

Optimal site conditions for dry grasslands of high conservation value in the canton of Zurich, Switzerland

Optimale Standortbedingungen für Trockenrasen mit hohem Naturschutzwert im Kanton Zürich, Schweiz

Marc-Olivier Büchler^{1,2}, Regula Billeter² & Jürgen Dengler^{2,3,4,*} 

¹Etzelstr. 52, 8820 Wädenswil, Switzerland;

²Vegetation Ecology Group, Institute of Natural Resource Sciences (IUNR), Zurich University of Applied Sciences (ZHAW), Grüentalstr. 14, 8820 Wädenswil, Switzerland

³Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany;

⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

*Corresponding author, e-mail: juergen.dengler@zhaw.ch

Abstract

Semi-dry semi-natural grasslands such as those of the alliance *Mesobromion (Festuco-Brometea)* are one of the most-diverse habitat types in Europe with regard to many taxonomic groups, but these remnants of traditional extensive agriculture are currently threatened throughout the continent. It is important to know how and where such valuable vegetation types could be best maintained (or re-established) under current environmental conditions. To address this question, we selected 27 dry grassland sites in the canton of Zurich, Switzerland, half of which had been classified as of “good” and half as of “poor” quality one decade ago. We sampled vegetation, soil and topographical data in three 1-m² plots in each of these sites. We then compared the current environmental conditions and plant species composition of the two original quality levels. Furthermore, we related four metrics of current conservation value (vascular plant species richness, evenness, forb/graminoid ratio and an *ad hoc* developed conservation score) to measured environmental predictors and mean ecological indicator values. We found that the “good” and “poor” sites differed in only few environmental predictors, such as good sites having higher pH, lower soil nitrogen and steeper slopes, while they had higher numbers and covers of typical semi-dry grassland species and a higher conservation value. The metrics of conservation value behaved inconsistently when relating them to various environmental predictors. Interestingly, species richness decreased with slope inclination, but was also marginally negatively related to soil phosphorus. Conservation score, in contrast, increased with inclination, but also with increasing litter cover and soil nitrogen. While evenness largely showed similar response as conservation score, those of the forb-graminoid ratio were reversed for several environmental predictors. Overall, our results indicate that the conservation value of semi-dry grasslands cannot simply be attributed to one or two main factors. As different metrics of conservation value behaved differently, taking just one as a proxy would not be sufficient. Despite some variation, generally lower nutrient status, higher pH and steeper slopes seem to favour the maintenance of dry grasslands of higher quality. Some of our counter-intuitive results such as the higher litter cover in the plots of higher conservation value may indicate that current conservation management of these grasslands is too extensive to maintain their quality, particularly given the high atmospheric nitrogen input in the region. We thus propose an experiment to test whether earlier and/or more frequent mowing helps in maintaining the quality of semi-dry grasslands.

Keywords: calcareous grassland, conservation value, eutrophication, *Festuco-Brometea*, *Mesobromion*, nutrient, semi-dry grassland, semi-natural, soil, nature conservation, species richness, Switzerland, typical species, underuse, vegetation

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Dry grasslands are among the world's most species-rich habitats and host most of the world records of fine grain vascular plant diversity (DENGLER 2012, WILSON et al. 2012). They harbour many rare plant species and attract other organisms, such as insects, birds and reptiles, for which they provide food and habitat (WASSMER 2004, DENGLER et al. 2020).

The area of dry grasslands has declined considerably throughout Europe since the 20th century, and they are now considered threatened (POSCHLOD & WALLISDEVRIES 2002, WALLISDEVRIES et al. 2002, JANSSEN et al. 2016). In Switzerland, LACHAT et al. (2010) estimated a decline in the area of dry grasslands of about 95% of the original area in 1900. Especially since World War II, dry grasslands have experienced a strong decline throughout Switzerland (ZOLLER et al. 1986). In Switzerland, all types of semi-natural dry grasslands are therefore included in the Red List of Habitats, among them the type 4.2.4 (*Mesobromion* – Mitteleuropäischer Halbtrockenrasen; growing on base-rich sites in the oceanic and sub-oceanic parts of Europe) as VU (vulnerable) (DELARZE et al. 2016). As a semi-natural habitat type, resulting from low-intensity agriculture, Central European semi-dry grasslands depend on regular management such as mowing or grazing to prevent succession towards forest (POSCHLOD & WALLISDEVRIES 2002, WALLISDEVRIES et al. 2002, DELARZE et al. 2015, BOCH et al. 2020).

Semi-dry, semi-natural grasslands like those of the alliance *Mesobromion* are mainly threatened by intensification on the one hand and abandonment on the other hand (POSCHLOD & WALLISDEVRIES 2002, WALLISDEVRIES et al. 2002, DELARZE et al. 2015, DENGLER & TISCHEW 2018, BOCH et al. 2020). However, also N-deposition seems to have a significant negative impact on species diversity and composition of semi-dry grasslands (DENGLER & TISCHEW 2018, DENGLER et al. 2020). BOBBINK et al. (1998) found, that eutrophication of soils through nitrogen inputs from the air influences species composition, as dominant grasses and nitrophytic species become dominant. For dry grasslands across Switzerland, BOCH et al. (2019) showed that vegetation has become denser over the last ten years. Mean indicator values of nutrients and moisture have increased, while that of light have decreased (BOCH et al. 2019).

For the conservation and restoration of *Mesobromion* stands, it is important to know under which soil (and other site) conditions these species-rich grasslands optimally develop. This knowledge would allow concentrating measures on areas that are promising from a pedological point of view. If necessary, soil conditions could also be restored, for example, by topsoil removal to provide the optimal conditions for restoration. Lastly, knowledge about optimal site conditions is also crucial when it comes to re-creating this habitat type in the context of ecological compensation measures, for example, on restored gravel pits and newly created road embankments. Despite the high conservation relevance of the *Mesobromion*, the knowledge on its site conditions is astonishingly limited. OBERDORFER & KORNECK (1993), ELLENBERG & LEUSCHNER (2010) and DELARZE et al. (2015), for example, provide only vague information, largely without concrete values for topographic and soil parameters. RÖDER et al. (2006) report in a local study that semi-dry grasslands (in their case

likely belonging to the alliance *Cirsio-Brachypodion*) had on average a pH (CaCl₂) of 6.4, a total N content of 0.6% and a C/N ratio of 12.1. Since these values are from a single nature reserve, it is unclear where in the overall range of possible site conditions of semi-dry grasslands they are positioned. Moreover, also climate and bedrock are different in the canton of Zurich, so that a specific regional study was needed.

Attributing conservation value to biological objects is necessarily a normative step, which cannot directly be derived from ecological assessment (ROMAHN 2003). Therefore, there are always different criteria possible, and their assessment should be reported in a transparent manner. BERG et al. (2014) proposed for plant communities in general to combine the occurrence of red-listed species, naturalness and the relevance of the assessed territory for the global distribution of the respective vegetation type as criteria. Often it is also argued that species rich communities are particularly important for nature conservation (DENGLER et al. 2020), while others rather focus on the presence of species “typical” for a community (EGGENBERG et al. 2001, DELARZE et al. 2015) and the absence of undesired species (such as neophytes). Specifically for nutrient-poor, but acidic grasslands it has been demonstrated that “deterioration” of the communities goes hand in hand with a relative increase of grass cover at the expense of forbs (DUPRÈ et al. 2010), making also the forb/graminoid ratio a potential measure of conservation value of grasslands.

Our study was carried out in cooperation with the Nature Conservation Agency of the Canton of Zurich, Switzerland. The canton of Zurich has an inventory of all dry grasslands, classifying them as “good” to “poor” in terms of vegetation composition. However, the classification of the quality levels is based on historical data, most of which date back more than ten years. Whether the classification still reflects the current state of the grasslands is unclear. In this study, we assessed and compared the soil conditions and plant species composition of 14 “good” and 13 “poor” grasslands.

We addressed two research questions: (1) Are the dry grasslands, according to the historical division into “good” and “poor”, still different in terms of soil conditions and plant species composition? (2) Which soil and other site conditions are driving the current conservation value of the sites as measured with a range of different metrics?

2. Methods

2.1 Study area

The study was conducted in dry grasslands in the upper and lower Töss valley, east and west of Winterthur, in the canton of Zurich, Switzerland (Fig. 1). Geographically, the study area belongs to the Swiss Plateau (No. 2), subregion Eastern Plateau (No. 23; GONSETH et al. 2001). The elevation ranges from 414 to 724 m a.s.l. The mean annual temperature of the nearest weather station (Winterthur) is 9.2 °C and the mean annual precipitation is 1049 mm (CLIMATE-DATA.ORG 2020). Geologically, the study area belongs to the Molasse basin with Tertiary sediments, mainly consisting of conglomerates, sandstones and marls (LABHART 1995, PFIFFNER 2019).

2.2 Sampling design

2.2.1 Site selection

Since our main aim was to determine which site factors discriminate between dry grasslands of different conservation value, we selected sites that were as similar as possible in other aspects, but covered a wide range of conservation values. We thus limited our study to the grasslands used as meadows

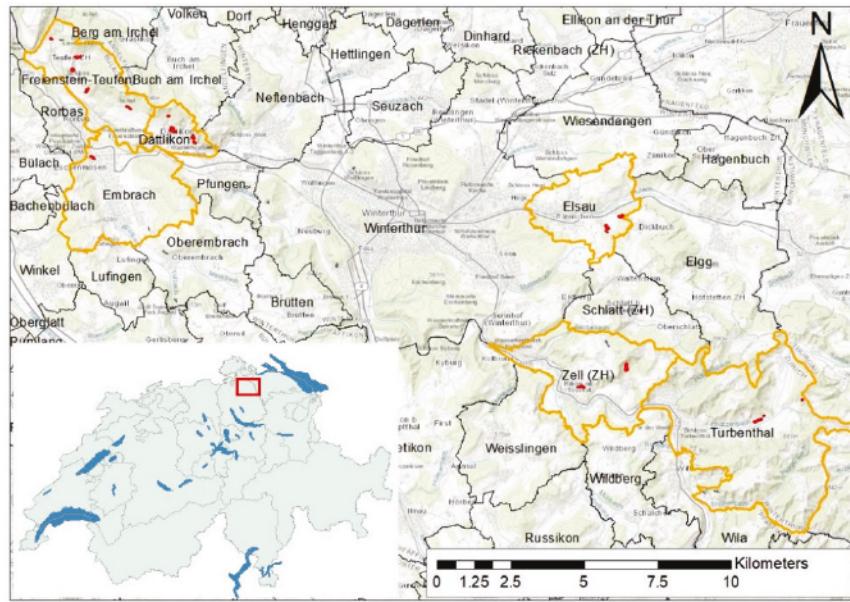


Fig. 1. Study area in the canton of Zurich, east and west of the city of Winterthur. Municipalities with studied sites (red) are outlined in orange (Source: Federal Office of Topography, swisstopo).

Abb. 1. Untersuchungsgebiet im Kanton Zürich, östlich und westlich von Winterthur. Gemeinden mit Untersuchungsflächen (rot) sind orange markiert (Quelle: Federal Office of Topography, swisstopo).

(not pastures), growing on calcareous brown soil in the Töss valley (limiting climatic variability). This pre-selection was done based on a GIS dataset from the Office of Landscape, Agriculture and Environment (OALE) of the Canton of Zurich, containing all dry grasslands registered in the national and cantonal inventories. Within this dataset, dry grasslands were rated by OALE as “good”, “medium” or “poor” quality, essentially referring to the number of typical dry grassland plant species found during the original survey, mostly more than 10 years back. To have a balanced dataset covering a wide range of different conservation values, we selected 14 dry meadows labelled as “good” and 13 labelled as “poor”. The two categories have the following meaning:

Dry grasslands of “good quality” are those that are registered as dry grasslands (TWW = *Trockenwiesen und -weiden*) of national importance according to Swiss legislation (EGGENBERG et al. 2001).

Dry grasslands of “poor quality” meet the basic criteria for a TWW object of national importance, but contain only four or five typical plant species per 28 m² (circle with 3 m radius) according to EGGENBERG et al. (2001), compared to at least six species for TWW of good quality.

Approximately, “good quality” means that the vegetation of a dry grassland at the time of survey belonged to the alliance *Mesobromion*, while “poor quality” would rather reflect an *Arrhenatherion* stand with some *Mesobromion* species (EGGENBERG et al. 2001, DELARZE et al. 2015). The selected 27 sites, with one exception, were all south-facing. They were mown once or twice a year, and three of them were additionally grazed from September onwards.

2.2.2 Size and arrangement of the vegetation plots

To cover the variability of the dry grassland sites, we selected in spring three squared plots of 1 m² size in each of the 27 sites. This was done according to the following procedure: (i) Three subareas representing differences in topography and vegetation physiognomy were mentally delimited, and in each of them one 1-m² plot was located haphazardly. (ii) Each 1-m² square plot was laid out with two

folding rules and the help of a compass exactly in North-South orientation to facilitate exact relocation in future studies. (iii) For exact relocation, a magnet (consisting of 6 disc magnets in a closed plastic tube) was buried in 5 cm depth in the northwest corner of the plot. The pairwise distance of the plots within one site typically was between 20 and 70 m, depending on the size of the site. To facilitate later retrieval of the plot, coordinates were taken with a handheld GPS device (Garmin eTrex 20).

2.3 Soil parameters

During March and April 2019, from each 1-m² plot a mixed soil sample from the four corners just outside the plot area was taken from the uppermost 15 cm with a gouge. The soil samples were then placed in a drying oven at 60 °C for at least 48 hours to dry completely. The dried soil samples were sieved through a 2-mm mesh sieve to obtain at least 80 g of fine soil (< 2 mm), which was crushed with a mortar for lab analyses.

The elemental analyses were carried out with a TruSpec Macro Analyser (LECO Instrumente GmbH). In the further analyses, we used organic carbon (C_{org}), total nitrogen (N_{tot}) and the C/N ratio (C_{org}/N_{tot}). Phosphorus was measured according to the Swiss Reference Method of ART & ACW (2010). Soil pH was measured electrometrically in a 0.01 molar CaCl₂ suspension according to the method of ART & ACW (2008).

2.4 Vegetation relevés

The vegetation was recorded between 29 July and 1 October 2019, but with sufficient time after mowing so that species could be well detected and their cover estimated. We consider the relatively late recording time as unproblematic because the *Mesobromion* hardly contains any spring therophytes or spring geophytes that would then not be visible anymore. The 1-m² plots were located precisely in the original position by searching the buried magnets with a magnetic locator (Schonstedt, model GA-92 XT) and arranging the folding rules in North-South direction using a compass. All vascular plant species were recorded with the shoot-presence method (DENGLER 2008) in per cent. Plant nomenclature follows the current Swiss checklist (JUILLERAT et al. 2017).

In each plot, we estimated the cover of the following layers in per cent: vegetation total, herb layer, forbs, graminoids, moss layer and litter. Shrub and tree layers were not present. Please note that these values do not normally sum up as component layers of an aggregate layer (e.g. herb layer total vs. forbs and graminoids separately) usually have some overlap.

Further, we measured elevation, inclination (with an App on the smartphone), microrelief (for method, see DENGLER et al. 2016) and mean soil depth (based on three measurements at random points inside each plot, following the method of DENGLER et al. 2016). Land-use intensity was quantified as number of land uses per year, based on interviews with the farmers, whereby each mowing event as well as the potential aftermath grazing in autumn were counted as 1, resulting in a maximum of 3.

The vegetation-plot data are provided to (and available from) the GrassPlot database (DENGLER et al. 2018) as well as an emerging Swiss national vegetation database ("Veg.CH"; Dengler et al. unpubl.).

2.5 Parameters derived from vegetation relevés

2.5.1 Mean indicator values

We used the program Vagedaz (KÜCHLER 2017) to calculate cover-weighted mean indicator values based on LANDOLT et al. (2010). We considered the following indicator values: temperature (T), continentality (K), light (L), moisture (F), reaction (R), nutrients (N), humus (H), aeration (D) and mowing tolerance (MW), which all range from 1 (low) to 5 (high), and moisture variability (W; range: 1–3). Furthermore, we considered the CSR strategies according to GRIME (2001), based on the values in LANDOLT et al. (2010), with C standing for competition, S for stress and R for ruderality. Here we used the convention that for a given species, and consequently as mean strategy per plot, the values sum up to 3. For instance, a pure C-strategist has C = 3, S = 0 and R = 0, while a CSR-strategist has C = 1, S = 1 and R = 1.

2.5.2 Species-related values

For each 1-m² plot, we calculated species richness, cover-based Shannon diversity and Shannon evenness for the vascular plants. We considered the following additional measures of vegetation “quality”: (i) \log_{10} (forb cover / graminoid cover) (further as forb-graminoid ratio; the logarithm was used to achieve normal distribution), (ii) conservation score = $4 \times$ cover (%) of Red List species of Switzerland (BORNAND et al. 2016) + $2 \times$ cover (%) character species of *Mesobromion* (DELARZE et al. 2015) + cover (%) of typical companion species of the *Mesobromion* (DELARZE et al. 2015) – $4 \times$ cover of (%) Black List and Watch List species (= invasive aliens) of Switzerland (BUHOLZER et al. 2014)

2.6 Statistical analyses

The statistical analyses were performed with the R 3.6.1 (R CORE TEAM 2018). The significance level was set to $p < 0.05$, while results with $0.05 \leq p < 0.10$ were considered as marginally significant.

2.6.1 Comparison of dry meadows according to a priori classification into "good" and "poor" quality

We assessed how the dry grasslands originally classified as “good” and “poor” differed in their current abiotic conditions and plant species composition. For the variables listed in Tables 1 and 2, we first tested for normal distribution with a Shapiro-Wilk test. If there was no significant deviation from normality, we applied the Welch *t*-test (default setting in R, which accounts for potentially unequal variances). Otherwise, we used a Wilcoxon rank-sum test.

2.6.2 Dependence of the current plant species composition on environmental parameters

We tested how the current plant species diversity (species richness, Shannon diversity, Shannon evenness) and vegetation quality (forb-graminoid ratio and conservation score) depended on the predictor variables listed in Table 1 with bivariate linear regressions. To account for inflation of Type I errors, when relating the same dependent variable to 25 different independent variables, we applied the sequential Bonferroni method of HOLM (1979) as recommended by QUINN & KEOUGH (2002). The residual plots were checked for deviations from normality and variance homogeneity of residuals (QUINN & KEOUGH 2002). No severe deviations were observed, and we thus used linear models.

3. Results

3.1 Site conditions and diversity of the plots

The surveyed dry grasslands typically occurred on slopes of moderate steepness (mean inclination: 21°) with relatively shallow soils (mean soil depth: 34 cm; Table 1). Soil pH values were relatively similar, mostly basic, rarely slightly acidic, with a mean of 7.23 (Table 1). In contrast, soil organic carbon and nutrient contents showed much higher variation, with 3.3-fold, 4.7-fold, 79-fold and 90-fold differences between richest and poorest sites for C_{org}, N_{tot}, P and C_{inorg}, respectively (Table 1).

Mean vascular plant species richness in 1 m² was about 20.8, with a range from 8 to 32 (Table 2). While character species of the *Mesobromion* according to DELARZE et al. (2015) were absent in most stands, character and typical companion species combined (diagnostic species) on average accounted for more than 1/4 of all species and reached a joint cover of nearly 60%. However, there were also stands without a single diagnostic species (Table 2). Nationally red-listed species and species of the Black/Watch List were rare with far less than one species of each group on average per plot (Table 3). Generally, forbs were predominant

Table 1. Independent variables with mean, standard deviation, minimum and maximum based on 1-m² plots ($n = 81$). Asterisks in columns #1 and #2 indicate which of the variables were used as predictors in which analyses (see sections 2.6.1 and 2.6.2, respectively).

Tabelle 1. Unabhängige Variablen mit Mittelwert, Standardabweichung, Minimum und Maximum basierend auf 1 m²-Vegetationsaufnahmen ($n = 81$). Sternchen in den Spalten #1 und #2 geben an, in welchen Analysen die entsprechenden Variablen als Prädiktoren genutzt wurden (vgl. Kapitel 2.6.1 bzw. 2.6.2).

Parameter [unit or range]	Mean	Standard deviation	Minimum	Maximum	#1	#2
Site parameters						
Elevation [m a.s.l.]	525	69	415	722	*	
Inclination [°]	20.5	6.7	6	40	*	*
Microrelief [cm]	5.0	2.0	1	12	*	*
Mean soil depth [cm]	34.0	7.3	16	55	*	*
Land-use intensity [yr ⁻¹]	1.8	0.6	1	3	*	*
Soil chemical parameters						
Organic carbon (C _{org}) [%]	2.74	1.15	0.19	5.63	*	*
Inorganic carbon (C _{inorg}) [%]	3.13	1.52	0.08	7.25		
Nitrogen (N _{tot}) [%]	0.34	0.08	0.19	0.62	*	*
C/N ratio	8.00	2.66	0.70	13.84	*	*
Phosphorus [ppm]	2.77	1.55	0.11	8.68	*	*
pH value (CaCl ₂)	7.23	0.42	5.70	7.60	*	*
Cover values						
Vegetation total [%]	86.7	9.5	60	100	*	*
Herb layer [%]	82.0	10.1	50	95	*	
Forbs [%]	60.0	13.9	20	90	*	
Graminoids [%]	50.1	16.2	10	80	*	
Moss layer [%]	14.7	12.8	0	55	*	*
Litter [%]	31.4	12.1	10	60	*	*
Mean indicator values						
Temperature [1–5]	3.72	0.33	2.47	4.45	*	*
Continentality [1–5]	2.92	0.28	1.80	3.47	*	*
Light [1–5]	3.66	0.24	3.14	4.30	*	*
Moisture [1–5]	2.81	0.20	2.05	3.19	*	*
Moisture variability [1–3]	1.96	0.28	1.29	2.54	*	*
Reaction [1–5]	3.54	0.29	2.66	4.33	*	*
Nutrients [1–5]	2.84	0.36	2.01	3.55	*	*
Humus [1–5]	2.99	0.33	1.63	3.63	*	*
Aeration [1–5]	2.44	0.52	1.55	4.40	*	*
Mowing tolerance [1–5]	1.04	0.34	0.29	1.97	*	*
Competition [0–3]	1.32	0.24	0.49	1.92	*	*
Stress [0–3]	0.75	0.25	0.36	1.56	*	*
Ruderality [0–3]	0.93	0.19	0.30	1.48	*	*

in the stands over graminoids with on average 1.45 times the cover of the latter, but the stands varied much in this respect from graminoids having three times more cover than forbs to forbs having nine times more cover than graminoids (Table 2).

Table 2. Dependent variables with mean, standard deviation, minimum and maximum based on 1-m² plots ($n = 81$). Cover refers to cumulative cover of the respective species group. Asterisks in columns #1 and #2 indicate which of the variables were used in which analyses (see sections 2.6.1 and 2.6.2, respectively).

Tabelle 2. Abhängige Variablen mit Mittelwert, Standardabweichung, Minimum und Maximum basierend auf 1 m²-Vegetationsaufnahmen ($n = 81$). Stemchen in den Spalten #1 und #2 geben an, in welchen Analysen die entsprechenden Variablen genutzt wurden (vgl. Kapitel 2.6.1 bzw. 2.6.2).

Parameter	Mean	Standard deviation	Minimum	Maximum	#1	#2
Species diversity						
Species richness	20.8	4.484	8	32	*	*
Shannon index	2.42	0.33	1.12	3.14	*	
Shannon evenness	0.80	0.09	0.47	0.92	*	*
Richness and cover of species groups						
Cover of Red List species [%]	0.3	1.4	0	10	*	
Number of Red List species	0.0	0.2	0	1	*	
Cover of Black/Watch List species [%]	0.1	0.5	0	3	*	
Number of Black/Watch List species	0.1	0.3	0	1	*	
Cover of character species [%]	1.0	4.9	0	35	*	
Number of character species	0.1	0.3	0	2	*	
Cover of typical companion species [%]	58.5	29.8	0	124	*	
Number of typical companion species	5.7	2.4	0	11	*	
Cover of character + typical companion species [%]	59.5	31.0	0	129	*	
Number of character + typical companion species	5.8	2.6	0	12	*	
Measures of vegetation quality						
Forb cover / graminoid cover	1.45	1.07	0.33	9.00	*	
\log_{10} (forb cover / graminoid cover)	0.09	0.23	-0.48	0.95	*	*
Conservation score	61.2	34.3	0.0	155.0	*	*

3.2 Comparison of dry meadows according to a priori classification into “good” and “poor” quality

From the eleven tested site and soil chemical parameters, only four differed significantly between good and poor sites (Table 3): Good sites grew on average on steeper slopes (Fig. 2) with bigger microrelief, lower nitrogen content (Fig. 2) and lower soil pH, but generally the differences between good and poor sites were small. Mean indicator values showed the strongest differences for nutrients (higher in “good” sites), competition (higher in “good” sites) and stress (lower in “good” sites).

From the species diversity measures, only the Shannon index differed significantly, with slightly higher values in “poor” sites (Table 3). Nevertheless, character and typical companion species were significantly more abundant (both in terms of species richness and cover) in the “good” sites, while Black/Watch List species were more frequent in the “poor” sites (Table 3). Consequently, the (current) conservation score was more than twice as high in sites originally classified as good vs. those classified as poor (Fig. 3).

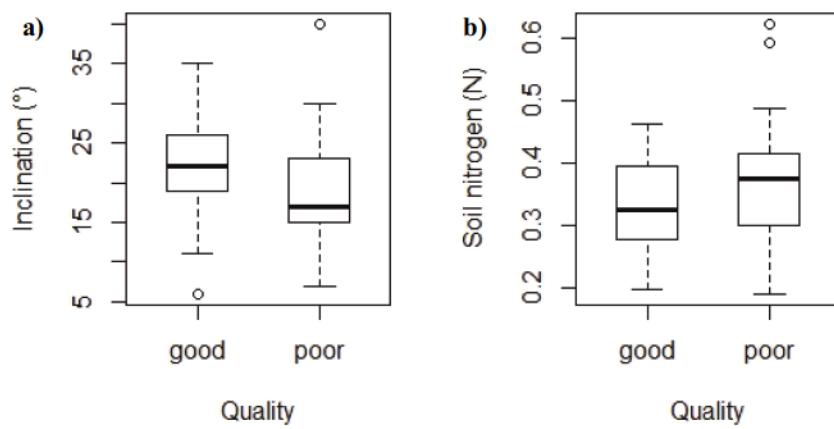


Fig. 2. Two environmental factors showing particularly strong differences between plots of semi-dry grasslands originally classified as “good” or “poor”: **a)** inclination ($p = 0.041$); **b)** soil nitrogen in % ($p = 0.031$). For details, see Table 3.

Abb. 2. Zwei Umweltvariablen, die sich besonders deutlich zwischen den Vegetationsaufnahmen der ursprünglich als „gut“ und „schlecht“ eingestuften Halbtrockenrasen unterscheiden. **a)** Hangneigung ($p = 0,041$); **b)** Stickstoffgehalt im Boden in % ($p = 0,031$). Detaillierte statistische Ergebnisse finden sich in Tabelle 3.

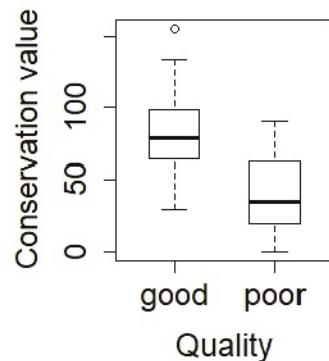


Fig. 3. Comparison of current conservation score between plots of semi-dry grasslands originally classified as “good” or “poor” ($p < 0.001$; see Table 3).

Abb. 3. Vergleich des aktuellen Naturschutzwertes zwischen Vegetationsaufnahmen von ursprünglich als “gut” oder “schlecht” eingestuften Halbtrockenrasen ($p < 0,001$; vgl. Tab. 3).

3.3 Dependence of conservation value on environmental parameters

From the four metrics of conservation value, species richness showed the fewest and weakest relationships to the 25 tested predictors (Supplement S1). Moreover, the findings for species richness were largely incongruent to the other three metrics (Shannon evenness, \log_{10} [forb cover / graminoid cover], conservation score), i.e., significant relationships occurred for predictors not influential for the other metrics (such as phosphorus and total vegetation

Table 3. Differences in the means of various variables between plots of semi-dry grasslands originally classified as “good” or “poor”. Depending on the normal distribution of variables, either a Wilcoxon test or a Welch *t*-test was applied. Significant differences are given in bold.

Tabelle 3. Unterschiede in den Mittelwerten verschiedener Variablen zwischen Aufnahmeflächen von Halbtrockenrasen, die ursprünglich als “gut” und als “schlecht” klassifiziert wurden. Abhängig von der Normalverteilung der Variablen wurde entweder ein Wilcoxon-Test oder ein Welch’ *t*-Test durchgeführt. Signifikante Unterschiede sind fett hervorgehoben.

Parameter	Good	Poor	Test	p	Sign.
Site parameters					
Elevation [m a.s.l.]	525	525	Wilcoxon test	0.496	n.s.
Inclination [°]	22	19	Welch <i>t</i> -test	0.041	*
Microrelief [cm]	5.5	4.5	Wilcoxon test	0.045	*
Mean soil depth [cm]	33.3	34.7	Wilcoxon test	0.431	n.s.
Land-use intensity [yr^{-1}]	1.9	1.7	Wilcoxon test	0.125	n.s.
Soil chemical parameters					
Total carbon (C_{tot}) [%]	6.1	5.7	Wilcoxon test	0.333	n.s.
Nitrogen (N_{tot}) [%]	0.32	0.36	Welch <i>t</i> -test	0.031	*
C/N ratio	7.9	8.1	Welch <i>t</i> -test	0.811	n.s.
Phosphorus [ppm]	2.4	3.1	Wilcoxon test	0.101	n.s.
pH value (CaCl_2)	7.3	7.1	Wilcoxon test	0.009	**
Cover values					
Vegetation total [%]	88	86	Wilcoxon test	0.321	n.s.
Herb layer [%]	82	82	Wilcoxon test	0.950	n.s.
Forbs [%]	59	61	Wilcoxon test	0.242	n.s.
Graminoids [%]	52	48	Wilcoxon test	0.214	n.s.
Moss layer [%]	16	13	Wilcoxon test	0.045	*
Litter [%]	36	27	Wilcoxon test	< 0.001	***
Mean indicator values					
Temperature [1–5]	3.7	3.7	Welch <i>t</i> -test	0.321	n.s.
Continentality [1–5]	2.9	3.0	Welch <i>t</i> -test	0.134	n.s.
Light [1–5]	3.6	3.7	Welch <i>t</i> -test	0.010	*
Moisture [1–5]	2.8	2.8	Welch <i>t</i> -test	0.226	n.s.
Moisture variability [1–3]	2.0	1.9	Welch <i>t</i> -test	0.736	n.s.
Reaction [1–5]	3.6	3.5	Welch <i>t</i> -test	0.013	*
Nutrients [1–5]	3.0	2.7	Welch <i>t</i> -test	< 0.001	***
Humus [1–5]	2.9	3.0	Wilcoxon test	0.064	.
Aeration [1–5]	2.4	2.5	Welch <i>t</i> -test	0.367	n.s.
Mowing tolerance [1–5]	1.1	1.0	Welch <i>t</i> -test	0.258	n.s.
Competition [0–3]	1.4	1.2	Wilcoxon test	0.001	**
Stress [0–3]	0.7	0.8	Wilcoxon test	0.002	**
Ruderality [0–3]	0.9	0.9	Wilcoxon test	0.545	n.s.
Species diversity					
Species richness	20.4	21.1	Welch <i>t</i> -test	0.501	n.s.
Shannon index	2.37	2.46	Wilcoxon test	0.022	*
Shannon evenness	0.79	0.81	Wilcoxon test	0.101	n.s.
Richness and cover of species groups					
Cover of Red List species [%]	0.4	0.1	Wilcoxon test	0.345	n.s.
Number of Red List species	0.1	0.0	Wilcoxon test	0.351	n.s.
Cover of Black/Watch List species [%]	0.0	0.3	Wilcoxon test	0.004	**

Parameter	Good	Poor	Test	p	Sign.
Number of Black/Watch List species	0.0	0.2	Wilcoxon test	0.004 **	
Cover of character species [%]	2.0	0.0	Wilcoxon test	0.008 **	
Number of character species	0.2	0.0	Wilcoxon test	0.008 **	
Cover of typical companion species [%]	75	41	Wilcoxon test	< 0.001 ***	
Number of typical companion species	7.0	4.3	Welch t-test	< 0.001 ***	
Cover of character + typical companion species [%]	77	41	Welch t-test	< 0.001 ***	
Number of character + typical companion species	7.1	4.3	Welch t-test	< 0.001 ***	
Measures of vegetation quality					
Forb cover / graminoid cover	1.27	1.64	Wilcoxon test	0.202 n.s.	
\log_{10} (forb cover / graminoid cover)	0.06	0.12	Welch t-test	0.253 n.s.	
Conservation score	81	40	Welch t-test	< 0.001 ***	

cover) or even pointing into a different direction as in the case of inclination and moss layer cover for conservation score. In contrast, evenness and conservation score reacted largely consistently to the relevant predictors, while the forb-graminoid ratio for various parameters showed the opposite relationship (Supplement S1).

For species richness, strong negative relationships occurred with inclination (Fig. 4) and moss layer cover, a marginally negative one for soil phosphorus (Supplement S1). In contrast, species richness was strongly and positively related to the mean indicator value of moisture and marginally significantly related to that of soil humus and to total vegetation cover (Supplement S1). In the case of evenness, we did not find any significant relationship to the measured site and soil chemical parameters, but many to cover values and mean indicator values (Supplement S1). The strongest negative relationships were for litter cover and indicator values of humus and continentality, the strongest positive ones occurred for indicator values of nutrients and reaction (Supplement S1). The forb-graminoid ratio had the strongest negative relationships with litter cover, the indicator values for reaction and nutrients as well as inclination (Fig. 4) and particularly strongly positive relationships with indicator values of continentality and light. Among the four metrics of vegetation quality, conservation score had the highest number of significant predictors (Supplement S1). Particularly strong positive relationships occurred with inclination (Fig. 4), litter cover and the indicator values of reaction, nutrients and competition, and particularly negative ones with the indicator values of continentality, light and stress.

4. Discussion

4.1 Site conditions and plant diversity

The site conditions observed in this study were rather uniform in relation to soil pH, but showed a high variability for nutrient contents of the soil. This high variability may be explained by the fact, that some of the sites surveyed in this study are close to intensively used agricultural areas. This proximity but also possible former management such as the application of manure can lead to higher nutrient contents (BAUR 2003). When comparing our results to those of one of the few other studies that actually measured soil conditions in semi-dry grasslands of good quality ("Altheide" of the nature reserve Garchinger Heide near Munich; RÖDER et al. 2006), albeit belonging to a different phytosociological alliance (*Cirsio-Brachypodion*), it turns out that our stands on average had higher pH (7.2 vs. 6.4),

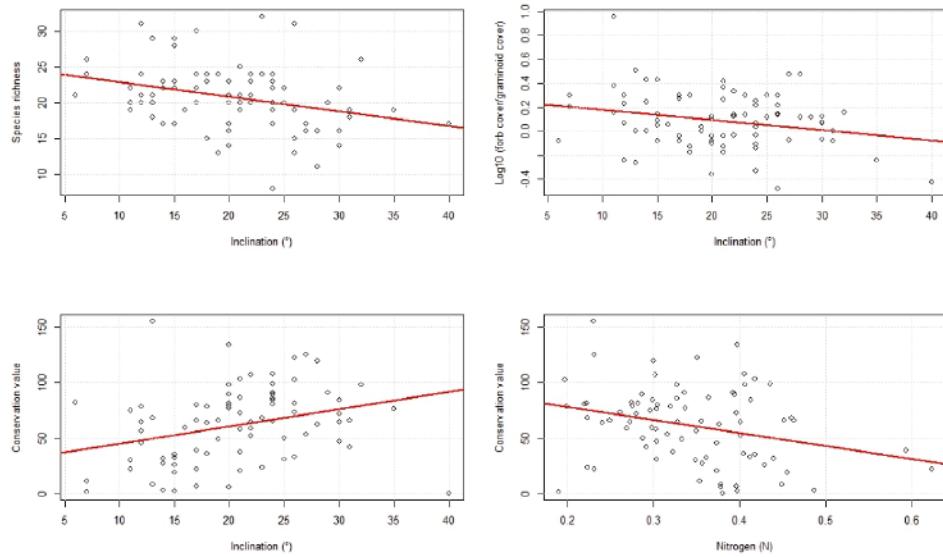


Fig. 4. Regressions of measures of current vegetation quality with environmental predictors. Top left: species richness (1 m^2) vs. inclination ($p = 0.084$); top right: \log_{10} (forb cover / graminoid cover) vs. inclination ($p = 0.029$); bottom left: conservation score vs. inclination ($p = 0.006$); bottom right: conservation score vs. soil nitrogen in % ($p = 0.023$). The regression equations can be found in Supplement S1.

Abb. 4. Regressionen von Maßen der aktuellen Vegetationsqualität gegen Umweltvariablen. Oben links: Artenreichtum (1 m^2) vs. Hangneigung ($p = 0,084$); oben rechts: \log_{10} (Deckung Kräuter / Deckung Grasartige) vs. Hangneigung ($p = 0,029$); unten links: Naturschutzwert vs. Hangneigung ($p = 0,006$); unten rechts: Naturschutzwert vs. Stickstoffgehalt im Boden in % ($p = 0,023$). Die Regressionsgleichungen sind in Anhang S1 angegeben.

lower P (2.8 vs. 7.0), lower N_{ges} (0.34 vs. 0.60) and lower C/N ratio (8.0 vs. 12.1). This is astonishing because the “Altheide”, based on the available descriptions, is much richer in rare dry grassland species than our stands were. From nature conservation point of view, it would thus be desirable to have more measurements of soil parameters of semi-dry grasslands of high and low conservation value, growing under different geological and climatic conditions.

With an average of 21 species in 1 m^2 , the species richness of vascular plants was below the reported average of approximately 24 vascular plants for semi-dry (meso-xeric) grasslands across the Palaearctic biogeographic realm (DENGLER et al. 2020). This could be an indication that some of the plots studied here already belonged to mesic rather than semi-dry grasslands, for which the Palaearctic average is about 18 species in 1 m^2 (DENGLER et al. 2020).

4.2 Comparison of dry meadows according to *a priori* classification into "good" and "poor" quality

When comparing the meadows of formerly “good” and “poor” quality, no consistent picture emerged. The measured variables showed only few significant relationships with the historical classification of dry grasslands. The significant differences in case of inclination,

microrelief and soil conditions (pH, N) suggested that dry grassland of (formerly) higher floristic quality occur on steeper slopes with a more heterogeneous topography, have lower nitrogen content and higher pH. However, the differences between “good” and “poor” semi-dry grasslands were generally small. While the mean indicator value for soil reaction was in parallel with measured soil pH, mean indicator values for nutrients and competition pointed into opposite direction than the measured N contents.

While site conditions and mean indicator values showed at best weak differences between the two quality levels, the occurrences of the species groups (invasive species, character species, and typical companion species) were all significant and in the expected direction, except for red-listed species, which did not differ between “good” and “poor” grasslands. Likewise, our conservation score, which combined the information of all these species groups, was about twice as high in the sites classified as “good” vs. those classified as “poor”. This difference in species-group based indices was expected as the original classification in “good” and “poor” habitats was based on the number of typical species of semi-dry grasslands (EGGENBERG et al. 2001). It showed that the overall floristic composition did not change very much since the original inventory. Interestingly, all three diversity measures were slightly lower in the “good” sites, albeit the difference was only significant for the Shannon index. It is rather speculative, but it might be that the good sites are underused and this could lead to dominance of some taller species, reducing both evenness and richness at the fine grain size of 1 m².

4.3 Dependence of the current vegetation on environmental parameters

Species richness and the forb/graminoid-ratio were strongly negatively related to inclination. This is in contrast to conservation score, which increased with inclination. The latter result was in accordance with the results of OLSSON et al. (2009), who found in Danish dry grasslands that the occurrence of Red List species is positively related to increasing inclination. However, in contrast to OLSSON et al. (2009), species richness behaved differently and decreased with increasing inclination. TURTUREANU et al. (2014) described in their study that increasing inclination was negatively related to species richness at similar spatial scales as in our study. The discrepancy to the results of our study may be due to typical and rare species of dry grasslands being more likely to grow on steep slopes than common species.

Another important aspect was litter cover of dry grasslands. Litter cover showed a negative relationship to the forb/graminoid-ratio, meaning that the relative forb cover decreased with increasing litter, and the same was true for species evenness. In other studies (e.g. FOSTER & GROSS 1998, RUPRECHT & SZABÓ 2012), litter cover has been described as a factor negatively influencing the establishment of herbaceous plant seedlings. Litter acts as a “trap” for seeds and can prevent them from reaching the soil (RUPRECHT & SZABÓ 2012). Litter thus acts as a mechanical barrier, but it can also have an allelopathic effect on the seedlings of herbaceous plants (FOSTER & GROSS 1998). Although there was no significant negative relationship of species richness to litter cover, “good” quality dry meadows contained on average fewer species and had a higher average litter cover. The accumulation of litter could result from over-extensive use of “good” semi-dry grasslands (RÖDER et al. 2006, WALLISDEVRIES et al. 2002), while the more productive “poor” grasslands were more attractive for farmers, used more intensively and thus showed less litter. A too extensive use of semi-dry grasslands could lead to a relative increase of grass cover in the vegetation due to the lack of light on the ground, thus constraining the establishment of seedlings of forb species (RÖDER et al. 2006, RUPRECHT & SZABÓ 2012) and leading to a decline of typical dry

grassland species, which require a higher amount of light (RÖDER et al. 2006). This assumption was supported by the significant relationship between the forb/graminoid-ratio and the average indicator value for light. Deviating from the results of other studies in nutrient-poor grasslands (e.g. DUPRÈ et al. 2010), in our system higher relative graminoid cover was not associated with lower conservation score or evenness.

The measured soil parameters had very little influence on species richness, evenness or forb/graminoid ratio, with only species richness showing a marginally significant negative relationship to soil phosphorus. Conservation score, on the other hand, did not react sensitively to the phosphorus content of the soil, but negatively to the nitrogen- and the organic carbon content. Many studies (BOBBINK et al. 1998, CRITCHLEY et al. 2002, DE SCHRIJVER et al. 2011, ROTH et al. 2013) showed that eutrophication leads to an impoverishment of species richness. Especially in oligo- to mesotrophic soils, the effect of nitrogen inputs and the resulting displacement of characteristic species by nitrophilous species is strong (BOBBINK et al. 1998). It is therefore not surprising that species richness and particularly conservation score reacted negatively to soil nutrient content. One issue might be the small size of most of the studied dry grasslands assessed in this study. Spill-over of nutrients/fertiliser is particularly important in small-sized semi-dry grasslands as it was found by BAIER & TISCHEW (2004). They reported that the closer a dry grassland is to arable land, the higher is the degree of eutrophication. Therefore, special attention must be paid to the management of the surrounding agricultural land in order to preserve the typical and rare species of semi-dry grasslands. A reduction of nutrients such as nitrogen (N), phosphorus (P) or potassium (K) within sites could be achieved by increasing the mowing frequency, benefitting typical and rare species of dry grasslands (RÖDER et al., 2006). However, RÖDER et al. (2006) mention that the decrease of phosphate (P) and potassium (K) contents by mowing takes a long time. SMITS et al. (2008) found that former fertilization of a meadow with phosphorus-rich fertilizer had an effect up to 25 years after its last addition.

4.4 Conclusions and outlook

The quality of dry grasslands depends on various interacting environmental drivers, including management, soil conditions as well as other environmental site conditions. Generally, our data indicate that lower soil N and P concentrations, higher pH values and steeper slopes favour dry grasslands of higher conservation score. Unexpectedly, however, total species richness behaved differently than conservation score. The latter only took into account typical and noxious species but not the large number of ubiquitous species found in semi-dry grasslands. Likewise, DIEKMANN et al. (2014) found in *Mesobromion* stands in NW Germany that over the years, species richness (positive) and number of typical species (negative) showed opposite trends. Since natural science cannot provide arguments which is the better measure of conservation value, it seems reasonable to consider both and potentially further metrics to capture more different facets of biodiversity conservation.

Also unexpected was the finding that conservation score significantly increased with litter cover, while many studies have shown that in dry grasslands high litter cover is negative for plant diversity in general and for many low-competitive target species in particular. This finding might point to an underuse of the originally most valuable sites in our study area. Additionally, the significantly higher indicator values for nutrients and competition in the originally “good” sites seemed to indicate that current land use might be too extensive to maintain the conservation score of the sites and rather favours litter accumulation and the spread of competitive non-target species. Moreover, the relatively low species richness in

relation to the Palaearctic average of meso-xeric grasslands might indicate that in many sites a succession towards mesic grasslands, i.e., from *Mesobromion* to *Arrhenatherion*, is ongoing. Such a tendency was also reported for dry grasslands across Switzerland by BERGAMINI et al. (2019). While one rather late cut might have been the historical use of the *Mesobromion* in Switzerland (see DELARZE et al. 2015; also the conservation regulations are based on this assumption), it might not be sufficient for their maintenance under current conditions anymore. Here one needs to bear in mind that the study regions receives a particularly high atmospheric nitrogen input of 15 to more than 40 kg ha⁻¹ yr⁻¹ (RIHM & ACHERMANN 2016). With this in mind, we recommend trying earlier and more cuts in the semi-dry grasslands of the canton of Zurich to maintain their quality in the medium run. However, such an adjustment in management should be applied thoughtfully (e.g. a second cut only every second year) and be accompanied by scientific monitoring to ensure that the desired effects are maximised and undesired side-effects are avoided.

Erweiterte deutsche Zusammenfassung

Einführung – Halbnatürliche Halbtrockenrasen wie jene des Verbandes *Mesobromion* (Klasse *Festuco-Brometea*) gehören zu den artenreichsten Habitattypen Europas in Bezug auf Gefäßpflanzen und zahlreiche andere taxonomische Gruppen (WILSON et al. 2012, DENGLER et al. 2020). Zugleich unterliegen sie einem erheblichen Flächenverlust (POSCHLOD & WALLISDEVRIES 2002, LACHAT et al. 2010) und gehören heutzutage zu den gefährdeten Lebensräumen (DELARZE et al. 2016, JANSSEN et al. 2016). In der Schweiz sind die Trockenwiesen und -weiden (TWW), zu denen das *Mesobromion* gehört, in nationalen und kantonalen Inventaren geschützt, abhängig vom jeweiligen Naturschutzwert (EGGENBERG et al. 2001). Für einen effektiven Schutz vorhandener Halbtrockenrasen wie auch ihre Neuschaffung (etwa an Straßenböschungen oder in rekultivierten Kiesgruben) ist es wichtig zu wissen, unter welchen Standortbedingungen (Boden, Topographie) sie sich am besten entwickeln können, doch gibt es dazu in einschlägigen Standardwerken kaum konkrete Zahlen (ELLENBERG & LEUSCHNER 2010, DELARZE et al. 2015). Zugleich ist es eine normative Frage, die unterschiedlich beantwortet werden kann, wann ein Halbtrockenrasen besonders wertvoll ist. Oftmals wird Naturschutzwert mit Artendiversität, dem Vorkommen typischer oder dem Fehlen unerwünschter Arten in Verbindung gebracht. Ziel der vorliegenden Arbeit war es daher, im Auftrag des Kantons Zürich herauszufinden, (1) ob und wie sich die Halbtrockenrasen, die vor gut einem Jahrzehnt in solche „guter“ und „schlechter“ Qualität eingestuft worden sind, immer noch unterscheiden und (2) wie Vegetations- und Bodeneigenschaften vier verschiedene Aspekte des Naturschutzwerts dieser Flächen heute beeinflussen.

Methoden – Das Untersuchungsgebiet liegt im Kanton Zürich im Schweizer Mittelland. Die untersuchten Kalkhalbtrockenrasen (*Mesobromion*) befinden sich im nordöstlichen Teil des Kantons östlich und westlich der Stadt Winterthur (Abb. 1), stocken alle auf Kalkbraunerden und werden gemäht. Wir haben 14 ehemals als „gut“ und 13 ehemals als „schlecht“ kategorisierte Trockenrasen ausgewählt (vgl. EGGENBERG et al. 2001). Innerhalb jedes Trockenrasens haben wir dann drei 1 m² große Probeflächen in möglichst unterschiedlichen Teilbereichen für die Untersuchungen ausgewählt und dauerhaft mit Bodenmagneten markiert. Auf diesen somit 81 Probeflächen wurden Vegetationsaufnahmen angefertigt, bei denen die Deckung aller Gefäßpflanzarten und der einzelnen Schichten in % geschätzt wurde (Tab. 1). Weiterhin wurden topografische und bodenchemische Parameter erfasst (Tab. 1). Aus den Vegetationsaufnahmen haben wir mittlere ökologische Zeigerwerte nach LANDOLT et al. (2010), drei Diversitätsmaße (Artenreichtum, Shannon-Evenness, Shannon-Diversität) und verschiedene weitere Maße des Naturschutzwertes berechnet (Tab. 2). Eines davon ist log₁₀ (Deckung Kräuter / Deckung Grasartiger), da bekannt ist, dass vielfach mit einer „Verschlechterung“ der Qualität nährstoffarme Grasländer der Gräseranteil steigt (DUPRÉ et al. 2010). Ein weiteres Kriterium sind die von uns ad hoc definierten „Naturschutzpunkte“, für die wir gewichtet die Deckungen typischer und gefährdeter Arten zusammenzählen und davon jene der Neophyten abziehen. Wir haben dann je nach Erfüllung der

Voraussetzungen mit Welch' *t*-Test oder mit dem Wilcoxon-Test geprüft, ob sich die Mittelwerte der Vegetationsaufnahmen in den ehemals „guten“ und „schlechten“ Halbtrockenrasen bezüglich topografischen und bodenchemischen Parametern, Deckungen der Schichten, mittleren ökologischen Zeigerwerten, Artendiversität und verschiedenen Maßen des Naturschutzwertes unterscheiden. Für vier Maße des Naturschutzwertes (Artenreichtum auf 1 m², Shannon-Evenness, log₁₀ (Deckung Kräuter / Deckung Grasartiger) und die Naturschutzpunkte) haben wir zudem mittels bivariater Regressionen getestet, ob und wie sie von topografischen und bodenchemischen Parametern, Deckungen der Schichten sowie mittleren ökologischen Zeigerwerten beeinflusst werden.

Ergebnisse – Die untersuchten Halbtrockenrasen wuchsen meist an Hängen mittlerer Steilheit (Mittel: 21°) und auf relativ flachgründigen Böden (mittlere Bodentiefe: 34 cm). Die Nährstoffgehalte variierten dagegen stark (Tab. 1). Der Gefäßpflanzenartenreichtum auf 1 m² reichte von 8 bis 31 und betrug im Mittel 20,8. Der Vergleich der beiden Halbtrockenrasenqualitäten zeigte viele Unterschiede (Tab. 3). Unter anderem waren Hangneigung (Abb. 2), Mikrorelief, Streudeckung, pH-Wert und Naturschutzpunkte (Abb. 3) in den Vegetationsaufnahmen aus den Flächen „guter“ Qualität signifikant höher. Die Halbtrockenrasen „schlechter“ Qualität wiesen einen signifikant höheren Stickstoffgehalt (Abb. 2) auf. Hingegen waren bei Halbtrockenrasen „guter“ Qualität die durchschnittliche Lichtzahl signifikant tiefer und die durchschnittliche Nährstoffzahl signifikant höher. Rote-Liste-Arten und Charakterarten waren in Halbtrockenrasen „schlechter“ Qualität nicht zu finden. Bei den Regressionen der vier aktuellen Maße des Naturschutzwertes gegen die verschiedenen Prädiktoren zeigten sich inkonsistente Ergebnisse (Beilage S1, Abb. 4). Artenreichtum auf 1 m² nahm mit zunehmender Moosdeckung und Hangneigung ab, mit zunehmendem Phosphorgehalt aber marginal signifikant zu. Die Naturschutzpunkte zeigten dagegen positive Zusammenhänge mit der Hangneigung, der Streudeckung, den mittleren Reaktions- und Nährstoffzahlen sowie der relativen Häufigkeit von Konkurrenzstrategien, aber negative mit der mittleren Lichtzahl und der relativen Häufigkeit von Stressstrategien, sowie dem Stickstoffgehalt im Boden. Abgesehen von einer entgegengesetzten Reaktion bezüglich Streudeckung waren die Umweltbeziehungen der Shannon-Evenness ähnlich denen der Naturschutzpunkte, während das Verhältnis von Kräutern zu Grasartigen weitgehend entgegengesetzt reagierte. Insbesondere nahm der Kräuteranteil mit zunehmender Streudeckung sowie höheren Reaktions- und Nährstoffzahlen ab. Von den vier betrachteten Wertigkeitsmaßen zeigte die Naturschutzzahl signifikante Beziehungen zu den meisten der 25 betrachteten Prädiktoren (8 nach sequentieller Bonferroni-Korrektur nach HOLM 1979), der Artenreichtum dagegen zu den wenigsten (nur 1 nach sequentieller Bonferroni-Korrektur).

Diskussion – Im Vergleich zu einer der wenigen anderen Arbeiten, in der konkrete Werte für bodenchemische Parameter in einem gut ausgebildeten Halbtrockenrasen publiziert wurden (RÖDER et al. 2006; Naturschutzgebiet Garchinger Heide bei München), weisen unsere Standorte im Mittel einen höheren pH-Wert, aber niedrigere P- und N-Gehalte sowie C/N-Verhältnisse auf. Es zeigt sich, dass ein großer Bedarf für weitere Messungen topografischer und bodenchemischer Parameter in Halbtrockenrasen hohen und niedrigen Naturschutzwertes unter unterschiedlichen klimatischen und geologischen Rahmenbedingungen besteht. Nur so kann diese Information wirklich eingeordnet und für den Naturschutz nutzbar gemacht werden. Unsere Gefäßpflanzen-Artenzahlen auf 1 m² sind mit einem Mittelwert von 20,8 unterdurchschnittlich im Vergleich zum Gesamtmittelwert für Kalkhalbtrockenrasen in der Paläarktis von etwa 24 (DENGLER et al. 2020). Dies könnte darauf hindeuten, dass manche Bestände sich im Übergang zum *Arrhenatherion* befinden oder gar schon zu diesem gehören. Interessanterweise unterschieden sich die vor gut 10 Jahren in „gut“ und „schlecht“ eingeteilten Halbtrockenrasen aktuell in vielen (damals nicht erhobenen) Umwelt- und Vegetationsparametern. Wenn man die Regressionsmodelle der vier Maße des aktuellen Naturschutzwertes vergleicht, die wir exemplarisch ausgewählt haben, zeigen sich zahlreiche Inkonsistenzen bis hin zu signifikanten Effekten desselben Prädiktors in gegenteilige Richtung. Dies unterstreicht, dass man eine Naturschutzbewertung nicht auf ein einziges Diversitäts- oder Wertigkeitsmaß stützen sollte. Trotzdem zeigen sich, wenn man das historische und die vier aktuellen Gütemaße zusammennimmt, einige allgemeine Trends, auch wenn sie nicht 100 % konsistent waren: Generell scheinen niedrigerer Nährstoffgehalt, höherer pH-Wert und steilere Hanglagen vorteilhaft für die Erhaltung von Halbtrockenrasen höheren Naturschutzwertes zu sein. Einige

kontraintuitive Ergebnisse wie die höhere Naturschutzwertanzahl für Aufnahmeflächen mit höherer Streudeckung könnten auf eine verzögerte Reaktion der Vegetation hindeuten. Möglicherweise sind die ehemals besten Halbtrockenrasen zugleich die unproduktivsten und werden daher zu wenig genutzt, weswegen sich Streu ansammelt. Während das bislang noch nicht zu einer erheblichen floristischen „Verschlechterung“ geführt hat, ist eine solche bei Fortbestehen der gegenwärtigen Managements zu befürchten, insbesondere in Anbetracht der sehr hohen atmogenen Stickstoffdeposition im Gebiet (RIHM & ACKERMANN 2016). Wir empfehlen daher, experimentell zu prüfen, ob ggf. häufigere (durchschnittlich 1,5–2× jährlich) oder frühere Mahd auf die Artenzusammensetzung und den Naturschutzwert auswirken, um ggf. Managementvorschriften evidenzbasiert anpassen zu können.

Author contribution statement

M.-O.B. conducted the research for his Bachelor thesis under the supervision of J.D. and R.B. All three authors jointly wrote the article and approved its content.

Acknowledgements

We thank the Canton of Zurich for provision of information and cooperation. We are grateful to two anonymous reviewers and to the co-ordinating editor, Thomas Becker, for very detailed and helpful comments on the initial version of the manuscript.

ORCIDs

Jürgen Dengler  <https://orcid.org/0000-0003-3221-660X>

Supplements

Supplement S1. Results of bivariate linear regressions of the four response variables representing different facets of conservation value (y) to 25 predictor variables (x).

Beilage S1. Ergebnisse der bivariaten linearen Regressionen für die vier abhängigen Variablen (y), die unterschiedliche Aspekte des Naturschutzwertes von 25 Prädiktorvariablen (x) repräsentieren.

References

- ART & ACW (Eds.) (2008): Schweizerische Referenzmethoden der Forschungsanstalten Agroscope, Band 2, E2.056.d, Methode pH-C. – Agroscope, Zürich.
- ART & ACW (Eds.) (2010): Schweizerische Referenzmethoden der Forschungsanstalten Agroscope, Band 1, E1.056.d, Methode H2O10-P. – Agroscope, Zürich.
- BAIER, A. & TISCHEW, S. (2004): Naturschutz-Management auf Xerothermrassenstandorten in Sachsen-Anhalt – Gefährdungsanalyse und Entwicklungsstrategien am Beispiel des Naturschutzgebietes „Lämmerberg und Vockenwinkel“. – Hercynia N.F. 37: 201–230.
- BAUR, B. (2003): Auswirkungen von Flächenverlust, Verinselung und Nutzungsaufgabe auf die Biodiversität. – Bauhinia 17: 51–72.
- BERG, C., ABDANK, A., ISERMANN, M., JANSEN, F., TIMMERMANN, T. & DENGLER, J. (2014): Red Lists and conservation prioritization of plant communities – a methodological framework. – Appl. Veg. Sci. 17: 504–515.
- BERGAMINI, A., GINZLER, C., SCHMIDT, B.R. ... HOLDERECKER, R. (2019): Zustand und Entwicklung der Biotope von nationaler Bedeutung: Resultate 2011–2017 der Wirkungskontrolle Biotopschutz Schweiz. – WSL Ber. 85: 1–104.
- BOBBINK, R., HORNUNG, M. & ROELOFS, J.G.M. (1998): The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. – J. Ecol. 86: 717–738.

- BOCH, S., BEDOLLA, A., ECKER, T.K., GRAF, U., KÜCHLER, H., KÜCHLER, M., HOLDEREgger, R. & BERGAMINI, A. (2019): Mean indicator values suggest decreasing habitat quality in Swiss dry grasslands and are robust to relocation error. – *Tuexenia* 39: 315–334.
- BOCH, S., BIURRUN, I. & RODWELL, J. (2020): Grasslands of Western Europe. – In: GOLDSTEIN, M.I., DELLASALA, D.A. & DiPAOLO, D.A. (Eds.): Encyclopedia of the world's biomes. Vol. 3: Forests – trees of life. Grasslands and shrublands – sea of plants: 678–688. Elsevier, Amsterdam.
- BORNAND, C., GYGAX, A., JUILLERAT, P., JUTZI, M., MÖHL, A., ROMETSCH, S., SAGER, L., SANTIAGO, H. & EGGENBERG, S. (2016): Rote Liste Gefäßpflanzen. Gefährdete Arten der Schweiz. – Bundesamt für Umwelt, Bern: 178 pp.
- BUHOLZER, S., NOBIS, M., SCHÖNENBERGER, N. & ROMETSCH, S. (2014). Schwarze Liste –August 2014: Liste der gebietsfremden invasiven Pflanzen der Schweiz, Stand 2014. – Info Flora, Bern: 2 pp. – URL: https://www.infoflora.ch/de/assets/content/documents/neophyten/neophyten_diverse/Schwarze%20Liste_Watch%20Liste_2014.pdf [accessed 2020-06-08].
- CLIMATE-DATA.ORG (2020): Klima Winterthur (Schweiz). – URL: <https://de.climate-data.org/europa/schweiz/zuerich/winterthur-5980/> [accessed 2020-07-28].
- CRITCHLEY, C.N.R., CHAMBERS, B.J., FOWBERT, J.A., BHOGAL, A., ROSE, S.C. & SANDERSON, R.A. (2002): Plant species richness, functional type and soil properties of grasslands and allied vegetation in English Environmentally Sensitive Areas. – *Grass Forage Sci.* 57: 82–92.
- DE SCHRIJVER, A., DE FRENNE, P., AMPOORTER, E., VAN NEVEL, L., DEMEY, A., WUYTS, K. & VERHEYEN, K. (2011): Cumulative nitrogen input drives species loss in terrestrial ecosystems. – *Glob. Ecol. Biogeogr.* 20: 803–816.
- DELARZE, R., GONSETH, Y., EGGENBERG, S. & VUST, M. (2015): Lebensräume der Schweiz. Ökologie – Gefährdung – Kennarten. 3rd ed. – Ott, Bern: 456 pp.
- DELARZE, R., EGGENBERG, S., STEIGER, P., BERGAMINI, A., FIVAZ, F., GONSETH, Y., GUNTERN, J., HOFER, G., SAGER, L. & STUCKI, P. (2016): Rote Liste der Lebensräume der Schweiz. Aktualisierte Kurzfassung zum technischen Bericht 2013 im Auftrag des Bundesamtes für Umwelt (BAFU). – BAFU, Bern: 33 pp.
- DENGLER, J. (2008): Pitfalls in small-scale species-area sampling and analysis. - *Folia Geobot.* 43: 269–287.
- DENGLER, J. (2012): Europäische Trockenrasen schlagen tropische Regenwälder. – *Biol. Unserer Zeit* 42: 148–149.
- DENGLER, J. & TISCHEW, S. (2018). Grasslands of Western and Northern Europe – between intensification and abandonment. – In: SQUIRES, V.R., DENGLER, J., FENG, H. & HUA, L. (Eds.): Grasslands of the world: diversity, management and conservation: 27–63. CRC Press, Boca Raton.
- DENGLER, J., BOCH, S., FILIBECK, G. ... BIURRUN, I. (2016): Assessing plant diversity and composition in grasslands across spatial scales: The standardised EDGG sampling methodology. – *Bull. Eurasian Dry Grassl. Group* 32: 13–30.
- DENGLER, J., WAGNER, V., DEMBICZ, I. ... BIURRUN, I. (2018): GrassPlot – a database of multi-scale plant diversity in Palaearctic grasslands. – *Phytocoenologia* 48: 331–347.
- DENGLER, J., BIURRUN, I., BOCH, S., DEMBICZ, I. & TÖRÖK, P. (2020): Grasslands of the Palaearctic biogeographic realm: introduction and synthesis. – In: GOLDSTEIN, M.I., DELLASALA, D.A. & DiPAOLO, D.A. (Eds.): Encyclopedia of the world's biomes. Vol. 3: Forests – trees of life. Grasslands and shrublands – sea of plants: 617–637. Elsevier, Amsterdam.
- DIEKMANN, M., JANDT, U., ALARD, D., BLEEKER, A., CORCKET, E., GOWIN, D.J.G., STEVEN, C.J. & DUPRÈ, C. (2014): Long-term changes in calcareous grassland vegetation in North-western Germany – no decline in species richness, but a shift in species composition. – *Biol. Conserv.* 172: 170–179.
- DUPRÈ, C., STEVENS, C.J., RANKE, T., BLEEKER, A., PEPPLER-LISBACH, C., GOWIN, D.J.G., DISE, N.B., DORLAND, E., BOBBINK, R. & DIEKMANN, M. (2010): Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. – *Glob. Change Biol.* 16: 344–357.
- EGGENBERG, S., DALANG, T., DIPNER, M. & MAYER, C. (2001).: Kartierung und Bewertung der Trockenwiesen und -weiden von nationaler Bedeutung. Technischer Bericht. – BUWAL, Bern: 249 pp.
- ELLENBERG, H. & LEUSCHNER, C. (2010): Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. 6th ed. – Ulmer, Stuttgart: 1333 pp.
- FOSTER, B.L. & GROSS, K.L. (1998): Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. – *Ecology* 79: 2593–2602.

- GONSETH, Y., WOHLGEMUTH, T., SANSONNES, B. & BUTTLER, A. (2001): Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. – BUWAL, Bern: 47 pp.
- GRIME, J.P. (2001): Plant strategies, vegetation processes, and ecosystem properties. 2nd ed. – Wiley, Chichester: 417 pp.
- HOLM, S. (1979): A simple sequentially rejective multiple test procedure. – Scand. J. Stat. 6: 65–70.
- JANSSEN, J.A.M., RODWELL, J.S., GARCIA CRIADO, M. ... VALACHOVIĆ, M. (2016): European Red List of habitats – Part 2. Terrestrial and freshwater habitats. – European Union, Luxembourg: 38 pp.
- JUILLERAT, P., BÄUMLER, B., BORNAND, C., EGGENBERG, S., GYGAX, A., JUTZI, M., MÖHL, A., NYFFELER, R., SAGER, L. & SANTIAGO, H. (2017). Flora Helvetica Checklist 2017 der Gefäßpflanzenflora der Schweiz. – Info Flora, Bern: 385 pp.
- KÜCHLER, M. (2017): Veedaz (Version 2017). – WSL, Birmensdorf. – URL: <https://www.wsl.ch/en/services-and-products/software-websites-and-apps/veedaz.html>.
- LABHART, T.P. (1995): Geologie der Schweiz. 3rd ed. – Ott Verlag, Thun: 211 pp.
- LACHAT, T., PAULI, D., GONSETH, Y., KLAUS, G., SCHEIDEGGER, C., VITTOZ, P. & WALTER, T. (2010): Wandel der Biodiversität in der Schweiz seit 1900: Ist die Talsohle erreicht? – Haupt, Bern: 435 pp.
- LANDOLT, E., BÄUMLER, B., ERHARDT, A. ... WOHLGEMUTH, T. (2010): Flora Indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. 2nd ed. – Haupt, Bern: 378 pp.
- OBERDORFER, E. & KORNECK, D. (1993): Klasse: *Festuco-Brometea* Br.-Bl. et Tx. 43. – In: OBERDORFER, E. (Ed.): Süddeutsche Pflanzengesellschaften – Teil II: Sand- und Trockenrasen, Heide- und Borstgras-Gesellschaften, alpine Magerrasen, Saum-Gesellschaften, Schlag- und Hochstaudenfluren. 3rd ed.: 86–180. Fischer, Stuttgart.
- OLSSON, P.A., MÄRTENSSON, L.-M. & BRUUN, H.H. (2009): Acidification of sandy grasslands – consequences for plant diversity. – Appl. Veg. Sci. 12: 350–361.
- PIIFFNER, O.A. (2019): Landschaften und Geologie der Schweiz. – Haupt, Bern: 358 pp.
- POSCHLOD, P. & WALLISDEVRIES, M.F. (2002): The historical and socioeconomic perspective of calcareous grasslands-lessons from the distant and recent past. – Biol. Conserv. 104: 361–376.
- QUINN, G.P. & KEOUGH, M.J. (2002): Experimental design and data analysis for biologists. – Cambridge University Press, Cambridge: 537 pp.
- R CORE TEAM (2018): R: A language and environment for statistical computing. (3.6.1 for Windows). R Foundation for Statistical Computing, Wien. URL: <https://www.R-project.org/>.
- RIHM, B. & ACHERMANN, B. (2016): Critical loads of nitrogen and their exceedances. Swiss contribution to the effects-oriented work under the Convention on Long-range Transboundary Air Pollution (UNECE). – FOEN, Bern: 78 pp.
- RÖDER, D., JESCHKE, M. & KIEHL, K. (2006): Vegetation und Böden alter und junger Kalkmagerrasen im Naturschutzgebiet "Garchinger Heide" im Norden München. – Forum Geobot. 2: 24–44.
- ROMAHL, K.S. (2003): Rationalität von Werturteilen im Naturschutz. – Theor. Ökol. 8: 1–217.
- ROTH, T., KOHLI, L., RIHM, B. & ACHERMANN, B. (2013): Nitrogen deposition is negatively related to species richness and species composition of vascular plants and bryophytes in mountain grassland. – Agric. Ecosyst. Environ. 178: 121–126.
- RUPRECHT, E. & SZABÓ, A. (2012): Grass litter is a natural seed trap in long-term undisturbed grassland. – J. Veg. Sci. 23: 495–504.
- SMITS, N.A.C., WILLEMS, J.H. & BOBBINK, R. (2008): Long-term after-effects of fertilisation on the restoration of calcareous grasslands. – Appl. Veg. Sci. 11: 279–286.
- TURTUREANU, P.D., PALPURINA, S., BECKER, T., DOLNIK, C., RUPRECHT, E., SUTCLIFFE, L.M.E., SZABÓ, A. & DENGLER, J. (2014): Scale- and taxon-dependent biodiversity patterns of dry grassland vegetation in Transylvania. – Agric. Ecosys. Environ. 182: 15–24.
- WALLISDEVRIES, M.F., POSCHLOD, P. & WILLEMS, J.H. (2002): Challenges for the conservation of calcareous grasslands in northwestern Europe: Integrating the requirements of flora and fauna. – Biol. Conserv. 104: 265–273.
- WASSMER, A. (2004): Über einige Magerwiesen des Aargauer Juras: Floristisch-ökologische Vergleichsstudien. – Abteilung Landschaft und Gewässer, Baudepartement Aargau, Aarau: 110 pp.
- WILSON, J.B., PEET, R.K., DENGLER, J. & PARTEL, M. (2012): Plant species richness: The world records. – J. Veg. Sci. 23: 796–802.

ZOLLER, H., WAGNER, C. & FREY, V. (1986): Nutzungsbedingte Veränderungen in *Mesobromion*-Halbtrockenrasen in der Region Basel – Vergleich 1950–1980. – Abh. Westf. Mus. Naturkd. Münster 48(2/3): 93–107.

Büchler et al: Optimal site conditions for dry grasslands of high conservation value in the canton of Zurich, Switzerland

Supplement S1. Results of bivariate linear regressions of the four response variables representing different facets of conservation value (y) to 25 predictor variables (x). The colour and the slope of the regression equation indicate the direction (and size) of the effect. Green: Significantly positive at $\alpha = 0.1$ after application of a “sequential Bonferroni” correction (HOLM 1979); light green: significantly positive at $\alpha = 0.1$ without “sequential Bonferroni”; red: significantly negative at $\alpha = 0.1$ after application of “sequential Bonferroni”; light red: significantly negative at $\alpha = 0.1$ without “sequential Bonferroni”.

Beilage S1. Ergebnisse der bivariaten linearen Regressionen für die vier abhängigen Variablen (y), die unterschiedliche Aspekte des Naturschutzwertes repräsentieren (von links nach rechts: Artenreichtum auf 1 m², Shannon Evenness, log₁₀(Deckung Krautige / Deckung Grasartige), Naturschutzpunkte) von 25 Prädiktorvariablen (x). Die Farbe und die Steigung der Regressionsgleichung geben die Richtung (und Größe) des Effektes an. Grün: signifikant positiv bei $\alpha = 0.1$ nach der Anwendung einer sequentiellen Bonferroni-Korrektur (HOLM 1979); blassgrün: signifikant positiv bei $\alpha = 0.1$ ohne Anwendung einer sequentiellen Bonferroni-Korrektur; rot: signifikant negativ bei $\alpha = 0.1$ nach der Anwendung einer sequentiellen Bonferroni-Korrektur; blassrot: signifikant negativ bei $\alpha = 0.1$ ohne Anwendung einer sequentiellen Bonferroni-Korrektur.

Predictor variable (x)	Species richness (1 m ²)		Shannon evenness		$\log_{10}(\text{forb cover} / \text{graminoid cover})$		Conservation score	
	p	Equation	p	Equation	p	Equation	P	Equation
Site parameters								
Inclination [°]	0.005	$y = 25 - 0.2 x$	0.158		0.029	$y = 0.26 - 0.01 x$	0.006	$y = 29.42 + 1.55 x$
Microrelief [cm]	0.238		0.327		0.549		0.087	$y = 44.57 + 3.32 x$
Mean soil depth [cm]	0.139		0.145		0.144		0.867	
Land-use intensity [yr ⁻¹]	0.197		0.234		0.140		0.349	
Soil chemical parameters								
Organic carbon (C _{org}) [%]	0.421		0.282		0.236		0.045	$y = 79.49 - 6.67 x$
Nitrogen (N _{tot}) [%]	0.458		0.691		0.851		0.023	$y = 96.72 - 103.35 x$
C/N ratio	0.591		0.389		0.142		0.392	
Phosphorus [ppm]	0.084	$y = 22.3 - 0.6 x$	0.817		0.335		0.819	
pH value (CaCl ₂)	0.999		0.695		0.253		0.350	
Cover values								
Vegetation total [%]	0.073	$y = 12.6 + 0.1 x$	0.687		0.899		0.310	
Moss layer [%]	<0.001	$y = 22.7 - 0.13 x$	0.010	$y = 0.83 - 0.002 x$	0.722		0.093	$y = 53.82 + 0.5 x$
Litter [%]	0.132		0.001	$y = 0.89 - 0.003 x$	<0.001	$y = 0.32 - 0.01 x$	<0.001	$y = 21.92 + 1.25 x$
Mean indicator values								
Temperature [1–5]	0.582		0.047	$y = 1.02 - 0.06 x$	0.922		0.200	
Continentality [1–5]	0.505		0.001	$y = 0.47 + 0.11 x$	<0.001	$y = -0.91 + 0.34 x$	0.002	$y = 180.84 - 40.95 x$
Light [1–5]	0.391		0.024	$y = 0.46 + 0.09 x$	0.009	$y = -0.93 + 0.28 x$	<0.001	$y = 318.66 - 70.38 x$
Moisture [1–5]	0.006	$y = 1.8 + 6.74 x$	0.053	$y = 0.46 + 0.09 x$	0.014	$y = 0.98 - 0.32 x$	0.443	
Moisture variability [1–3]	0.297		0.013	$y = 0.97 - 0.09 x$	0.040	$y = 0.47 - 0.19 x$	0.038	$y = 5.19 + 28.64 x$
Reaction [1–5]	0.120		0.011	$y = 1.11 - 0.09 x$	<0.001	$y = 1.28 - 0.33 x$	0.001	$y = -96.28 + 44.51 x$
Nutrients [1–5]	0.919		0.006	$y = 1.02 - 0.08 x$	<0.001	$y = 0.84 - 0.26 x$	<0.001	$y = -94.84 + 54.86 x$
Humus [1–5]	0.075	$y = 12.77 + 2.67 x$	0.001	$y = 0.51 + 0.1 x$	0.321		0.136	
Aeration [1–5]	0.318		0.806		0.023	$y = -0.18 + 0.11 x$	0.421	
Mowing tolerance [1–5]	0.338		0.174		0.248		0.881	
Competition [0–3]	0.970		0.291		0.245		<0.001	$y = -23.70 + 64.4 x$
Stress [0–3]	0.436		0.011	$y = 0.73 + 0.1 x$	0.582		<0.001	$y = 99.90 - 51.65 x$
Ruderality [0–3]	0.272		0.375		0.025	$y = 0.38 - 0.31 x$	0.460	