

Vegetation change in meso-xeric grasslands of the Swiss Jura Mts. over 40 years

Vegetationsveränderungen in Kalkhalbtrockenrasen des Schweizer Juras über 40 Jahre

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Abstract

Meso-xeric grasslands have declined sharply in Central Europe during the last century. These species-rich habitats are threatened by intensification or abandonment of agricultural use, eutrophication, climate change and landscape fragmentation. However, different studies in various regions of Central Europe are inconsistent in their findings about degree and direction of changes. We thus resurveyed the historical vegetation plots of the alliance *Mesobromion* in the Swiss Jura Mts. In 2020, we re-sampled 28 quasi-permanent vegetation plots originally recorded in 1980 to quantify potential vegetation change. Frequency of individual species, species diversity, 11 ecological indicator values and four functional traits, as well as the presence of diagnostic species of phytosociological alliances, were analysed. Further, a habitat classification and detrended correspondence analysis (DCA) were also performed. Species richness, indicator values for light availability and temperature, seed dispersal by animals and seed persistence had significantly decreased by 2020. Conversely, ecological indicator values for nutrient availability and soil moisture as well as community-weighted means for seed mass and canopy height had significantly increased. There were significantly fewer ruderal species, stress-tolerators, therophytes and herbaceous chamaephytes in 2020. In contrast, highly competitive species and hemicryptophytes had increased. Together, these findings indicate an increase in productivity over time. There were fewer specialized species in 2020 than in 1980, indicating a homogenization of the vegetation and a shift towards nutrient-rich pastures and meadows. The shift towards a later successional stage might indicate reduced grazing disturbance. Most of these sites are currently not included in an agri-environmental scheme. Partial differences of our findings from those reported elsewhere in Central Europe highlight the importance of regionally adapted conservation strategies in order to stop biodiversity loss in meso-xeric grasslands.

Keywords: *Arrhenatherion elatioris*, biodiversity loss, ecological indicator value, eutrophication, *Mesobromion*, land-use change, quasi-permanent plot, resurvey, Swiss Jura Mts., vegetation change

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Meso-xeric grasslands are meadows and pastures on semi-dry, nutrient-poor soils, usually over calcareous bedrock (DELARZE et al. 2015, DENGLER & SCHAMINÉE 2016). Within Central Europe, they represent a successional stage that can only be maintained by regular and moderately intense cyclic disturbance. In this intermediate state, species diversity and interspecific competition reach their maximum (PETRAITIS et al. 1989; SCHEINER & WILLIG 2011). Meso-xeric meadows and pastures are the habitats with the greatest small-grain plant species richness in Central Europe and globally (ZOLLER 1954, DENGLER 2012, DENGLER et al. 2020).

During the past decades meso-xeric pastures and meadows have experienced a continuous decline (SILVA et al. 2008, DENGLER & TISCHEW 2018), mostly due to the double threats of intensification and abandonment (DENGLER & TISCHEW 2018, DENGLER et al. 2020, BOCH et al. 2021a). It is assumed that since 1900 95% of the dry grasslands in the wider sense (i.e. xeric and meso-xeric types) have disappeared in Switzerland (LCHAT et al. 2010). Although landscape fragmentation and the structural impoverishment of cultivated landscapes have a significant impact on biodiversity (FERANEC et al. 2016), eutrophication from agricultural fertilizers and atmospheric nitrogen deposition seem to be primarily responsible for biodiversity and habitat loss as well as floristic changes (ROTH et al. 2013, DENGLER et al. 2014, HETTELINGH et al. 2017, DENGLER et al. 2020, BOCH et al. 2021b). Additionally, the loss of faunistic and floristic diversity might be accelerated by the effects of global warming (SCHUCH et al. 2012, FISCHER et al. 2020, SCHILS et al. 2020). In addition to the decline in biodiversity, a change in the floristic composition of meso-xeric grasslands is also occurring. The trend observed on calcareous sites shows that specialists are most threatened and are increasingly replaced by generalists (FISCHER & STÖCKLIN 1997, STÖCKLIN et al. 1999, 2000, BOCH et al. 2019a).

While patterns and drivers of the decline of meso-xeric grasslands and their biodiversity in Central Europe are well known, vegetation changes at local scales may still differ from the general trend because they depend first on local climatic, geological and agricultural conditions (BRUELHEIDE & JANDT 2007, SOCHER et al. 2012, DENGLER et al. 2014, DENGLER & TISCHEW 2018, KUMMLI et al. 2021). In the Swiss Jura Mts., only few resurvey studies have been conducted on the vegetation of meso-xeric grasslands. ZOLLER et al. (1986) showed in a resurvey study (1986 vs. 1950) that many rare and endangered species, such as orchids, had declined. To this end, they noted a homogenization of communities within the vegetation of meso-xeric grasslands. Later, STÖCKLIN et al. (2000) found that specialists are especially endangered. However, no decrease in species richness was observed in these studies. However, we are not aware of more recent studies of vegetation change in meso-xeric grasslands in the Swiss Jura. For this purpose, determining vegetation change at the local level is essential for implementing an effective conservation strategy (PALPURINA 2017, BOCH et al. 2020).

Resurveys of historical vegetation plots are a valuable tool for understanding the long-term dynamics of plant communities (HÉDL et al. 2017). Relocation inaccuracy, differences between observers and inconsistent recording times during the year are the three main challenges for resurveys (KAPFER et al. 2017). However, using ecological indicator values for data analysis is largely robust with respect to relocation inaccuracy (BOCH et al. 2019b).

In this study, we resurveyed 40-year-old vegetation plots of meso-xeric grasslands, originally recorded in the year 1980 (HEDINGER 1983). In 1980, these grasslands, mainly belonging to the alliance *Mesobromion*, were extensively grazed by sheep. The objective of this

study was to quantify possible changes in the diversity and composition of vascular plants over this time period. For this purpose, biodiversity indices, community-weighted means of ecological indicator values and functional traits as well as sociological affinities of plots were compared between the two time periods, and a joint ordination of the old and new plots was performed.

2. Study area

All investigated sites were located in the north-western part of Switzerland, in the cantons of Aargau, Basel-Landschaft, Jura and Solothurn (Fig. 1). The study area covers an east-west extension of 67.5 km and a north-south extension of 13.5 km. The area belongs to the Folded Jura and Jura Massif and is dominated by sedimentary rocks such as limestone, marl and sandstone (GNÄGI & LABHART 2014). The elevation of the sites ranges from 420 m a.s.l. to 800 m a.s.l., all of them belonging to the colline belt.

The Atlantic climate of the region is characterized by humid air from the northwest and a complementary dry air supply from the east. For Rünenberg at 611 m a.s.l. in the centre of the study area, the mean annual temperature 1981–2010 was 9.0 °C and the mean annual

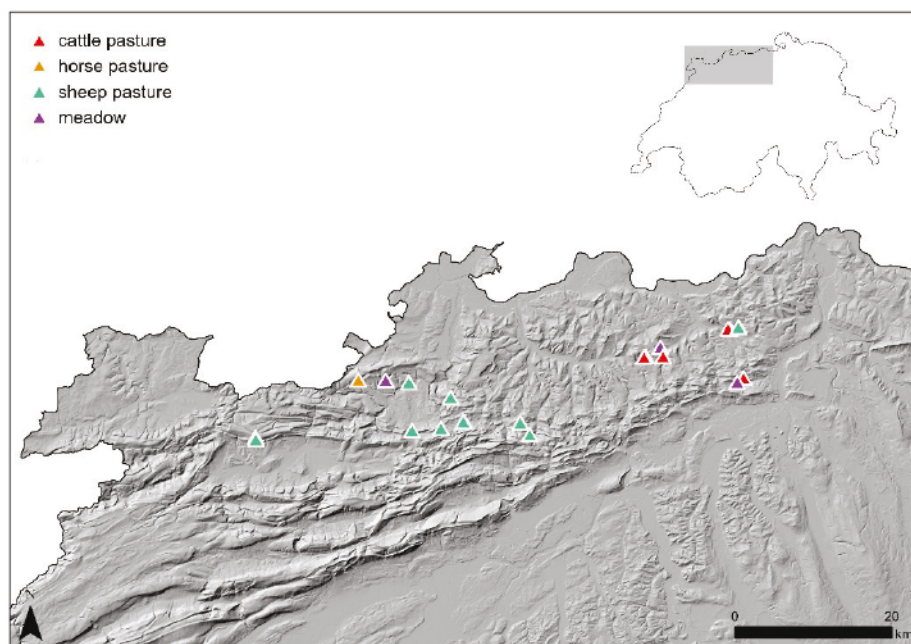


Fig. 1. Location of the study sites in the Jura Mts. in Northwest Switzerland. The 19 sites (with 1–3 plots each) are color-coded according to their current land use (copyright geodata: swisstopo DV084370). Note that some sites are so close together that their symbols are overlapping.

Abb. 1. Lage der Untersuchungsflächen im Schweizer Jura. Die 19 Trockenrasengebiete (mit jeweils 1–3 Aufnahmeflächen) sind entsprechend ihrer aktuellen Landnutzung eingefärbt (Copyright geodata: swisstopo DV084370). Man beachte, dass einige Trockenrasengebiete so nahe beisamen liegen, dass ihre Symbole sich überlappen.

precipitation 1009 mm (METEOSCHWEIZ 2021). From 1961 to 2020 annual precipitation slightly increased, although this was only observed in winter (METEOSCHWEIZ 2020). The average local temperature has risen by about one and a half degrees between 1964 and 2020. The effects of climate change are noticeable throughout the year, with milder seasonal values in winter and heat waves and longer periods of sunshine in summer (METEOSCHWEIZ 2020).

3. Methods

3.1 Field sampling

The original study included a total of 68 plots, each sampled with three visits throughout the season in 1980 (HEDINGER 1983). At that time all of them were used as sheep pastures. In 2020, a significant fraction of the original sites had either a different agricultural use than in the past (cereal crops, orchards, very intensive management with extremely low vegetation cover) or a non-agricultural use (forest, urban area). From those that were still used as grasslands, we selected 28 plots for resurvey during summer 2020 (June – July) (for two examples, see Fig. 2). These plots were distributed in 19 grasslands, each with one to three plots, depending on the size, with a typical distance between the plots of 100 m (minimum: 36 m). The land uses now, apart from the still prevailing sheep pastures, also included horse and cattle pastures as well as hay meadows (Fig. 1). The plots were relocated using the geographical coordinates from HEDINGER (1983), who provided them with 10 m precision. Given the fine-structured land use and topography, we assume that the relocation error was on average around 10 m, but 20 m at most.

The size of the original plots ranged from 48 to 400 m², with 100 m² prevailing (Supplement E1), while the plot shape was not recorded. In the resurvey, we used the same plot size as in the corresponding historical plot and square shape throughout. All plots were oriented in cardinal direction and permanently marked with a magnet buried in the SE corner to allow future resurveys without relocation error.

In the original survey, HEDINGER (1983) used a modified version of the cover-abundances scale of BRAUN-BLANQUET (1964; see Supplement E2), while in 2020 we estimated the cover directly in percent, disregarding abundance. In both surveys, all vascular plant species were recorded. To enable a comparison of the data between 1980 and 2020, the cover-abundance categories were replaced by the geometric mean of the upper and lower limits of the respective percentage cover range (Supplement E2).

In 2020, the species were identified with the current Swiss floras (BINZ & HEITZ 1990, EGGENBERG & MÖHL 2013, LAUBER et al. 2018) and named according to the Swiss checklist (JUILLERAT et al. 2017). To allow a statistical comparison of the two studies, the nomenclature of the old species data was adapted to the current nomenclature and taxa aggregated on a higher taxonomic level if needed. “*Festuca ovina* aggr. s.l.” stands for *Festuca ovina* aggr. + *Festuca valesiaca* aggr. sensu JUILLERAT et al. (2017).

The header data of both surveys are provided in Supplement E3, the species cover data in Supplement E4. The vegetation-plot data will be provided to the emerging Swiss National Vegetation Database (J. Dengler et al. in prep.) and the ReSurveyEurope initiative (F. Essl et al. in prep., see <http://euroveg.org/eva-database-re-survey-europe>).

3.2 Data analyses

The Shannon index, Shannon evenness and species richness were used to assess biodiversity. The threatened species (including the category NT, i.e. near-threatened species) were determined according to the national Red List (BORNAND et al. 2016). A large set of mean ecological indicator values as well as CSR strategy types from LANDOLT et al. (2010) were used for the data analysis (Table 1). Using the program VEGEDAZ (KÜCHLER 2019), we calculated them in two variants, as unweighted means and



Fig. 2. Two examples of the resurveyed grasslands. **a)** site ID 43 in Wittnau (AG) was used as meadow in 2020, was rather species poor and now can be assigned to the *Arrhenatherion*. **b)** Lower photo: site ID 21 in Himmelried (BL) was used as a sheep pasture in 2020, was moderately species rich and still can be considered as a *Mesobromion* (Photos: J. Dengler, 08.07.2020 und 22.07.2020).

Abb. 2. Zwei Beispiele der untersuchten Grasländer. **a)** Die Aufnahme­fläche Nr. 43 in Wittnau (AG) wurde 2020 als Wiese genutzt, war eher artenarm und kann aktuell dem *Arrhenatherion* zugeordnet werden. **b)** Die Aufnahme­fläche Nr. 21 in Himmelried (BL) wurde 2020 als Schafweide genutzt, war mittelartenreich und kann auch heute noch dem *Mesobromion* zugeordnet werden (Fotos: J. Dengler, 08.07.2020 und 22.07.2020).

as cover-weighted means. We also compared the community-weighted means (CWMs) of the three “standard” functional traits proposed by WESTOBY (1998) for assessing the strategy type of species (LHS traits: specific leaf area, seed mass and crown height), using the \log^{10} -transformed mean trait values from the LEDA trait database (KLEYER et al. 2008). Further, we used the supervised classification implemented in VEGEDAZ (KÜCHLER 2019) to quantify to which degree each plot is matching

Table 1. Ecological indicator values, CSR strategies and plant functional traits from LANDOLT et al. (2010) used in this analysis.

Tabelle 1. Ökologische Zeigerwerte, CSR-Strategietypen und funktionelle Pflanzenmerkmale aus LANDOLT et al. (2010), die in dieser Untersuchung genutzt wurden.

Category	Parameter	Ordinal range or nominal categories
Indicator values	Temperature	1 to 5
	Continentality	1 to 5
	Light	1 to 5
	Moisture	1 to 5
	Reaction	1 to 5
	Nutrients	1 to 5
	Humus	1 to 5
	Mowing tolerance	1 to 5
CSR-strategies	Competitive strategy	0 to 3
	Ruderal strategy	0 to 3
	Stress tolerant strategy	0 to 3
Functional traits	Seed longevity	1 to 5
	Dispersal of diaspores	Anemochory, zoochory
	Life form	Phanerophyte, nanophanerophyte, woody chamaephyte, herbaceous chamaephyte, nanophanerophyte-hemicryptophyte, chamaephyte-hemicryptophyteperennial, hemicryptophyte, geophyte, therophyte, climber, hemiparasite

different types of the Swiss habitat typology (DELARZE et al. 2015). This supervised classification approach uses weighting factors for the different categories of diagnostic species in DELARZE et al. (2015) as proposed by S. Eggenberg (Info Flora, Bern; see DENGLER et al. 2019). We then determined the scores for the following habitat types, approximately corresponding to the phytosociological alliances *Mesobromion*, *Arrhenatherion*, *Cynosurion*, *Trifolion medii*, *Xerobromion*, *Polygono-Trisetion*, *Stipo-Poion*, *Diplachnion*, *Cirsio-Brachypodion*, *Poion alpinae* and *Geranion sanguinei* and standardised them so that they sum up to 1.

To test for differences in metric parameters between the two survey periods, we used paired Welch *t*-tests (default in R). To test whether individual species had become more or less frequent over the 40 years, we applied a sign test (binomial test). All statistical analyses were carried out with the program R (R CORE TEAM 2021). We assumed a significance level of $\alpha = 0.05$.

To visualise the vegetation change over the 40 years and the potentially underlying factors, we conducted a detrended correspondence analysis (DCA). The mean indicator values for temperature, continentality, light, soil reaction, nutrients, moisture, stress and competition, the CWMs of specific leaf area, seed mass and seed persistence, as well as the relative cover of hemicryptophytes, herbaceous chamaephytes and therophytes were correlated post-hoc with the axes of the ordination graph.

4. Results

4.1 Frequency changes of individual species

A total of 20 species found in 1980 (12.3%) were significantly less frequent in 2020 (Table 2). Conversely, eight of the 175 species found in 2020 (4.6%) had become more frequent compared to 1980 (Table 2). The strongest decrease (from 82% to 14% frequency) was found for *Linum catharticum*, the strongest increase (from 25% to 86%) for *Arrhenatherum elatius* (Table 2).

Table 2. List of species that became significantly less or more frequent in the 28 quasi-permanent plots over the study period.

Tabelle 2. Liste der Arten, die in den 28 quasi-permanenten Aufnahme­flächen während der Untersuchungsperiode signifi­cant seltener oder häufiger wurden.

Taxon	Occurrences in 1980	Occurrences in 2020	<i>p</i> -value
Decrease			
<i>Linum catharticum</i>	23	4	<0.001
<i>Bellis perennis</i>	16	2	<0.001
<i>Veronica arvensis</i>	11	0	0.001
<i>Myosotis arvensis</i>	10	0	0.002
<i>Poa trivialis</i>	10	0	0.002
<i>Sedum sexangulare</i>	12	1	0.003
<i>Carlina acaulis</i>	9	0	0.004
<i>Vicia sativa</i>	10	1	0.004
<i>Campanula rotundifolia</i> aggr.	13	3	0.006
<i>Leontodon hispidus</i>	19	9	0.006
<i>Prunus spinose</i>	8	0	0.008
<i>Teucrium chamaedrys</i>	10	2	0.008
<i>Festuca ovina</i> aggr. s.l.	21	10	0.013
<i>Cirsium acaule</i>	9	2	0.016
<i>Ajuga reptans</i>	9	1	0.021
<i>Cerastium fontanum</i>	20	11	0.022
<i>Agrostis capillaris</i>	6	0	0.031
<i>Bromus hordeaceus</i>	6	0	0.031
<i>Potentilla verna</i>	13	4	0.035
<i>Helictotrichon pubescens</i>	8	1	0.039
Increase			
<i>Potentilla reptans</i>	3	19	<0.001
<i>Arrhenatherum elatius</i>	7	24	<0.001
<i>Festuca arundinacea</i>	0	12	<0.001
<i>Centaurea jacea</i> subsp. <i>jacea</i>	6	20	0.001
<i>Phleum pratense</i> aggr.	0	7	0.016
<i>Festuca rubra</i> aggr.	9	19	0.021
<i>Rosa</i> sp.	2	10	0.021
<i>Carex flacca</i>	9	18	0.022

Threatened and near-threatened species accounted only for a small proportion of the total floristic composition (2 of 169 in 1980; 1 of 175 in 2020). The vulnerable *Gentiana cruciata*, which previously occurred in four of the 28 plots, completely vanished (n.s.). Likewise, the near-threatened *Anacamptis pyramidalis* with formerly two occurrences was not found at all in the resurvey (n.s.). By contrast, the vulnerable *Cynoglossum officinale* newly occurred in one plot (n.s.).

4.2 Biodiversity

Mean species richness per plot (of mostly 100 m²) decreased significantly from 47 in 1980 to 42 in 2020 ($p = 0.022$). By contrast, the Shannon index ($p = 0.257$) and the Shannon evenness ($p = 0.968$) did not change significantly during this 40-year period.

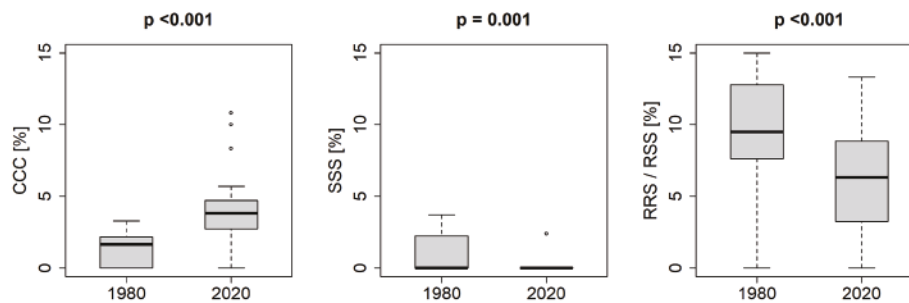


Fig. 3. Three strategy types that showed significant changes in relative richness between 1980 and 2020. CCC = pure competitors, SSS = pure stress-tolerators, RRS/RSS = ruderal stress-tolerators.

Abb. 3. Drei Strategietypen, deren relativer Artenreichtum sich zwischen 1980 und 2020 signifikant verändert hat. CCC = reine Konkurrenzstrategen, SSS = reine Stressstrategen, RRS/RSS = ruderale Stressstrategen.

4.3 Ecological indicator values and CSR strategies

Over the 40 years, species adapted to nutrient-rich sites had increased, both in number and in cover (Supplement E5). In parallel, the mean ecological indicator values for continentality, light and reaction decreased (Supplement E5). Species with highly competitive ability were more numerous and covered a larger area in 2020 than in 1980 (Supplement E5). Conversely, ruderal species and stress-tolerant species were more numerous in 1980, while their percentage cover values remained similar (Supplement E5). When analysing the individual CSR strategy types separately, pure competitive strategists (CCC) had increased, while both stress-tolerant ruderals (RRS/RSS) and pure stress-tolerators (SSS) had decreased (Fig. 3, Supplement E5). The intermediate CSR-strategy prevailed both in 1980 (50.1% cover) and 2020 (45.7%), with no significant change.

4.4 Life forms and functional traits

Hemicryptophytes covered a larger area in 2020 than in 1980. Conversely, the cover of therophytes and chamaephytes was significantly smaller in 2020 (Supplement E5 and Fig. 4). Considering the coverage of each species, the LHS strategy analysis (Supplement E5 and Fig. 5) showed canopy height and seed mass were significantly greater in 2020. On average, seed longevity of the communities was higher in 1980 than in 2020, when based on presence-absence, but not when cover-weighted (Supplement E5). The analysis of seed dispersal methods showed that zoochorous species were more numerous in 2020, but their cumulative cover remained unchanged (Supplement E5).

4.5 Sociological affinity and ordination

The relative score of *Mesobromion* species had decreased significantly ($p = 0.035$) from 1980 to 2020, while that of *Arrhenatherion* species had increased ($p = 0.005$). The ordination (Fig. 6) demonstrates a clear separation of the historic plots in the lower right corner from the present plots in the upper left corner. This trajectory coincides more or less with

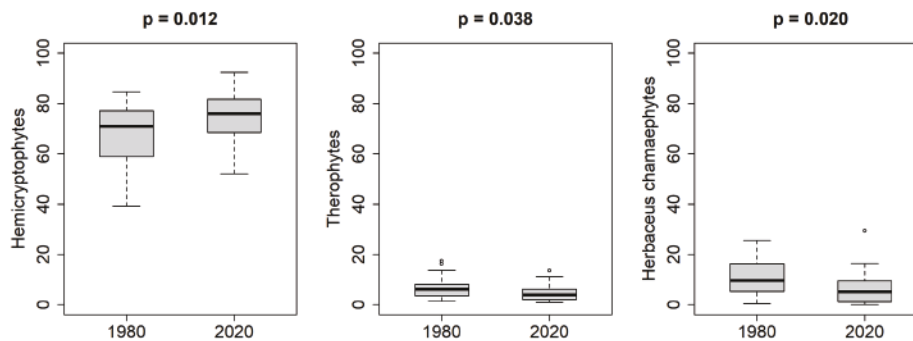


Fig. 4. Three life forms that showed significant changes in relative cover between 1980 and 2020.

Abb. 4. Drei Lebensformen, deren relative Deckung sich zwischen 1980 und 2020 signifikant verändert hat.

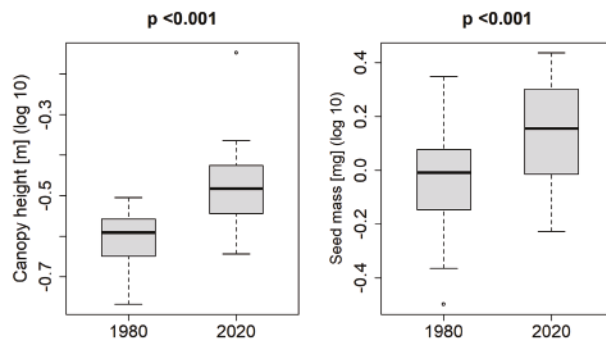


Fig. 5. Community-weighted means of functional traits that significantly changed between 1980 and 2020.

Abb. 5. Deckungsgewichtete Mittelwerte funktioneller Merkmale, die sich zwischen 1980 und 2020 signifikant geändert haben.

higher SLA, higher seed mass and more pronounced competition strategy, but fewer therophytes and herbaceous chamaephytes, while other variables were more or less orthogonal to the mean trajectory.

5. Discussion

5.1 Biodiversity

In Swiss meso-xeric grasslands, the average vascular plant species richness is 58 in 100 m² (GrassPlot Diversity Explorer v. 2.10; <https://edgg.org/databases/GrasslandDiversityExplorer>; BIURRUN et al. 2021), which is about the same average number of species for this grassland type in Western Europe (DENGLER et al. 2020). In this study, as well as in the initial study by HEDINGER (1983), below-average species richness was found (47 species in 1980 vs. 42 in 2020). This could mean that the study sites were already floristically impoverished in 1980 or, more likely, that they are for biogeographic reasons not as rich as in other parts of Europe.

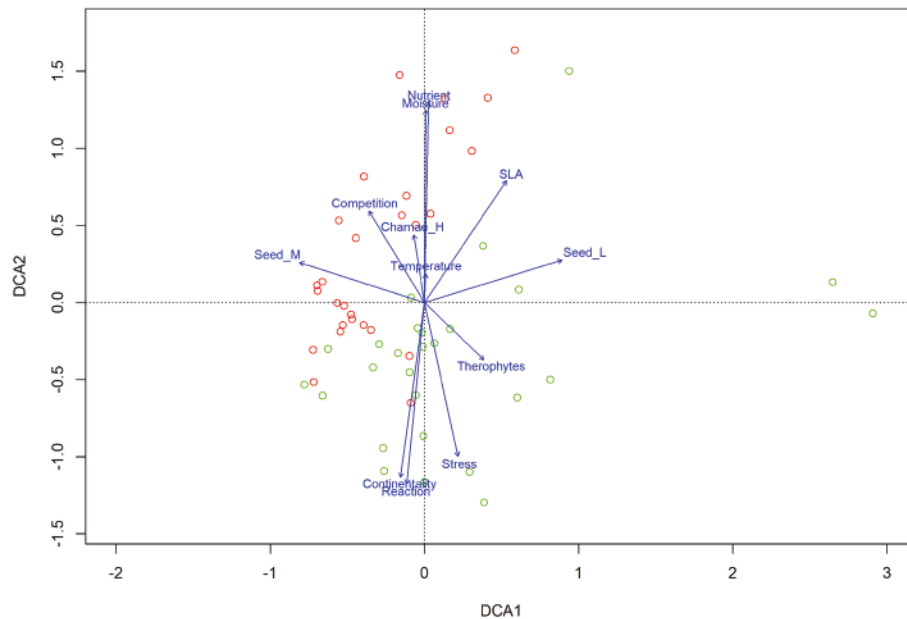


Fig. 6. Joint detrended correspondence analysis (DCA) of the old and new plots. Green circles = 1980, red circles = 2020. Significantly correlated variables were fitted *post hoc* to the two axes. Chamae_H = herbaceous chamaephytes, Seed_M = seed mass, Seed_L = seed longevity.

Abb. 6. Gemeinsame trendbereinigte Korrespondenzanalyse (DCA) der alten und neuen Vegetationsaufnahmen. Grüne Kreise = 1980, rote Kreise = 2020. Signifikant Variablen wurden nachträglich mit den zwei Achsen korreliert. Chamae_H = krautige Chamaephyten, Seed_M = Samenmasse, Seed_L = Langlebigkeit der Samen.

A significant decrease in the number of species was observed in 2020. However, considering the degree of coverage of the individual species by means of the Shannon index and Shannon evenness, the biodiversity remained unchanged between 1980 and 2020. It follows that the more dominant plants did not experience significant changes between 1980 and 2020, but that the species with lower presence decreased or disappeared in 2020. Those results are similar to the trend observed in a meta-analysis of resurvey vegetation studies in the UK and Germany (DIEKMANN et al. 2019), which highlighted a decline in species richness in semi-natural grasslands caused by a combination of poor management, increased fertilization and nitrogen deposition.

5.2 Ecological indicator values

The vegetation composition of 2020 indicated more nutrient-rich soils than in 1980. Finding indications of eutrophication in semi-dry grasslands, is in line with what ZOLLER et al. (1986) reported for the same region and JANDT et al. (2011) for Germany. By contrast, KUMMLI et al. (2021) did not find any sign of eutrophication in mesic grasslands of the city of Zurich. This difference, however, might be attributable to the urban situation and a land-use change from pasture to meadow that had occurred there. During the fieldwork, it could be observed that most of the sites were surrounded by intensively cultivated land. It is therefore plausible that nutrient input from surface runoff occurs if the intensive areas are located

above the study sites. The fact that the soil reaction value had decreased significantly can be seen as an indirect effect of soil ammonium ions enrichment through manure application and atmospheric deposition, as the oxidation of NH_4^+ to NO_3^- releases protons, leading to soil acidification. Studies have found that the indirect role of soil acidification has a greater influence on the composition of the herb layer than nutrient input *per se* (BERG et al. 2011). The origin of the nutrient input cannot be clearly defined. In Switzerland, however, an average of 24 kg of nitrogen per hectare of land and year is deposited (AUGUSTIN & ACHERMANN 2012, SEITLER et al. 2016). Across Switzerland, about 12% of nitrogen inputs come from atmospheric nitrogen deposition and about 88% from agricultural fertilization (PURGHART et al. 2014).

The increase of nutrient and moisture values in 2020 also gives an indication of the improved nutrient and water storage capacity of the soil. This allows for a higher biomass productivity (DENGLER et al. 2014), which is disadvantageous for the typical species of nutrient-poor grasslands. The analysis of plant sociological behaviour also confirms that species characteristic of nutrient-poor grasslands (*Mesobromion*) had decreased and species of nutrient-rich grasslands (*Arrhenatherion*) had increased.

5.3 Plant strategies and functional traits

According to GRIME's (2001) model, decreases in ruderal and stress-tolerant species and an increase in highly competitive species indicate an increase in biomass productivity as well as a decrease in disturbance intensity. In a study based on analyses of a large German vegetation-plot database (JANDT et al. 2011), an increase in competitive species was also observed. Perennial species (mostly hemicryptophytes) generally have a more competitive strategy than annual and biennial species (GUREVITCH et al. 2006), and the slight increase in cover of these species in 2020 indicates an increase in competitive strategy.

The decline in ruderal species indicates that the meadows and pastures had shifted to a later successional stage with lower disturbance intensity. Such a trend was also observed in by MOOG et al. (2005), who studied effects of land use abandonment on meadows on nutrient-poor soils. Since the sites in the study are all under agricultural use, abandonment cannot be the reason in our case. Rather it is that the sites in 1980 were partly overgrazed while they are now used in an agronomically optimised way, meaning that the creation of bare patches is avoided by proper management. Likewise, also the stress-tolerant species declined. However, from the biodiversity point-of-view this more sustainable land use has disadvantages as the niches of therophytes and low competitive chamaephytes (such as *Sedum* spp.) disappear.

Two of the key functional traits of WESTOBY (1998), canopy height and seed mass, had significantly increased over the 40 years. Higher canopy height and seed mass indicate a lower level of disturbance compared to 40 years back. According to current knowledge, seed dispersal by animals (zoochory) allows seeds to be transported over greater distances than by wind (VITTOZ & ENGLER 2007). The mode of seed dispersal can be an important survival factor for species, especially when the landscape is fragmented. In the Swiss Jura Mts., fragmentation has been found to play a major role in the decline of rare species (NIEMELÄ & BAUR 1998, STÖCKLIN et al. 1999, 2000). However, the hypothesis that seed dispersal strategy adaptation occurs in isolated plant communities is tenuous. In this study, the increase in zoochory and the constant rate of anemochory (the two principal dispersal types for species of meso-xeric meadows and pastures) suggest a diversification of seed dispersal strategies.

5.4 Changes of species frequencies

Among the significantly decreased species, *Sedum sexangulare*, *Potentilla verna*, *Campanula rotundifolia* aggr. and *Festuca ovina* aggr. s.l. are indicators of dry conditions and *Potentilla verna*, *Campanula rotundifolia* aggr., *Linum catharticum*, *Carlina acaulis* and *Festuca ovina* aggr. s.l. of nutrient-poor soils (LANDOLT et al. 2010). By contrast, species such as *Potentilla reptans*, *Festuca arundinacea* and *Carex flacca* which are more adapted (to rich and) intermittently moist soils, became more frequent in the studied meadows and pastures. These observations point to the general eutrophication of the studied sites and indicate an increase in soil moisture. Increased density of the vegetation cover (BOCH et al. 2020) and strong shading are probable causes of the increase in soil moisture, since both curb soil evaporation.

5.5 Conclusions

In a recent resurvey of grasslands in the city of Zurich, KUMMLI et al. (2021) found that urban mesic grasslands did not undergo eutrophication or significant changes in floristic composition and concluded that the low land-use pressure in urban areas plays a great role in preserving mesic grasslands. While these positive results can be observed in the city, the opposite is unfortunately true in the countryside, where agricultural activity exerts permanent pressure on the vegetation of extensively managed areas. In this study, a total of 25 variables showed a statistically significant difference between 1980 and 2020. Except for the increase in zoochory, all observed changes are consistent with the trend of increasing productivity. Nutrients and moisture play an essential role in the equilibrium of ecological interactions and processes in meso-xeric grasslands. The observed higher productivity, as well as the increase in plants of intermittently wet sites, show that water and nutrients are now less limiting than in the past, leading to a shift in floristic composition towards that of nutrient-rich pastures. This threatens many vulnerable meso-xeric grassland species and leads also to a homogenization of plant diversity at the landscape level.

Since most of the study sites have not undergone any special protection measures during the last decades, they have been particularly exposed to nutrient enrichment and inappropriate agricultural management. Despite these unfortunate results in terms of nature protection and biodiversity, it is at least important to note that poor quality meso-xeric grasslands and pastures offer a window to the actual drivers of vegetation change in Europe as well as at a local scale.

The fact that it takes an average of 10 to 20 years for an enriched calcareous grassland to regain the characteristics of a nutrient-poor habitat (SMITS et al. 2008) indicates that the implementation of a targeted and successful protection strategy is conceivable in the medium term. This must limit as much as possible the progressive tendency of meso-xeric grasslands towards nutrient enrichment, homogenization and biodiversity loss.

Erweiterte deutsche Zusammenfassung

Einleitung – Kalkhalbtrockenrasen sind während des letzten Jahrhunderts in Mitteleuropa massiv zurückgegangen (LACHAT et al. 2010, DENGLER & SCHAMINÉE 2016). Diese artenreichen Lebensräume sind durch Intensivierung und Aufgabe der landwirtschaftlichen Nutzung, Eutrophierung, Klimawandel und Landschaftsfragmentierung gefährdet (DENGLER & TISCHEW 2018). Allerdings variieren die Ergebnisse zum Ausmaß und zur Richtung des dadurch bedingten Vegetationswandels zwischen

verschiedenen Studien in unterschiedlichen Regionen (DIEKMANN et al. 2019). Da allgemein noch recht wenig zum Vegetationswandel der Kalkhalbtrockenrasen im Schweizer Jura (Verband *Mesobromion*) bekannt war, untersuchten wir diesen mittels quasi-permanenten Aufnahmeflächen.

Untersuchungsgebiet – Unser Untersuchungsgebiet liegt im Schweizer Jura, in den Kantonen Aargau, Basel-Landschaft, Jura and Solothurn (Abb. 1). Der geologische Untergrund besteht aus Kalkstein, Mergel oder Sandstein (GNÄGI & LABHART 2014). Die Aufnahmeflächen liegen zwischen 420 und 800 m ü. d. M. Die für das Gebiet repräsentative Klimastation Rünenberg (611 m ü. d. M.) weist eine Jahresmitteltemperatur von 9,0 °C und einen Jahresniederschlag von 1009 mm auf (METEOSCHWEIZ 2021).

Methoden – Die Originalstudie umfasste 68 Vegetationsaufnahmen aus dem Jahr 1980 (HEDINGER 1983). Viele der Flächen werden heute aber anders genutzt (Acker, Wald, Siedlung). Von den verbleibenden wählten wir 28 Vegetationsaufnahmen in 19 Graslandgebieten, verteilt über das ganze Untersuchungsgebiet aus (zwei Beispiele in Abb. 2). Da die alten Vegetationsaufnahmen mit auf 10 m genauen Koordinaten registriert waren, gehen wir von einer Relokalisierungsungenauigkeit von maximal 20 m aus. Wir fertigten die neuen Vegetationsaufnahmen auf der gleichen Flächengröße wie die jeweils korrespondierende alte Vegetationsaufnahme an (48–400 m², meist 100 m²). Es wurden alle Gefäßpflanzen mit prozentualer Deckung erfasst. Wir berechneten Artenzahlen, Diversitätsindizes, mittlere Zeigerwerte und CSR-Strategien (nach LANDOLT et al. 2010), deckungsgewichtete funktionelle Merkmal (LHS nach WESTOBY 1998) basierend auf Daten aus LEDA (KLEYER et al. 2008), Anteile von Lebensformen und Affinität zu pflanzensoziologischen Verbänden (DELARZE et al. 2015). Alle diese Variablen wurden mit gepaarten *t*-Tests zwischen den beiden Aufnahmezeitpunkten verglichen. Weiterhin haben wir die Veränderungen in der Häufigkeit von Einzelarten mit Binomialtests geprüft. Schließlich wurde die Vegetationsveränderung mit einer gemeinsamen trendbereinigten Korrespondenzanalyse (DCA) der alten und neuen Vegetationsaufnahmen visualisiert.

Ergebnisse – Zwanzig der 1980 gefundenen Arten (12.3 %) waren 2020 signifikant weniger häufig, während acht der 175 aktuell gefundenen Arten (4.6 %) signifikant seltener waren als 1980 (Tab. 2). Der stärkste Rückgang (von 82 % zu 14 %) wurde bei *Linum catharticum* und die stärkste Zunahme bei *Arrhenatherum elatius* (von 25 % zu 86 %) festgestellt (Tab. 2). Der mittlere Artenreichtum pro Aufnahmefläche (überwiegend 100 m²) ging signifikant von 47 auf 42 Arten zurück, während Shannon-Evenness und Shannon-Index unverändert blieben. Unter den mittleren Zeigerwerten waren bei einer vorkommensbasierten Berechnung die Unterschiede meist größer als bei einer deckungsgewichteten Berechnung. Einzig die mittleren Nährstoffwerte zeigten bei beiden Berechnungsarten eine signifikante Änderung, und zwar hin zu nährstoffreicheren Verhältnissen. Von den CSR-Strategietypen zeigten die reinen Konkurrenzstrategen einen signifikanten Anstieg des relativen Artenreichtums, während reine Stresstrategen und ruderale Stresstrategen signifikant seltener wurden (Abb. 3). Unter den Lebensformen stieg der Deckungsanteil der Hemikryptophyten signifikant, während jener der krautigen Chamaephyten und der Therophyten signifikant zurückging (Abb. 4). Von den deckungsgewichteten funktionellen Merkmalen nahmen sowohl die vegetative Höhe als auch die Samenmasse signifikant zu, während sich die spezifische Blattfläche nicht signifikant änderte (Abb. 5). Die soziologische Affinität der Aufnahmen zeigte eine signifikante Tendenz weg vom *Mesobromion* und hin zum *Arrhenatherion* (Anhang E5). Die Ordination (Abb. 6) zeigt, dass die Aufnahmen von 1980 und heute sich systematisch unterscheiden.

Diskussion –Insgesamt zeigen die verschiedenen Ergebnisse, dass die Produktivität der Standorte in den letzten 40 Jahren deutlich zugenommen hat, was vermutlich mit indirekten Stickstoffeinträgen aus benachbarten Nutzflächen bzw. aus der Atmosphäre zu tun hat. Die Abnahme kleinwüchsiger Arten und von solchen mit Stresstrategie deutet auf ein zurückgehendes Störungsregime hin, d. h. es gibt heute offensichtlich weniger übernutzte, offene Stellen als seinerzeit. Das zeugt von einer agronomisch optimierten Nutzung, reduziert aber die Vorkommensmöglichkeiten konkurrenzschwacher Arten und führt letztlich zu einer floristischen Homogenisierung. Während die die meisten untersuchten Flächen

bislang keine Biodiversitätsförderflächen sind, würde eine Aufnahme in dieses Programm evtl. eine Chance bieten, dem Artenverlust entgegenzuwirken. Insgesamt zeigen unsere Ergebnisse viele Übereinstimmungen, aber auch manche Unterschiede zu anderen regionalen „Resurvey“-Studien von Kalkhalbtrockenrasen, was deutlich macht, dass Entwicklungen regional verschieden ablaufen können, und den Wert regionaler Untersuchungen unterstreicht.


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Author contributions

C.H. did the original plot sampling, while K.C. conducted the resampling and statistical analyses for his Bachelor thesis under the supervision of J.D. and M.B. The manuscript was drafted by K.C. with major contributions by J.D., while C.H., M.B. and S.W revised it critically.

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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. Site parameters recorded in summer 2020. Mean, minimum, maximum and standard deviation (SD).

Anhang E1. Mittelwerte, Minima, Maxima und Standardabweichungen (SD) Charakteristika der Aufnahmeflächen im Sommer 2020.

Supplement E2. Transformation of the variant of the Braun-Blanquet scale used by HEDINGER (1983) to percent cover.

Anhang E2. Transformation der Braun-Blanquet-Kategorien von HEDINGER (1983) zu Prozentwerten.

Supplement E3. Header data of the 28 resurvey plots in 1980 and 2020.

Anhang E3. Kopfdaten der 28 quasi-permanenten Aufnahmeflächen 1980 und 2020.

Supplement E4. Species cover data of the 28 resurvey plots in 1980 and 2020.

Anhang E4. Deckungsdaten der Arten in den 28 quasi-permanenten Aufnahmeflächen 1980 und 2020.

Supplement E5. All determined variables in comparison between 1980 and 2020.

Anhang E5. Alle zwischen 1980 und 2020 verglichenen Variablen.

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Supplement E1. Mean, standard deviation, minimum and maximum of plot size as well as the ecological and structural variables recorded in summer 2020.

Anhang E1. Mittelwerte, Standardabweichungen, Minima und Maxima der Flächengröße, der ökologischen und strukturellen Variablen im Sommer.

Variable	Mean	SD	Min	Max
Plot size [m ²]	125	85	48	400
Topography				
Elevation [m a.s.l.]	575	134	354	830
Southing	0.88	0.20	0.64	1.00
Inclination [°]	23	6	9	35
Maximum microrelief [cm]	10.9	3.8	4.0	22.0
Soil				
Mean soil depth [cm]	15.8	5.7	7.4	28.0
Stones and rocks [%]	1.0	1.7	0.0	5.0
Gravel [%]	2.6	2.2	0.0	10.0
Fine soil [%]	96.4	3.6	85.0	100.0
Vegetation structure				
Mean vegetation height [cm]	14.0	6.3	2.2	26.6
Total vegetation cover [%]	87	11	60	100
Shrub layer [%]	0.3	1.3	0.0	7.0
Herb layer [%]	84	10	60	99
Moss layer [%]	4	5	0	20
Litter [%]	16	10	3	50
Dead wood [%]	1.4	2.5	0.0	10.0

Supplement E2. Transformation of the variant of the Braun-Blanquet scale used by HEDINGER (1983) to percent cover. We generally applied the geometric mean of the lower and upper class boundaries.

Anhang E2. Definition der von HEDINGER (1983) verwendeten Braun-Blanquet-Kategorien und ihre Übersetzung in prozentuale Deckungen, basierend auf den geometrischen Mitteln der jeweiligen unteren und oberen Klassengrenze.

Cover-abundance category in HEDINGER (1983)	Definition in HEDINGER (1983)	% cover value used in numerical analyses
R	Very rare	0.1
+	<5%, sparse	0.5
1	<5%, numerous	2.5
>	5–15%	8.7
2	15–25%	19.4
3	25–50%	35.4
4	50–75%	61.2
5	75–100%	86.6

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Supplement E5. All determined variables in comparison between 1980 and 2020. P/A = presence/absence-based, CW = cover-weighted. Significant *p*-values are marked in bold.

Anhang E5. Übersicht aller zwischen 1980 und 2020 verglichenen Variablen. P/A = vorkommensbasiert, CW = deckungsgewichtet. Signifikante *p*-Werte sind fett hervorgehoben.

Variable	Weighting	Mean 1980	Mean 2020	<i>p</i> -value
Biodiversity metrics				
Species richness	n.a.	46.9	42.0	0.022
Shannon diversity	n.a.	2.79	2.70	0.257
Shannon evenness	n.a.	0.73	0.73	0.968
Ecological indicator values				
Temperature value	P/A	3.58	3.50	0.003
Temperature value	CW	3.51	3.44	0.217
Continental value	P/A	3.33	3.25	0.004
Continental value	CW	3.42	3.38	0.551
Light value	P/A	3.73	3.68	0.100
Light value	CW	3.69	3.75	0.204
Moisture value	P/A	2.42	2.56	< 0.001
Moisture value	CW	2.38	2.43	0.446
Reaction value	P/A	3.51	3.47	0.197
Reaction value	CW	3.58	3.47	0.029
Nutrient value	P/A	2.64	2.85	< 0.001
Nutrient value	CW	2.59	2.74	0.034
Humus value	P/A	3.02	3.01	0.782
Humus value	CW	3.00	2.99	0.722
Mowing tolerance value	P/A	2.66	2.64	0.836
Mowing tolerance value	CW	2.65	2.65	0.980
CSR strategies				
Competition value	P/A	1.03	1.18	< 0.001
Competition value	CW	1.10	1.28	0.001
Ruderality value	P/A	0.89	0.83	0.034
Ruderality value	CW	0.76	0.67	0.114
Stress value	P/A	1.08	0.99	0.006
Stress value	CW	1.14	1.05	0.167
CCC	P/A	1.24	4.05	< 0.001
CCC	CW	0.50	4.12	0.001
RRR	P/A	0.08	0.26	0.283
RRR	CW	0.06	0.04	0.741
SSS	P/A	1.03	0.09	0.001
SSS	CW	0.66	0.05	0.092
CCR/CRR	P/A	9.20	6.81	0.086
CCR/CRR	CW	4.50	3.37	0.490
CCS/CSS	P/A	20.38	21.71	0.379
CCS/CSS	CW	36.40	41.46	0.321
RRS/RSS	P/A	9.70	6.21	< 0.001
RRS/RSS	CW	4.88	2.39	0.013
CRS	P/A	49.21	50.11	0.586
CRS	CW	45.47	39.79	0.210
Life forms				
Phanerophyte	CW	0.01	0.57	0.098
Nanophanerophyte	CW	0.20	0.11	0.174
Woody chamaephyte	CW	1.95	0.59	0.121
Herbaceous chamaephyte	CW	10.30	6.35	0.020
Nanophanerophyte-hemicryptophyte	CW	0.00	0.07	0.206
Chamaephyte-hemicryptophyte	CW	0.00	0.01	0.171
Hemicryptophyte	CW	67.56	74.76	0.012
Geophyte	CW	4.91	3.78	0.362
Therophyte	CW	6.81	4.58	0.038
Climber	CW	0.13	1.02	0.005
Hemiparasite	CW	0.05	0.00	0.137
Plant functional traits (categorical)				
Anemochory	P/A	0.70	0.71	0.731
Anemochory	CW	0.59	0.56	0.055
Zoochory	P/A	0.84	0.82	0.569
Zoochory	CW	0.77	0.80	0.046
Plant functional traits (metric or ordinal)				
Seed longevity (ordinal)	CW	3.38	3.26	0.025
Canopy height (log ₁₀ (m))	CW	-0.61	-0.48	< 0.001
Seed mass (log ₁₀ (mg))	CW	-0.05	0.14	< 0.001
SLA (log ₁₀ (mm ² /mg))	CW	1.32	1.31	0.371
Phytosociological alliances (fractional score)				
Arrhenatherion	n.a.	0.10	0.12	0.005
Cirsio-Brachypodion	n.a.	0.04	0.05	0.560
Cynosurion	n.a.	0.09	0.09	0.948
Diplachnion	n.a.	0.06	0.06	0.290
Geranion sanguinei	n.a.	0.03	0.03	0.389
Mesobromion	n.a.	0.08	0.07	0.035
Poion alpinae	n.a.	0.08	0.07	0.210
Polygono-Trisetion	n.a.	0.07	0.07	0.841
Stipo-Poion	n.a.	0.04	0.04	0.745
Trifolion medii	n.a.	0.04	0.04	0.890
Xerobromion	n.a.	0.05	0.05	0.622