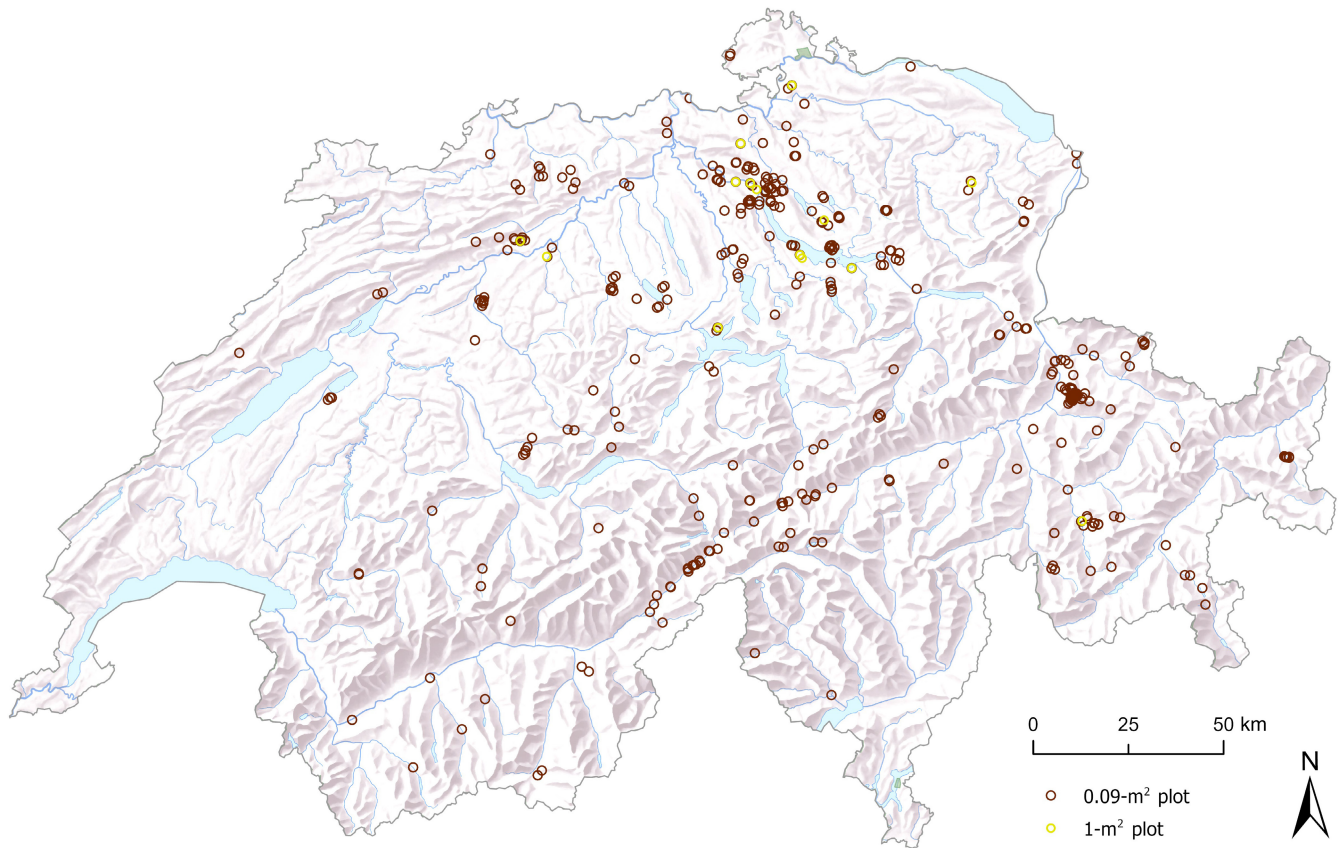


FIGURE 3 Frequency distribution of the grassland 0.09-m<sup>2</sup> plots over time and along the elevational gradient.



**FIGURE 4** Spatial distribution of the plots of the Historic Square Foot Dataset in Switzerland ( $n=580$  for  $0.09\text{-m}^2$  plots,  $n=43$  for  $1\text{-m}^2$  plots). Several plots had identical locality descriptions, resulting in 377 different potential areas (PAs) for the  $0.09\text{-m}^2$  plots and 14 for the  $1\text{-m}^2$  plots. Note that due to the proximity of some plots, they are not well separated on the map.

species group were then classified based on expert knowledge, considering the entire species list of the record as well as elevation and indications from the original authors. The remaining 74  $0.09\text{-m}^2$  plots remained unclassified. In order to prepare the data for the GrassPlot database, we derived the required variable “Grass-Plot\_vegetation\_type” (Biurrun et al., 2019) from the EUNIS habitat class or, in certain cases, from the phytosociological class and order (Mucina et al., 2016).

In total, we could assign the plots to 27 EUNIS habitat types (Table 1). Among the  $0.09\text{-m}^2$  plots, most frequent were “low and medium altitude hay meadow” (33%), followed by “mesic permanent pasture of the lowlands and mountains” (20%), “semi-dry perennial calcareous grassland (meadow steppe)” (11%) and “temperate acidophilous alpine grassland” (11%) (Table 1).

For further characterisation, we calculated unweighted mean ecological indicator values of the plots for moisture and nutrients (Landolt et al., 2010). To analyse species richness in relation to elevation, moisture and nutrients, we ran general linear models with the software R (R Core Team, 2022), using family “quasipoisson” to take overdispersion into account.

The ecological indicator values for moisture and nutrients reveal that the plots cover wide ecological gradients (Figures 5 and 6). Generally, the moisture gradient was relatively well covered in all elevational bands, with records of wet grasslands being more frequent at

lower elevations (Figure 5). Mean nutrient indicator values generally declined with elevation, except for unusually low values in the interval from 750 to 999 m a.s.l. A few plots on overfertilised soils near the alpine huts of Fürstenalp are responsible for the extreme values in the intervals from 1750 to 1999 m a.s.l. and from 2000 to 2249 m a.s.l.

## 7 | AVAILABILITY OF THE DATA SET

The Historic Square Foot Dataset comprises all available historic plots of both plot sizes and is registered in the Global Index of Vegetation-Plot Databases (Dengler et al., 2011) under EU-CH-013. The data are available in Appendices S1–S4, with S1 and S3 comprising the header data for the square-foot and the square-metre plots and Appendices S2 and S4 including the species composition data of the square-foot and the square-metre plots, and in the GrassPlot database (Dengler et al., 2018; <https://edgg.org/databases/GrassPlot>) as data set ID CH-P. The species nomenclature is standardised to Juillerat et al. (2017) with a few additional aggregates. Species importance values are given as fractional dry mass. We also provide a set of plot-level data (header data) which are explained in Table 2. Most importantly, we provide the coordinates and their imprecision as PA centroid and PA radius, respectively. Due to the inclusion



TABLE 1 Frequency distribution of the EUNIS habitat types (Chytrý et al., 2020) in the data set.

EUNIS class	EUNIS habitat name	Number of 0.09-m <sup>2</sup> plots	Number of 1-m <sup>2</sup> plots
<b>Q</b>	<b>Wetlands</b>	<b>11</b>	<b>1</b>
Q22	Poor fen	1	
Q24	Intermediate fen and soft-water spring mire	1	
Q41	Alkaline, calcareous, carbonate-rich small-sedge spring fen	1	
Q43	Tall-sedge base-rich fen	3	
Q51	Tall-helophyte bed	2	
Q53	Tall-sedge bed	3	1
<b>R</b>	<b>Grasslands and lands dominated by forbs, mosses or lichens</b>	<b>477</b>	<b>42</b>
R1A	Semi-dry perennial calcareous grassland (meadow steppe)	58	
R1B	Continental dry grassland (true steppe)	2	
R1M	Lowland to montane, dry to mesic grassland usually dominated by <i>Nardus stricta</i>	10	
R21	Mesic permanent pasture of lowlands and mountains	103	6
R22	Low and medium altitude hay meadow	167	32
R23	Mountain hay meadow	20	
R35	Moist or wet mesotrophic to eutrophic hay meadow	4	1
R36	Moist or wet mesotrophic to eutrophic pasture		1
R37	Temperate and boreal moist or wet oligotrophic grassland	14	
R41	Snow-bed vegetation	4	
R43	Temperate acidophilous alpine grassland	54	
R44	Arctic-alpine calcareous grassland	24	
R51	Thermophilous forest fringe of base-rich soils	1	
R55	Lowland moist or wet tall-herb and fern fringe	10	2
R56	Montane to subalpine moist or wet tall-herb and fern fringe	6	
<b>S</b>	<b>Heathlands, scrub and tundra</b>	<b>9</b>	
S21	Subarctic and alpine dwarf <i>Salix</i> scrub	1	
S22	Alpine and subalpine ericoid heath	4	
S25	Subalpine and subarctic deciduous scrub	1	
S42	Dry heath	3	
<b>U2a</b>	<b>Inland habitats with no or little soil and mostly with sparse vegetation</b>	<b>1</b>	
U2a	Siliceous high-mountain scree	1	
<b>V</b>	<b>Vegetated man-made habitats</b>	<b>5</b>	
V37	Annual anthropogenic herbaceous vegetation	5	

of specific terms and toponyms which cannot easily be translated, the descriptive spatial information is only available in the original language (German). Most variables are of descriptive nature, which means that they neither adhere to a standardised scale nor to standardised methods.

## 8 | HISTORIC GRASSLANDS – DIVERSITY AND MANAGEMENT

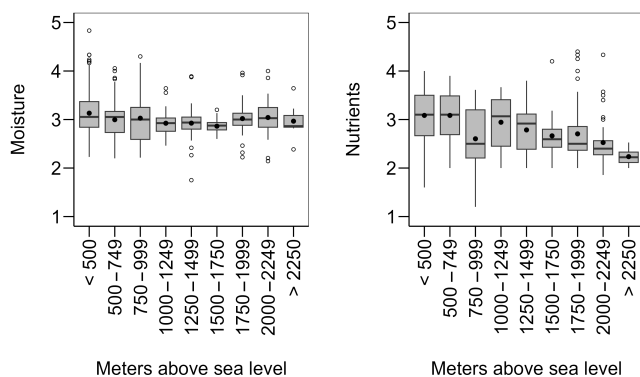
The species richness in the 0.09-m<sup>2</sup> plots ranged from 2 to 47, with an average of 19.7 species (Appendix S2). The maximum of 47

vascular plant species in a 0.09-m<sup>2</sup> plot stems from a “semi-dry perennial calcareous grassland (meadow steppe)” at 1480 m a.s.l. in the village of Says in the canton of Grisons. This grassland, which was mown once a year at that time, has a southern aspect and an inclination of 35°. This richness is higher than any published record on that spatial scale in any plant community worldwide. It is higher than the world record reported by Wilson et al. (2012) (43 species in 0.1 m<sup>2</sup> of a meso-xeric grassland in Romania, even though this plot was sampled with the shoot presence method and has an 11% larger area), which was itself also not surpassed by more recent compilations (Chytrý et al., 2015; Dengler et al., 2020). Apart from this plot, five more plots reach or exceed the mark of 43, amongst them two plots

in the lowlands located at around 500 and 600 m a.s.l. This indicates a recurring pattern of high species richness in this data set.

However, not only the maximum, but also the mean small-scale richness was exceptionally high, as the present-day mean across all available plots of 0.09/0.1 m<sup>2</sup> in the GrassPlot database (<https://edgg.org/databases/GrasslandDiversityExplorer>; see Biurrun et al., 2021) is only 11.8, or 9.6 if restricting the search to Switzerland and its neighbouring countries ( $n=3735$  and 775, respectively). When split into the main vegetation types, the mean richness values in 0.09 m<sup>2</sup> were much higher than present-day means, too (Appendix S5).

In the 1-m<sup>2</sup> plots, the species richness ranged from 8 to 36, with an average of 21.1 species (Appendix S4). Here the means are higher than in carefully collected plots of the same size from GrassPlot (<https://edgg.org/databases/GrasslandDiversityExplorer>; see Biurrun et al., 2021), for all plots and for mesic grasslands, too,

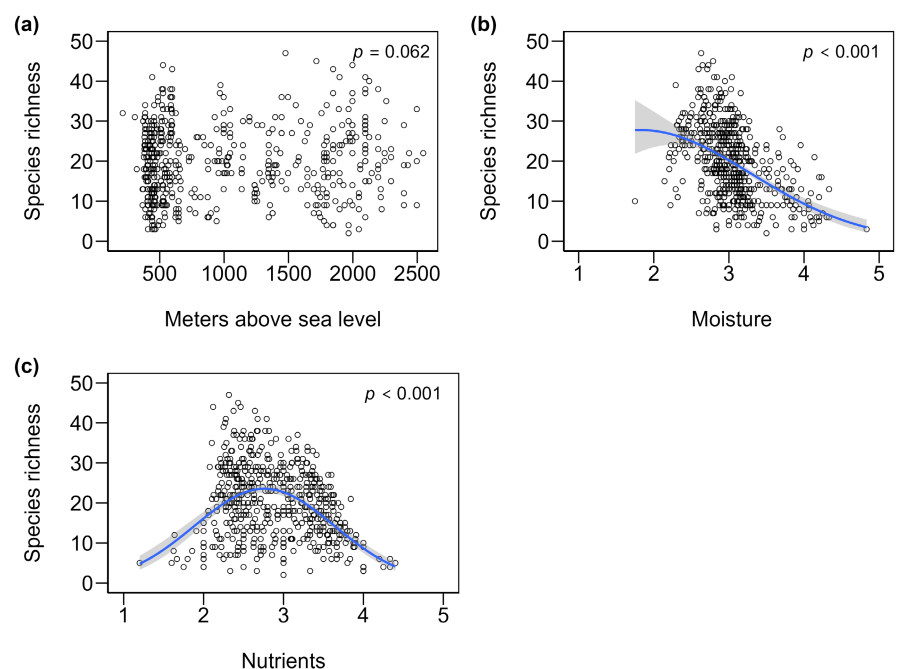


**FIGURE 5** Distribution of unweighted mean indicator values according to Landolt et al. (2010) for moisture (1 = very dry to 5 = flooded) and nutrients (1 = very infertile to 5 = very fertile and over-rich) in the 0.09-m<sup>2</sup> plots of the Historic Square Foot Dataset ( $n=580$ ) along the elevational gradient.

but the difference is not as pronounced as for the smaller plots (Appendix S5). The reason for the less outstanding richness in the larger plots is probably rooted in the fact that they mostly stem from intensively used mesic grasslands at around 400 to 500 m a.s.l. (see management data in Appendix S3). In addition, the sampling method might have been slightly less comprehensive, as the biomass was cut in the field and not in the laboratory.

Species richness showed a small and insignificant increase with elevation ( $p=0.062$ ) (Figure 6a). By contrast, species richness showed a unimodal relationship with the two niche axes determined by the mean indicator values for moisture ( $p<0.001$ , pseudo- $R^2=0.242$ ) and nutrients ( $p<0.001$ , pseudo- $R^2=0.213$ ). With increasing moisture, predicted richness decreased, whereas for nutrients, predicted richness was highest for intermediate nutrient availability (Figure 6b,c). Not having a significant change in species richness along an elevational gradient is quite unexpected from a present-day perspective. Nowadays one typically finds, at least in humid mountains, a mid-elevational peak of plot-level species richness (Descombes et al., 2017; Fontana et al., 2020), that is, a pronounced increase from the lowlands to the subalpine belt, followed by a decrease towards the nival belt. For example, in representative 10-m<sup>2</sup> plots of grasslands from the actual national biodiversity monitoring of Switzerland, the mean species richness doubles from the colline to the subalpine belt (Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2009; Dengler et al., unpublished).

The six most frequent taxa in the 0.09-m<sup>2</sup> plots were *Festuca rubra* aggr., *Anthoxanthum odoratum* aggr., *Trifolium repens*, *Dactylis glomerata*, *Trifolium pratense* and *Leucanthemum vulgare* aggr., while in the 1-m<sup>2</sup> plots these were *Dactylis glomerata*, *Poa trivialis*, *Ranunculus acris*, *Poa pratensis*, *Taraxacum* sp. and *Festuca pratensis* (Appendix S6), marking on average more nutrient-rich sites. Overall, the species frequencies in the 0.09-m<sup>2</sup> plots demonstrate that the



**FIGURE 6** Vascular plant species richness in 0.09-m<sup>2</sup> plots of the Historic Square Foot Dataset ( $n=580$ ) along three main environmental gradients: (a) elevation, (b) mean indicator values according to Landolt et al. (2010) for moisture (1 = very dry to 5 = flooded) and (c) mean indicator values for nutrients (1 = nutrient-poor to 5 = nutrient-rich and over-rich). Blue lines indicate significant relationships in quasi-Poisson GLMs of species richness vs the respective variable.

TABLE 2 Header data that are provided with the two data sets in Appendices S1 and S3. The column “Data source” provides information on the origin of the variable, with “Original data” indicating that a variable was part of the original recording protocol and “Square Foot Project 2021” indicating that it was newly derived during data editing.

Variable	Description	Data source
ID_2021	Id of the plot	Square Foot Project 2021
Center_x_coordinate	x coordinate of the center of the circle around the polygon (WGS 84)	Square Foot Project 2021
Center_y_coordinate	y coordinate of the center of the circle around the polygon (WGS 84)	Square Foot Project 2021
Precision	Radius of the circle around the polygons, proxy for imprecision of localisation [m]	Square Foot Project 2021
ID_pa	Id of the potential area of the plot	Square Foot Project 2021
All_ID_same_pa	All plots that share the same potential area	Square Foot Project 2021
Date	Date of record (tt/mm/yyyy)	Original data
Year	Year of the record	Original data
Canton	Canton of the record	Square Foot Project 2021
Municipality	Municipality of the record	Original data
Toponym_TA	Toponym of the record	Original data
Additional_location	Additional site description of the plot location	Original data
Elevation_original	Elevation of the plot [m a. s. l.] (Swiss reference level LN02–3.26 m)	Original data
Aspect	Cardinal direction, letters	Original data
Inclination	Inclination, degrees or descriptive	Original data
Soil	Descriptive, mainly texture	Original data
Content_of_Ca	From 0 = not calcareous to 3 = very calcareous	Original data
Bedrock	Bedrock	Original data
Water_balance	Humidity level, descriptive	Original data
Light_cond	Light condition, descriptive	Original data
Land_use	Land use of the plot	Original data
Nr_cuts	Number of cuts per year, where 0.5 is every second year	Original data
Nr_cuts_before_record	Number of cuts in the season before the record	Original data
Grazing animals	Species of the grazing animal	Original data
Fertil_y_n	Fertilised or not, derived from description	Original data
Fertil_freq	Frequency of fertilisation, descriptive	Original data
Fertil_type	Type of fertiliser	Original data
Fertil_treatment	Details of fertilisation treatment	Original data
Total_dry_matter	Sum of the harvested biomass on 0.09 m <sup>2</sup> resp. 1 m <sup>2</sup> [g]	Original data
Species_richness	Total number of species counted on the plot	Square Foot Project 2021
Mean_ecological_indicator_value_nutrient	Mean ecological indicator value for nutrients (Landolt et al., 2010), 1 = very infertile to 5 = very fertile and overrich	Square Foot Project 2021
Mean_ecological_indicator_value_moisture	Mean ecological indicator value for moisture (Landolt et al., 2010), 1 = very dry to 5 = flooded	Square Foot Project 2021
EUNIS_habitat_code	Chytrý et al. (2020)	Square Foot Project 2021
EUNIS_habitat_name	Chytrý et al. (2020)	Square Foot Project 2021
Type_of_classification	1 = automatically classified, 2 = classified according to Section 2 of the EUNIS-ESy, 3 = classified with expert knowledge	Square Foot Project 2021
GrassPlot_vegetation_type	Biurrun et al. (2019)	Square Foot Project 2021
Vegetation_class	Mucina et al. (2016)	Square Foot Project 2021
Vegetation_order	Mucina et al. (2016)	Square Foot Project 2021





studies have been conducted in all kinds of grassland, with a strong focus on cultivated mesic grassland. In the top-ten list we do not find any species of nutrient-poor grassland (see Appendix S6).

The context information on the recording sheets gives useful indications on the land use at that time. Unfortunately, this information has not been recorded for all plots and not with a standardised method; thus, we cannot differentiate between empty entries and null. For each vegetation record, the context information given in the header has been digitised and is available in the database (Appendices S1 and S3). The following summary only refers to the recordings where the corresponding information is available. In the sample, meadows are represented twice as often as pastures and litter meadows. Half of the entries for the 0.09-m<sup>2</sup> plots indicate a mowing frequency of one or two times per year and only a few a higher frequency, whereas nearly half of the 1-m<sup>2</sup> plots have been mown four or five times, which corresponds to the mowing frequency of many meadows in Swiss lowlands nowadays. Most of the 1-m<sup>2</sup> plots were fertilised compared to around half of the 0.09-m<sup>2</sup> plots. The limited amount of information on type of fertilisation suggests that manure was more frequently used than slurry. With Thomas slack (phosphate-rich side product of steel production) and superphosphate, the application of the emerging artificial fertilisers is documented on few plots only.

## 9 | CONCLUSIONS AND PERSPECTIVES

To our knowledge, the Historic Square Foot Dataset is the largest standardised vegetation data set in grasslands from the late 19th to the early 20th century, particularly when considering that the oldest known vegetation plot worldwide dates to 1864 (Dengler et al., 2011). The exceptional mean and maximum richness found at small scales in representative grasslands around 120 years ago emphasises the ensuing loss of diversity. Our data set provides unique insights into how grasslands were composed in Central Europe at that time and allows diverse options for research.

The originators of the data set are aware of the weaknesses of their method, namely measuring the parameters only at one point of time and, due to the small plot size, not accounting for the heterogeneity of the stand (Stebler & Schröter, 1887a). The great sampling and analysing effort involved in collecting these data cannot compensate for these limitations. Spatial-statistical thinking in ecology evolved about one century later, which is why the surveyors did not think of applying a random or systematic sampling. This puts some impediments on possible analyses. Yet, the surveyors covered the major geographic and ecological gradients of grasslands in Switzerland sufficiently well to allow general inferences.

In the ongoing [Square Foot Project](#), the historic plots are re-sampled with the modern approaches of resurvey studies (Ross et al., 2010; Kapfer et al., 2017). We expect to gain major insights into the changes in species diversity and composition which occurred over approximately 120 years across a major habitat type in an entire country, and to attribute these changes to potential drivers.

## AUTHOR CONTRIBUTIONS

Andreas Grünig discovered the hand-written record sheets at Agroscope. Together with Nina Richner and Serge Buholzer, he digitised the records. Susanne Riedel and Stefan Widmer cleaned and prepared the vegetation data, and together with Manuel Babbi constructed the polygons of the PAs. Jürgen Dengler and Felix Herzog planned the overall project of which this paper is part. Susanne Riedel conceived the idea and led the writing of the manuscript, with significant input by Jürgen Dengler, while Stefan Widmer conducted the analyses and produced the graphs. All authors revised the manuscript and approved it for publication.

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## DATA AVAILABILITY STATEMENT

The described data are provided in the online Appendices S1–S4. Additionally, they are available from the GrassPlot database (Dengler et al., 2018).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1** Header data of the square-foot plots

**Appendix S2** Species composition data of the square-foot plots

**Appendix S3** Header data of the square-meter plots

**Appendix S4** Species composition data of the square-meter plots

**Appendix S5** Mean and maximum richness values compared with contemporary data from GrassPlot

**Appendix S6** Species frequencies of the square-foot and square-meter plots

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