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Mean indicator values suggest decreasing habitat quality in Swiss dry grasslands and are robust to relocation error

Mittlere Zeigerwerte deuten auf eine sinkende Lebensraumqualität in Trockenrasen der Schweiz hin – die Relokalisierungsgenauigkeit der Untersuchungsflächen spielt dabei nur eine untergeordnete Rolle

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Abstract

Resurveys of historical plots are important to study vegetation changes over time. However, there is a high potential of relocation error, as historical plots were usually not permanently marked, which might result in misleading interpretations of changes. Quasi-permanent plots can relatively well be relocated, because of available information on their position (e.g. GPS coordinates). This minimizes relocation error. Quasi-permanent plots have thus been suggested to be suitable for vegetation resurveys. Land-use abandonment and intensification are the major drivers of habitat degradation and thereby cause biodiversity loss. To counteract the ongoing decline of biodiversity in Swiss grasslands, the dry grasslands of national importance, comprising a total of 3631 sites across Switzerland (0.5% of its total area) were legally protected in 2010. These grassland sites represent various vegetation types and cover a wide elevational gradient. From 1995 to 2006, several thousand quasi-permanent vegetation plots of 28 m^2 were surveyed in the nationally important dry grassland sites. For each plot, GPS coordinates and a metric measure of post-processed GPS inaccuracy were recorded. In a set of 384 sites, 538 of the historical plots were resurveyed between 2011 and 2017. We tested the effects of GPS inaccuracy and elevation on temporal changes of species richness, species turnover and mean ecological indicator values. Overall, mean indicator values for light and stress significantly decreased, and those for moisture, nutrients and ruderality significantly increased within only one decade. However, the temporal change of the mean indicator values for nutrients and moisture was more pronounced at higher than at lower elevation, indicating a particularly strong decrease of habitat quality at high elevation sites. While changes of in mean indicator values were largely robust to relocation error, the temporal turnover of key species significantly increased with increasing GPS inaccuracy. These results indicate that quasi-permanent plots are suitable to study changes in mean indicator values, but probably not to compare species composition and turnover across time.

Keywords: dry grasslands, ecological indicator values, *Festuco-Brometea*, GPS inaccuracy, habitat conservation, quasi-permanent plots, relocation error, resurvey, species turnover, vegetation change

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Resurveys of vegetation plots have become an important tool to detect environmental and vegetation changes over time. However, when aiming to evaluate the effectiveness of conservation strategies, the accurate assessment of temporal changes is of particular importance. In previous studies on temporal vegetation changes, relocation bias has been proposed as one of the most important sources of error, maximized in heterogeneous habitats (KAPFER et al. 2017). To minimize relocation error, long-term permanently marked plots are suggested for monitoring programs (ROSS et al. 2010). However, permanent marking of plots has only been done in rather recent studies, and resurveys based on permanently marked plots are still scarce (but see LÜDI 1936, FISCHER et al. 2010, KOORDINATIONSSTELLE BDM 2014, BOCH et al. 2018a, KUDERNATSCH et al. 2019). As historical plots were usually not permanently marked and thus cannot be exactly relocated, there is high potential for relocation error in vegetation resurveys, which might result in wrong and misleading conclusions on found vegetation changes (BAKKER et al. 1996, KAPFER et al. 2017). Among non-permanent plots, two categories are distinguished: first, quasi-permanent plots can relatively well be relocated, because their coordinates or other accurate information are available (IMMOOR et al. 2017). The relocation error of quasi-permanent plots can potentially be kept within an acceptable range (KAPFER et al. 2017). Second, non-traceable plots have no information on their exact position within a given sampling site (STIX & ERSCHBAMER 2018). As the relocation error of non-traceable plots is large, they are not suitable to interpret temporal vegetation changes and should be avoided (KAPFER et al. 2017).

In addition, in most historical surveys vegetation plots were not randomly but subjectively selected by their vegetation composition to represent the most ‘typical’ vegetation of often only limited spatial extent. Thus, when repeating a vegetation relevé, a random spatial deviation from the original plot might result in pseudo-changes, since the resurveyed plot will almost inevitably be placed in less typical vegetation. Therefore, temporal effects can often not be separated from the effects of relocation error (ROSS et al. 2010, VERHEYEN et al. 2018). Moreover, as a resurvey is usually conducted by a different observer than that of the historical survey, observer error is likely to occur (KAPFER et al. 2017, VERHEYEN et al. 2018). The species identification error, resulting in pseudo-turnover and thereby compositional differences over time (MILBERG et al. 2008, BURG et al. 2015) might be reduced by using species aggregates for species that are notoriously difficult to identify and by ensuring high botanical skills of observers.

While the effects of relocation and observer error on species richness patterns in resurveys have been well studied, their effects on ecological indicator values has not been evaluated so far. Ecological indicator values are – beside species diversity and vegetation composition – an important component to describe differences among vegetation types (e.g. GHEZA et al. 2019, WITTIG et al. 2019) and in the interpretation of vegetation changes (ELLENBERG et al. 2001, LANDOLT et al. 2010, Czortek et al. 2018). They describe the realized niche optimum of a species on an ordinal scale. The respective values are not based on measurements, but on the experience of field botanists. They do better describe longer-term site conditions than exact point measurements (WAMELINK et al. 2002). For the comparison of historical and recent vegetation surveys ecological indicator values are particularly suitable, since they can indicate ecological changes in time (DIEKMANN 2003, IMMOOR et al. 2017, KÜCHLER et al. 2018). In addition, ecological indicator values can be used to describe spatial environmental changes, i.e. along elevational gradients. In Switzerland, the vegetation composition progressively changes along the large elevational gradient from warmer and drier low-elevation to colder and wetter high-elevation conditions. While species richness-elevation relationships are well explored, with a mid-elevational peak being the most common relationship (McCain & Grytnes 2010), it is largely unknown whether temporal changes of mean ecological indicator values based on vegetation changes differ along elevational gradients. For instance, one might expect changes of mean indicator values to be stronger at lower than at higher elevations, because of larger anthropogenic effects at lower elevations, i.e. high land-use intensity and nitrogen deposition in the lowlands (Güsewell et al. 2012).

The data used in the present study originated from the monitoring of nationally important habitats in Switzerland. To protect its biodiversity and to prevent habitat loss and the extinction of endangered species, Switzerland designated close to 7000 sites of national importance. These sites are legally protected and include fens, bogs, dry grasslands and flood plain habitats as well as amphibian breeding sites. They range from the lowlands to high mountain areas above 2500 m. The dry grasslands of national importance comprise 3631 sites and consist of meadows and pastures of various vegetation types. Between 1995 and 2006 about 10,000 vegetation plots were surveyed within these sites (for details see Eggenberg et al. 2001, Bafu 2017a, b). In 2011, the long-term program "monitoring the effectiveness of habitat conservation in Switzerland" has been established to monitor changes in the nationally important habitats. Data are collected using remote sensing and field surveys. For the analyses of temporal vegetation changes, 788 of the approximately 7000 sites of national importance were selected. Of these, 409 are dry grassland sites. In total, around 7000 permanent plots with a size of 10 m^2 were established and surveyed between 2011 and 2017 (for details see Boch et al. 2018a). 538 of the above mentioned historically sampled plots in Swiss dry grasslands of national importance were resurveyed. These sites covered an elevational gradient of more than 2000 m. As historical GPS-derived coordinates with information on the post-processed GPS inaccuracy of each plot were available, the historical plots are as quasi-permanent. This allowed a comparison of the vegetation data of the historical survey and the resurvey.

We hypothesized (1) stronger changes in mean indicator values, reduced number of dry grassland species and higher species turnover with increasing GPS inaccuracy of the historical plots because of increasing relocation error (Kapfer et al. 2017, Verheyen et al. 2018) and (2) changes of mean indicator values and number of dry grassland species to be stronger at lower than at higher elevations because of larger anthropogenic impact at lower elevations.

2. Methods

2.1 Study system and methodological details of the historical survey

To counteract the ongoing decline of diversity in dry grasslands in Switzerland, the dry grasslands were included in a national inventory of sites of national importance. The inventory comprises 3631 dry grasslands of national importance across Switzerland, representing about 0.5% of the country's land area (Bafu 2017c). The sites were selected based on their dominating vegetation types, ranging from very dry inner alpine steppes and continental dry grasslands of the *Festucetalia valesiacae* order, and Central European dry grassland communities of the *Xerobromion erecti* alliance, semi-dry *Mesobromion erecti* and *Arrhenatheretalia elatioris* (with a high proportion of dry grassland species) communities to subalpine mountain grasslands such as *Seslerion variae*, *Festucion variae*, *Caricion ferrugineae* and *Nardion strictae* communities (syntaxon names according to Eggenberg et al. 2001).

During the historical survey, plots were selected subjectively within sites to represent the most 'typical' vegetation. In addition, observers classified the vegetation into 19 different vegetation types using a classification scheme. In total 10,059 circular plots with a size of 28 m^2 were surveyed in the 3631 sites between 1995 and 2006. Unfortunately, not all species but only a defined subset of key species were recorded, representing character species of the 19 vegetation types (lists of historically recorded key species of each of the 19 vegetation types are given in EGGENBERG et al. 2001). In addition, to avoid identification efforts, many species aggregates were used, in cases where species identification was difficult. The abundance of each taxon was estimated using the combined abundance-cover scale of Braun-Blanquet. GPS coordinates were recorded, and a metric measure of post-processed GPS inaccuracy was calculated based on the 68% mean square error of the multiple measures (> 100) per plot. The plots can thus be regarded as quasi-permanent plots. The average sampling time was limited to 20 min per plot (for details see EGGENBERG et al. 2001).

2.2 Selection of the resurveyed plots and methods of resurvey

As part of the program monitoring the effectiveness of habitat conservation in Switzerland, a weighted sample of 409 sites out of the pool of the above 3631 dry grassland sites was taken, representing all vegetation types in all biogeographic regions of Switzerland (for methodological details see TILLÉ & ECKER 2014).

Based on the size of each site, we selected one or two of the historical relevés per site for our resurvey. Selection criteria were the availability of GPS-derived coordinates with information on GPS inaccuracy, and complete vegetation relevés (as based on an available historical field estimate indicating that approximately > 90% of occurring key species were sampled). Among all suitable plots per site, the selection criteria for the resampling plots were the maximum distance between all plots at a site and rare vegetation types (i.e. down-weighting common *Arrhenatherion elatioris* and *Seslerion variae* communities). Moreover, if two plots were selected per site it was ensured that they represented different vegetation types (based on the historical vegetation classification).

From 2011 to 2017, 538 of the historically sampled 28 m^2 plots were resurveyed from mid-May to end of July (depending on the elevation of plots), at a date comparable to the survey date of the historical survey and when vegetation was well developed. We used the available coordinates from the historical survey to relocate the quasi-permanent plots with a Trimble Geo 7X H-Star – a real time differential GPS with 10 cm precision after post processing. We therefore consider the GPS inaccuracy of the resurvey as negligible and did not further account for it in the analysis. The resurveyed sites were distributed across Switzerland and covered an elevational gradient from 230 m to 2320 m a.s.l. (Fig. 1). In resurveyed plots, all occurring vascular plant species (not only key species; all taxa identified to the species level) were recorded and the cover of each species was estimated using a modified Braun-Blanquet scale (r ≙ < 0.1%, + ≙ 0.1% – < 1%, 1 ≙ 1% – < 5%, 2 ≙ 5% – < 25%, 3 ≙ 25% – < 50%, 4 ≙ 50% – < 75%, 5 ≙ 75% – < 100%).

To ensure the comparability of the resurveyed dataset with the historical one, we first aggregated species to the historically used species aggregates and excluded all non-key species prior to analysis. However, the possibilities for comparative analyses were limited by the historical sampling method. For instance, as only native and "typical" plant species were historically recorded, it was not possible to study whether neophytes or generalist species were invading the quasi-permanent plots (i.e. homogenization on the expense of specialist species; GOSSNER et al. 2016). In addition, it was not possible to analyze changes in the number of threatened taxa, because no information on the conservation status was available for species aggregates (BAFU 2011, BORNAND et al. 2016). However, to test for vegetation changes, the mean indicator values for temperature, light, moisture, nutrients, ruderality and stress for the historical and the resampled relevés according to LANDOLT et al. (2010) were calculated. For the ruderality and stress values, the information given in LANDOLT et al. (2010), which is based on Grime's C-S-R triangle (GRIME 1974), was transformed to a numerical value ranging from 0 to 3. For instance, to a species with triple 's' in LANDOLT et al (2010), indicating the highest stress tolerance, a value of

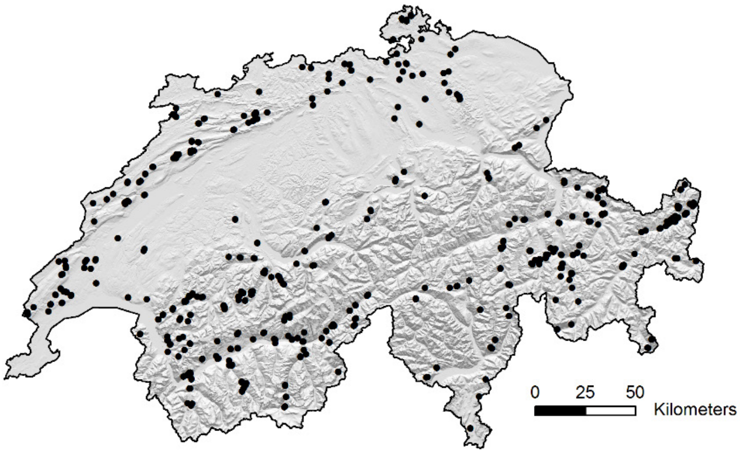

Fig. 1. Location of the 384 selected sites (black dots; 538 plots) of dry grasslands of national importance in Switzerland.

Abb. 1. Lage der für diese Studie ausgewählten 384 Trockenwiesen und -weiden von nationaler Bedeutung (schwarze Punkte, 538 Untersuchungsflächen).

3 was assigned. As it was not possible to estimate the bias in abundance estimation of the different observers, we used the unweighted arithmetic mean of indicator values of occurring species per plot instead of the commonly used abundance weighted mean (cf. KLAUS et al. 2012).

2.3 Statistical analysis

All statistical tests were performed in R version 3.5.1 (R CORE TEAM 2018). To avoid large differences in the variances among factors and to improve model convergence, we first standardized all continuous variables to a mean of 0 and standard deviation of 1. We then used linear mixed-effect models (lmerTest package; KUZNETSOVA et al. 2017) to test the effects of elevation, GPS inaccuracy and survey period (historical survey vs. resurvey) on the number of key species and ecological indicator values. We fitted plot-identification as a random factor to first correct for plot-specific differences and ensure the paired comparison of temporal changes within a plot. As non-linear relationships between elevation and species richness are common for many taxa including vascular plants (MCCAIN & GRYTNES 2010), we further included elevation as a quadratic term (Table 1). We did not use the quadratic term of elevation in models testing effects on indicator values, because it yielded no major improvement in the explained variation of the models and because there was no plausible hypothesis to test for a non-linear indicator value-elevation relationship. To test for differences in the strength of the effects between the historical survey and the resurvey along the elevational gradient, we included the interaction between survey period and elevation (in case of the key species richness model also the interaction of survey and the quadratic elevation term; Table 1). As GPS inaccuracy was taken from the data of the historical survey, we also included the interaction between GPS inaccuracy and survey to test whether the GPS inaccuracy affects the strength of the differences between the historical survey and the resurvey (Table 2). Moreover, we calculated the turnover (Sørensen dissimilarity) of taxa between the historical survey and the resurvey for each plot (SØRENSEN 1948): Turnover = b+c/ 2a+b+c, where b is the number of species present in the historical survey but not the resurvey, c is the number of species present in the resurvey but not in the historical survey and a is the number of species present in both surveys. We used a linear model to test the effects of elevation and GPS inaccuracy on turnover (Table 3). For all models, we further calculated the R^2 as the marginal coefficient of determination for mixed models, which represents the variance explained by the fixed effects (MuMin package; BARTON 2018).

3. Results

3.1 General findings

In the 538 plots, 469 certainly identified key species were recorded in both surveys (449 in the resurvey). The relationship of the number of key species with elevation followed an optimum curve (indicated by the significant quadratic elevation term; Table 1) peaking with an average of 39.0 species per plot at 1620 m (Fig. 2). With increasing elevation, the mean indicator values for light, moisture and stress increased, while the mean indicator values for temperature, nutrients and ruderality decreased (Table 2). The temporal turnover of key species ranged from 14% to 76% and was high with an average of 34% (±0.1 SD). Species turnover was not affected by elevation (Table 3).

Table 1. Summary of linear mixed-effect models with plot-identification fitted as random factor, separating the effects of elevation (including a quadratic term), GPS inaccuracy, survey period (historical vs. resurvey) as well as the interactions of elevation (and the quadratic term) and GPS inaccuracy with the survey period on the number of key species. Significant differences are indicated by bold *p*-values at $p < 0.05$. R^2 denotes the marginal coefficient of determination for mixed models which represents the variance explained by fixed effects.

Tabelle 1. Linear gemischte Modelle der Anzahl Schlüsselarten. Es wurden die Effekte der Höhe ü.M. (einschließlich quadratischer Term), der GPS-Ungenauigkeit, des Aufnahmezeitpunkts (Erst- vs. Folgeerhebung) und die Interaktionen zwischen Höhe ü.M. (einschließlich quadratischer Term) und GPS-Ungenauigkeit mit dem Aufnahmezeitpunkt auf die Anzahl Schlüsselarten getestet (Untersuchungsfläche wurde als Zufallsvariable getestet). Die Steigung gibt die Richtung des Effekts an. Signifikante Unterschiede sind durch fett gedruckte P-Werte gekennzeichnet.

		Number of key species	
	df	*Slope*	*p*
Intercept	1	-0.02	0.677
Elevation	1	0.23	**<0.001**
Elevation^2	1	-0.17	**<0.001**
GPS inaccurracy	1	-0.07	0.071
Survey period (historical vs. resurvey)	1	0.45	**<0.001**
Elevation × survey period	1	0.09	**0.016**
Elevation^2 × survey period	1	-0.06	0.122
GPS inaccurracy × survey period	1	-0.01	0.741
			$R^2 = 0.18$

3.2 Temporal vegetation changes

On average, the number of key species was 12% higher in the resurvey compared to the historical survey (+4.13 species; Table 1, 4). Unexpectedly, the temporal change in the number of key species was more pronounced at higher than at lower elevation (indicated by the significant elevation × survey period interactions; Fig. 2, Table 1). In addition, the mean indicator values for light and stress significantly decreased, and the ones for moisture, nutrients and ruderality significantly increased between the historical survey and the resurvey

Table 2. Summary of linear mixed-effect models with plot-identification fitted as random factor, separating the effects of elevation, GPS inaccuracy, survey period (historical vs. resurvey) as well as the interactions of elevation and GPS inaccuracy with survey period on mean indicator values. Significant differences are indicated by bold p-values at $p < 0.05$. R^2 denotes the marginal coefficient of determination for mixed models which represents the variance explained by fixed effects.

Tabelle 2. Linear gemischte Modelle der mittleren Zeigerwerte. Es wurden die Effekte der Höhe ü.M., der GPS-Ungenauigkeit, des Aufnahmezeitpunkts (Erst- vs. Folgeerhebung) und die Interaktionen zwischen Höhe ü.M. und GPS-Ungenauigkeit mit dem Aufnahmezeitpunkt auf die mittleren Zeigerwerte getestet (Untersuchungsfläche wurde als Zufallsvariable getestet). Die Steigung gibt die Richtung des Effekts an. Signifikante Unterschiede sind durch fett gedruckte P-Werte gekennzeichnet.

		Indicator value for											
		Temperature		Light		Moisture		Nutrients		Ruderality		Stress	
	df	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*	*Slope*	*p*
Intercept	1	0.01	0.94	0.1	**0.021**	-0.07	0.077	-0.08	**0.036**	-0.07	0.052	0.1	**0.011**
Elevation	1	-0.85	**<0.001**	0.03	0.481	0.37	**<0.001**	-0.42	**<0.001**	-0.59	**<0.001**	0.3	**<0.001**
GPS inaccurracy	1	0.05	**0.039**	-0.01	0.887	-0.03	0.45	0.01	0.801	-0.04	0.278	0.05	0.184
Survey period	1	-0.01	0.733	-0.2	**<0.001**	0.14	**<0.001**	0.17	**<0.001**	0.13	**<0.001**	-0.21	**<0.001**
Elevation × survey period	1	0.01	0.204	-0.02	0.409	0.04	**0.003**	0.07	**0.002**	-0.01	0.665	-0.04	0.13
GPS inaccurracy × survey period	1	-0.02	0.056	0.01	0.755	0.03	**0.039**	0.01	0.77	0.03	0.349	-0.04	0.149
		$R^2 = 0.71$		$R^2 = 0.01$		$R^2 = 0.16$		$R^2 = 0.15$		$R^2 = 0.36$		$R^2 = 0.09$	

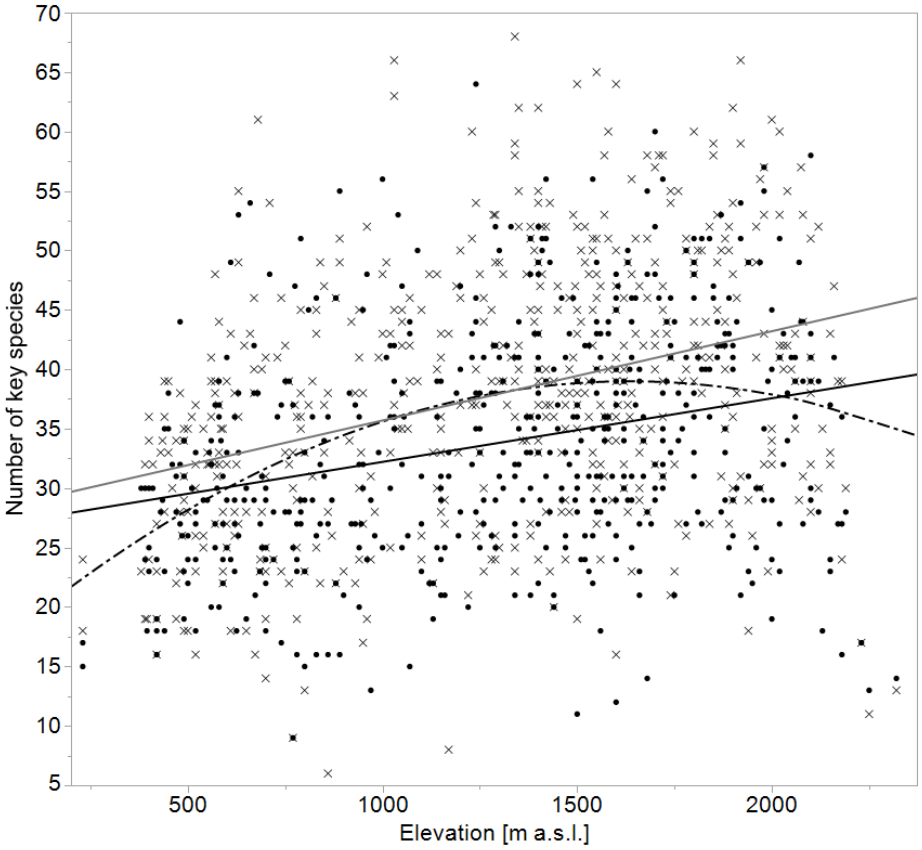

Fig. 2. Overall quadratic relationship between number of key species and elevation (dashed line), as well as the linear relationship between number of key species and elevation for the historical survey (black dots and black line) as well as the corresponding linear relationships for the resurvey (grey crosses and grey line; 538 plots; untransformed raw data). The trend lines represent significant relationships (Table 1).

Abb. 2. Unimodale Beziehung zwischen der Schlüsselartenzahl und der Höhe ü.M. (gestrichelte Linie), sowie lineare Beziehungen zwischen Schlüsselartenzahl und der Höhe ü.M. für die Ersterhebung (schwarze Punkte und schwarze Linie) sowie für die Folgeerhebung graue Kreuze und graue Linie; 538 Untersuchungsflächen, untransformierte Werte). Die Trendlinien zeigen signifikante Beziehungen an (Tab. 1).

(Table 2, 4). Again, the temporal change of the mean indicator value for nutrients and moisture was more pronounced at higher than at lower elevation (indicated by the significant elevation × survey period interactions; Table 2, Fig. 3, 4).

3.3 Relocation error

The GPS inaccuracy in the historical survey ranged from 0.33 m to 4.98 m and was on average 1.48 m (± 0.72 m SD). However, we found almost no effects of the GPS inaccuracy on the temporal changes of the mean indicator values between the historical survey and the resurvey. Only the mean indicator value for moisture significantly increased with increasing

Table 3. Summary of linear model, separating the effects of elevation and GPS inaccuracy on the turnover of key species. Significant differences are indicated by bold p-values at $p < 0.05$. R^2 denotes the marginal coefficient of determination which represents the variance explained by fixed effects.

Tabelle 3. Lineares Modell der Artenfluktuation über die Zeit. Es wurden die Effekte der Höhe ü.M. und der GPS-Ungenauigkeit auf Artenfluktuation getestet. Die Steigung gibt die Richtung des Effekts an. Signifikante Unterschiede sind durch fett gedruckte P-Werte gekennzeichnet.

		Turnover of key species	
	df	*Slope*	*p*
Intercept	1	< 0.01	1.000
Elevation	1	-0.06	0.056
GPS inaccurracy	1	0.08	**0.007**
			$R^2 = 0.19$

Table 4. Mean number of key species and mean ecological indicator values in the 28 m^2 plots of the historical survey and the resurvey (untransformed mean ± SE).

Tabelle 4. Mittelwerte der Schlüsselartenzahl und der Zeigerwerte in den 28 m^2 großen Untersuchungsflächen (untransformierte Mittelwerte ± Standardfehler) für die Erst- und Folgeerhebung.

	Historical survey		Resurvey	
	Mean	SE	Mean	SE
Number of key species	33.81	0.42	37.94	0.48
Indicator value				
Temperature	3.10	0.03	3.10	0.03
Light	3.82	0.01	3.80	0.01
Moisture	2.33	0.02	2.38	0.02
Nutrients	2.38	0.01	2.41	0.01
Ruderality	0.62	0.01	0.64	0.01
Stress	1.19	0.01	1.17	< 0.01

GPS inaccuracy (indicated by the significant GPS inaccuracy × survey period interaction; Table 2). However, the temporal turnover of key species significantly increased with increasing GPS inaccuracy (Table 3, Fig. 5)

4. Discussion

4.1 General elevational effects on species richness and mean indicator values

Plant species richness relationships to elevation are diverse and differ among biogeographic regions from linearly declining species richness with increasing elevation (metabolic theory of ecology assuming a decline of species richness and productivity from warm to cold regions; Brown et al. 2004) over several non-linear relationships to even linearly increasing relationships (e.g. because of increasing precipitation; McCain & Grytnes 2010). Our finding of a mid-elevational peak of species richness corresponds well to the most common species richness-elevation relationship found for many taxa. It can be explained by the overlap of distribution ranges of low- and high-elevation species and by less extreme

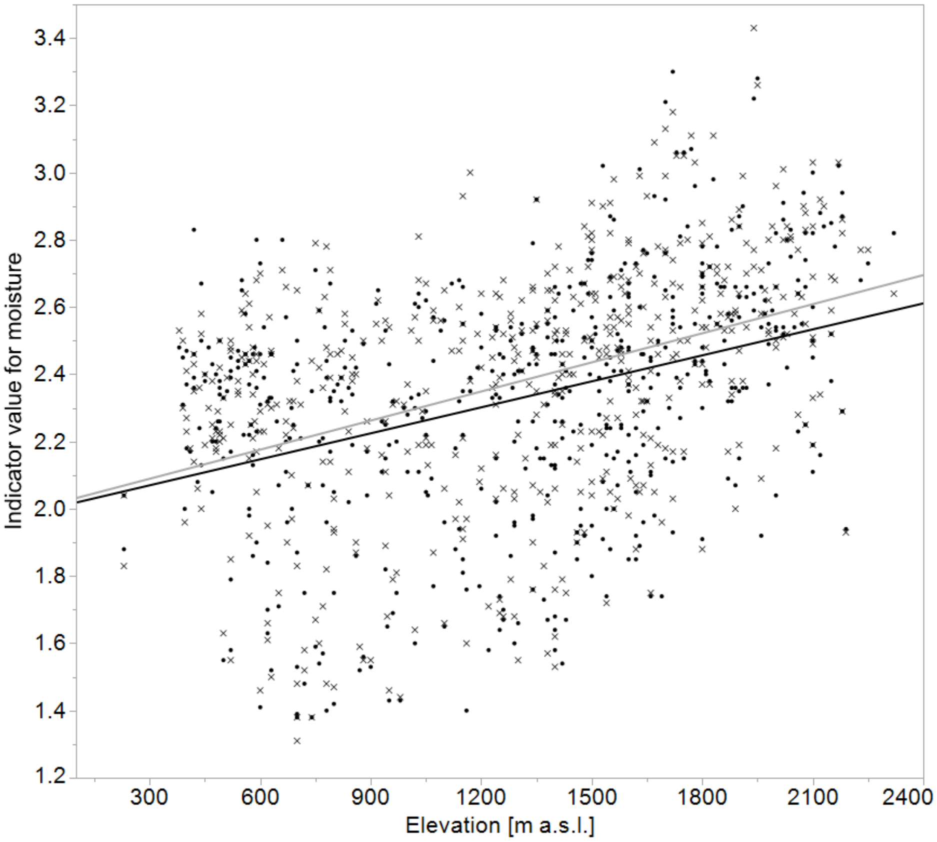

Fig. 3. Relationship between mean indicator value for moisture and elevation for the historical survey (black dots and black line) and the resurvey (grey crosses and grey line; 538 plots, untransformed raw data). The trend lines indicate significant relationships (Table 2).

Abb. 3. Beziehung zwischen der mittleren Feuchtezahl und der Höhe ü.M. für die Ersterhebung (schwarze Punkte und schwarze Linie) sowie für die Folgeerhebung (graue Kreuze und graue Linie; 538 Untersuchungsflächen, untransformierte Werte). Die Trendlinien zeigen signifikante Beziehungen an (Tab. 2).

environmental conditions at intermediate elevation (e.g. climatic conditions are often harsher at low and high elevations than at intermediate elevations), promoting high speciation and low extinction (reviewed in McCain & Grytnes 2010).

The findings of increasing mean indicator values for light, moisture and stress and at the same time decreasing mean indicator values for temperature, nutrients and ruderality with increasing elevation are intuitive and correspond to the general change of various conditions with elevation: mean temperature is decreasing, the growing season is shorter, solar radiation and precipitation (at least in the European Alps) are higher at higher elevations. At the same time, mineralization rate and N deposition is lower at high than at low elevation (Körner 2003). As the mean indicator value for nutrients is only weakly related to soil nutrient content and mainly reflects the productivity in terms of plant biomass (Schaffers & Sykora 2000) or biomass nitrogen concentrations (Klaus et al. 2012), these elevational changes

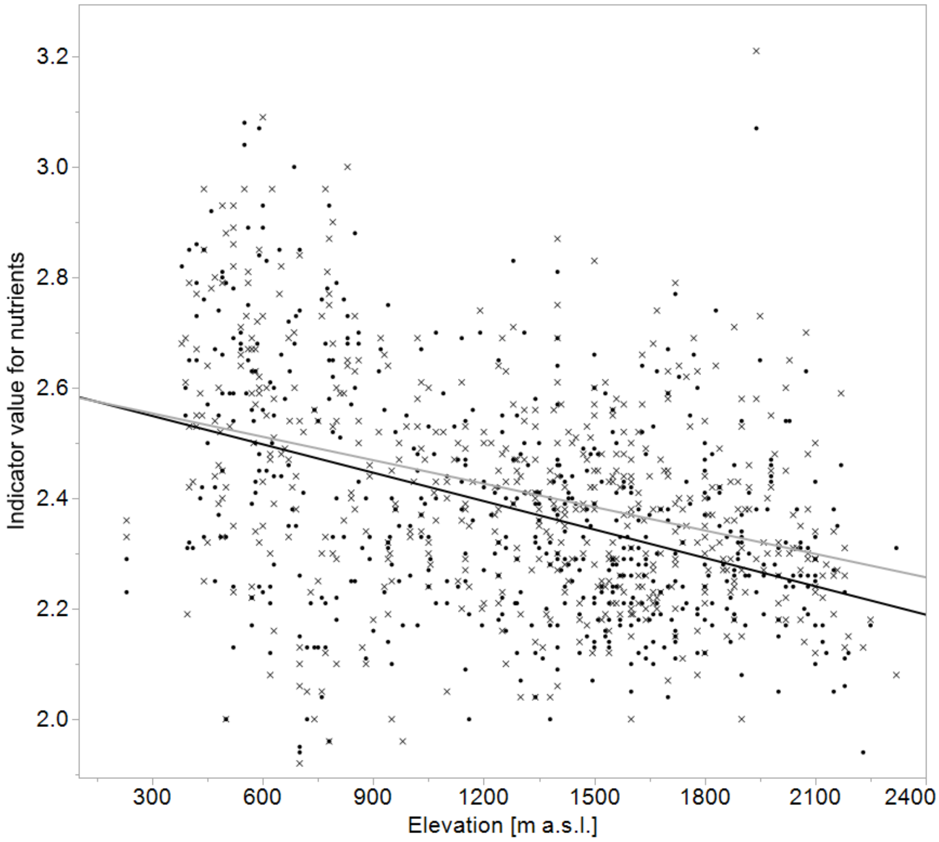

Fig. 4. Relationship between mean indicator value for nutrients and elevation for the historical survey (black dots and black line) and the resurvey (grey crosses and grey line; 538 plots; untransformed raw data). The trend lines indicate significant relationships (Table 2).

Abb. 4. Beziehung zwischen der mittleren Nährstoffzahl und der Höhe ü.M. für die Ersterhebung (schwarze Punkte und schwarze Linie) sowie für die Folgeerhebung (graue Kreuze und graue Linie; 538 Untersuchungsflächen, untransformierte Werte). Die Trendlinien zeigen signifikante Beziehungen an (Tab. 2).

reflect the decreasing productivity and increasing environmental stress because of harsher conditions with increasing elevation (VONLANTHEN et al. 2006). The findings of the present study also fit well to other studies which were investigating elevational changes of indicator values. For example, ODLAND (2009) generally found decreasing temperature and nutrient indicator values and increasing light values with increasing elevation based on floristic data from two areas in Norway. Similarly, GÜSEWELL et al. (2012) found decreasing nutrient indicator values with increasing elevation when analyzing vegetation plot data of the Swiss Biodiversity Monitoring Program (www.biodiversitymonitoring.ch).

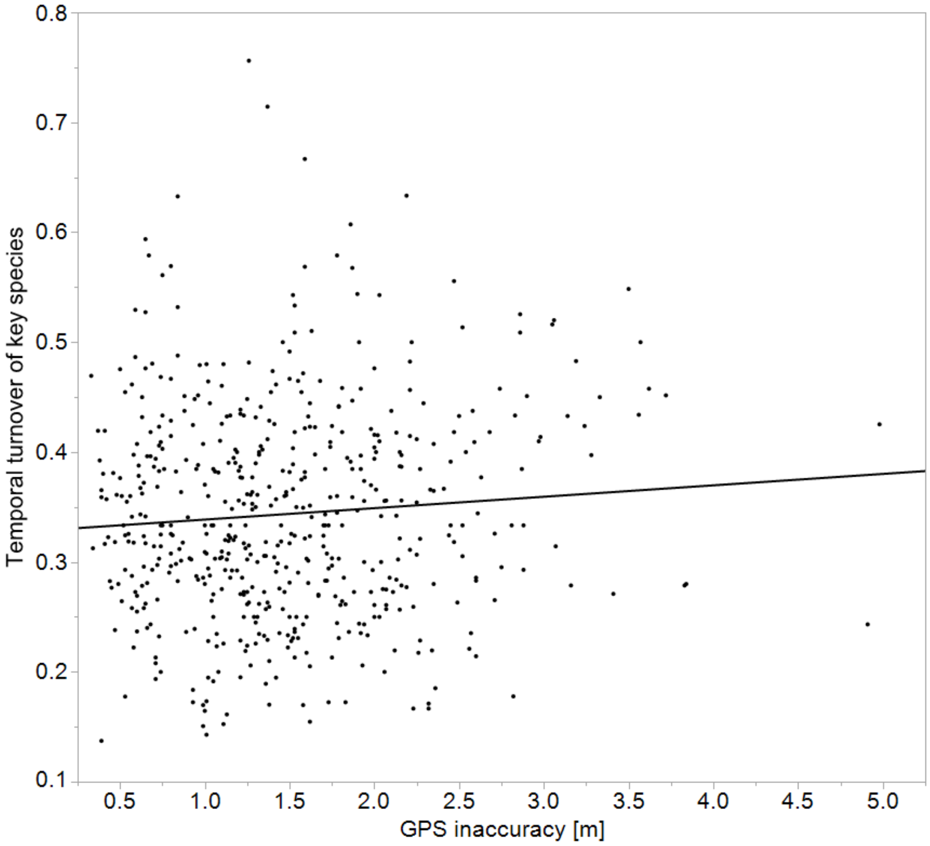

Fig. 5. Relationship between temporal turnover of key species (historical survey vs. resurvey) and GPS inaccuracy of the historical survey (538 plots; untransformed raw data). The trend line indicates a significant relationship (Table 3).

Abb. 5. Beziehung zwischen der Artenfluktuation und der GPS-Ungenauigkeit zwischen der Erst- und Folgeerhebung. Die Trendlinie zeigt eine signifikante Beziehung an (Tab. 3).

4.2 Temporal vegetation changes and the effect of relocation error

In contrast to previous studies reporting an effect of observer error on species richness (e.g. KAPFER et al. 2017, VERHEYEN et al. 2018), the overall higher number of key species in the resurvey compared to the historical survey was probably not caused by different observers, but rather was a methodological issue. In the resurvey, roughly one hour was spent surveying the vegetation per plot (note that all species and not only key species were recorded; BOCH et al. 2018a). In contrast, the sampling time of the historical survey was limited to 20 minutes per plot (EGGENBERG et al. 2001). As survey effort plays an important role in species (BORNAND et al. 2014), the longer time spent for recording species in the resurvey likely explains the large temporal increase in the mean number of key species. Similarly, the unexpected more pronounced temporal increase in the number of key species at higher than at lower elevation (significant elevation × survey period interaction; Fig. 2) can be attributed to the longer time spent during the resurvey. Given the fixed limited relevé time in the historical survey, more species have likely been overlooked in species-rich than in species-poor plots. As species richness increases with elevation in the present data set, the probability of overlooking species also increases with elevation when the effort remains similar. Furthermore, the longer time spent during the resurvey might also have affected pseudo-turnover, as the number of overlooked species logically increases the dissimilarity between two surveys.

Overall, the patterns of decreasing mean light and stress indicator values and increasing mean nutrient and ruderality indicator values between the historical survey and the resurvey indicated decreasing habitat quality over a time period of only about one decade. This might be attributed to habitat changes and degradation because of land-use abandonment, intensification and fragmentation. Land-use abandonment often goes along with habitat fragmentation and isolation of habitats, leading to the progressive loss of specialist species at a site (HELM et al. 2006, BOCH et al. 2019). More locally, abandonment can cause litter accumulation which lowers the germination rate of light demanding species, reduces microhabitat availability and thereby promotes homogenization because of few remaining competitive species on the expense of generally small specialist plants. In addition, shrub encroachment in abandoned grasslands decreases light values and results in grassland loss (reviewed in VALKÓ et al. 2018). On the other hand, land-use intensification, which includes fertilization, higher grazing pressures and increased mowing frequencies, reduces the overall diversity of plants and other taxa in grasslands, with fertilization having the largest negative effects (ALLAN et al. 2014, GILHAUS et al. 2017, BOCH et al. 2018b, c). Similarly to abandonment, land-use intensification also leads to biotic homogenization in grasslands, because competitive species are promoted, which outcompete specialists (ALLAN et al. 2014, GOSSNER et al. 2016, BUSCH et al. 2019). In general, species profiting from land-use intensification are fast growing species, which tend to have higher indicator values for nutrients and moisture than slower growing species occurring in low-intensively managed grasslands (e.g. higher relative growth rates and higher specific leaf area; BARTELHEIMER & POSCHLOD 2016, BUSCH et al. 2019). Winners of intensification rather indicate mesic, i.e., less stressful conditions (PFESTORF et al. 2013, BUSCH et al. 2019).

We found a stronger increase of the mean indicator value for moisture and a weaker decrease of the mean indicator value for nutrients with elevation in the resurvey compared to the historical survey (Fig. 3, 4). These results seem to be counterintuitive, but they may simply imply less effective conservation measures in dry meadows and pastures of national importance at higher compared to lower elevations. This might again be attributed to the abandonment of labor intensive traditional alpine land-use systems or the intensification of land use, because of better infrastructures allowing the use of modern agricultural machines even in mountainous regions (STÖCKLIN et al. 2007).

However, the temporal changes of indicator values between the historical survey and the resurvey were largely independent of the relocation error (non-significant GPS inaccuracy × survey period interaction; only the moisture indicator value increased with GPS inaccuracy). This result is clearly against expectations of stronger changes of mean indicator values with increasing relocation error. Although the relocation error of the quasi permanent plots of the historical survey was with an average of 1.48 m relatively low compared to other studies (VERHEYEN et al. 2018), the present study confirms the recommendations of KAPFER et al. (2017). The authors suggested that quasi-permanent plots are suitable for the resurvey of vegetation data, if relocation error can be minimized, i.e. by relatively precise historical GPS coordinates. The present findings further highlight the robustness of indicator values to explore vegetation change over time in quasi-permanent plots, even when these were subjectively selected to represent the most "typical" vegetation types at a site and the resurveyed plots are almost inevitably selected on a spot with less typical vegetation. This might be because of the balancing effect of using mean indicator values.

Turnover of species in resurveys can be attributed either to actual changes or to observer error. The observer error can be relatively high and cause a large pseudo-turnover, even when a permanent plot is sampled by different observers at the same date (VITTOZ & GUISAN 2007, VERHEYEN et al. 2018). Moreover, the observer error is likely to increase with changing phenology within the same year and across years (KAPFER et al. 2017). With the present data, one cannot separate pseudo-turnover caused by different observers from real species turnover because of vegetation changes.

However, in contrast to mean indicator values, and confirming our expectations, the temporal turnover of key species significantly increased with increasing GPS inaccuracy. This finding of a strong relocation error on species composition and turnover is in line with VERHEYEN et al. (2018), who resampled forest plots across Europe and reported a large species turnover because of relocation error. This finding indicates that quasi-permanent plots might not be suited for vegetation resurveys when exploring patterns of temporal variation in species composition. Thus, it is of particular importance to use truly permanent plots when the goal is to explore the effect of different factors on the community stability of taxa and species composition over time (BLÜTHGEN et al. 2016, GIARRIZZO et al. 2017).

5. Conclusions

The dry grasslands of national importance in Switzerland are – compared to the majority of Swiss grasslands – relatively well preserved because of legal protection and conservation objectives for each site (BAFU 2017a, b). Nevertheless, the results of the present study indicated decreasing habitat quality of these grasslands of national importance in a short time period of only about one decade. This decreasing habitat quality hold particularly true for sites at higher elevations. Our study therefore highlights the need for continuous monitoring of these grasslands using permanent plots in the framework of the program monitoring the effectiveness of habitat conservation in Switzerland (BOCH et al. 2018a). Moreover, better measures of land use and additional information on surrounding landscapes (e.g. connectivity) would be valuable to further explore the causes of the observed changes in dry grasslands. This would also facilitate the development of adaptive management strategies for the grasslands of national importance.

Moreover, our findings point to important methodological implications for resurvey studies, i.e., ensuring exact localization of the plots by permanent belowground marking, as well as compiling full species lists without restrictions to a specific subset of species and without time limitations. The findings further highlight the robustness of mean ecological indicator values to explore vegetation changes over time in quasi-permanent plots, at least when relocation error can be minimized. However, the increasing species turnover with relocation error indicated that the resurvey of historical quasi-permanent plots, even with a relatively small relocation error, might not be suitable to study patterns of temporal variation in species composition and functional diversity measures.

Erweiterte deutsche Zusammenfassung

Einleitung – Der hier verwendete Datensatz stammt aus dem Monitoringprogramm Wirkungskontrolle Biotopschutz Schweiz. Um wertvolle Lebensräume und die Artenvielfalt zu bewahren, hat die Schweiz seit Beginn der 1990er-Jahre rund 7000 Biotope von nationaler Bedeutung ausgewiesen. Dazu zählen Hoch- und Übergangsmoore, Flachmoore, Trockenwiesen und -weiden, Auen und Amphibienlaichgebiete. Die Wirkungskontrolle Biotopschutz Schweiz untersucht mittels verschiedener Methoden – darunter Vegetationsaufnahmen und Luftbildanalysen, ob sich die Biotope von nationaler Bedeutung gemäß ihren Schutzzielen entwickeln und in ihrer Qualität erhalten bleiben.

Folgeerhebungen von historischen Vegetationsaufnahmen gewinnen heutzutage an Popularität, da sich dadurch Umwelt- und Vegetationsveränderungen über die Zeit erkennen lassen. Es gibt jedoch eine Reihe von möglichen Fehlerquellen, die es zu minimieren gilt, um Fehlinterpretationen von Ergebnissen und irreführende Schlussfolgerungen zu vermeiden. Neben einem nicht zu vermeidenden Bearbeitendeneffekt (Fehlbestimmung von Arten, Pseuo-Artenfluktuation, etc.), der sich nur durch stetes Training der Artenkenntnis minimieren lässt, ist die ungenaue Lokalisierung der Untersuchungsflächen bei der Folgeerhebung eine der häufigsten Fehlerquellen (BAKKER et al. 1996, KAPFER et al. 2017, VERHEYEN et al. 2018). Es liegt auf der Hand, dass die Abweichung der Artenzusammensetzung steigt, je weiter die Stelle der Erst- und Folgeerhebung voneinander entfernt liegt. Nur permanent markierte Untersuchungsflächen (z. B. mit Magnetsonden) erlauben die Wiedererhebung der exakt gleichen Fläche. Permanente Markierungen bilden jedoch immer noch die Ausnahme in Monitoring- oder Forschungsprojekten. Im Rahmen Wirkungskontrolle Biotopschutz Schweiz wurden 538 der während der Inventarisierung der Trockenwiesen und -weiden von nationaler Bedeutung beprobten Vegetationsaufnahmen wiederholt. Die Untersuchungsflächen decken einen Höhengradienten von über 2000 m ab. Bei der Ersterhebung wurden die Koordinaten der Untersuchungsflächen mit Angaben zur postprozessierten GPS-Ungenauigkeit erfasst. Man spricht von quasi-permanenten Untersuchungsflächen.

Basierend auf dem Vergleich der Erst- und Folgeerhebung wurden die folgenden Hypothesen getestet: (1) Eine zunehmende GPS-Ungenauigkeit der Ersterhebung bedingt eine stärkere Änderung der mittleren Zeigerwerte, eine verringerte Anzahl von Trockenrasenarten und eine höhere Artenfluktuation; (2) Die Änderungen der mittleren Zeigerwerte und der Anzahl der Trockenrasenarten über die Zeit sind aufgrund der ausgeprägten anthropogenen Einflüsse in tieferen stärker sind als in höheren Lagen.

Methoden – Von 1995 bis 2006 wurden bei der Inventarisierung der 3631 Trockenwiesen und -weiden von nationaler Bedeutung über 10.000 kreisförmige, 28 m^2 große Vegetationsaufnahmen erstellt. Dabei wurden nicht alle, sondern nur sogenannte Schlüsselarten erfasst. Dies waren Charakterarten der 19 untersuchten Vegetationstypen (Details in EGGENBERG et al. 2001). Die Flächen wurden nicht permanent markiert, aber jeweils eine Koordinate der Untersuchungsfläche mit Angaben zur postprozessierten GPS-Ungenauigkeit verzeichnet.

Von 2011 bis 2017 wurden im Rahmen der Wirkungskontrolle Biotopschutz Schweiz 538 der obigen historischen Vegetationsaufnahmen in Trockenwiesen und -weiden von nationaler Bedeutung wiederholt. Die Untersuchungsflächen deckten alle biogeografischen Regionen der Schweiz und einen Höhengradienten von über 2000 m ab (Abb. 1). Die Flächen wurden anhand der Koordinaten der Ersterhebung mit einem leistungsfähigen GPS (Trimble Geo 7X H-Star) zur zentimetergenauen Einmessung bestimmt und das Zentrum mit einer Magnetsonde permanent unterirdisch markiert. Wir erfassten alle Gefäßpflanzenarten und schätzten ihre Deckung. Um die Vergleichbarkeit der Erst- und Folgeerhebung zu gewährleisten, wurden nur die in der Ersterhebung verwendeten Schlüsselarten in den Analysen berücksichtigt.

Wir berechneten mittlere Zeigerwerte für Temperatur, Licht, Feuchtigkeit, Nährstoffe, Ruderalität und Stress nach LANDOLT et al. (2010). Mittels gemischter Modelle errechneten wir danach die Effekte von Höhenlage, GPS-Ungenauigkeit und Aufnahmezeitpunkt (Erst- vs. Folgeerhebung) auf die Anzahl der Schlüsselarten und die mittleren Zeigerwerte (Tab. 1, 2). Mit einem linearen Modell errechneten wir außerdem wie die Artenfluktuation von Erst- zu Folgeerhebung (Sørensen-Unähnlichkeit; SØRENSEN 1948) durch Höhenlage und GPS-Ungenauigkeit beeinflusst wurden (Tab. 3).

Ergebnisse – Die Anzahl Schlüsselarten folgte einer Kurve entlang des Höhengradienten mit einem Höchstwert von 39,0 Arten bei 1620 m ü.M. Bei der Folgeerhebung war die Anzahl Schlüsselarten 12 % höher als bei der Ersterhebung. In höheren Lagen war die Veränderung der Anzahl Schlüsselarten jedoch höher als in niedrigen Lagen (Abb. 2, Tab. 1).

Mit zunehmender Höhe stieg die mittlere Licht-, Feuchte- und Stresszahl, während die Temperatur-, Nährstoff- und Ruderalitätszahl abnahm (Tab. 2). Darüber hinaus sank die mittlere Licht- und Stresszahl von der Erst- zur Folgeerhebung, bei gleichzeitigem Anstieg der Feuchte -, Nährstoff- und Ruderalitätszahl (Tab. 2, 4). Auch hier war die zeitliche Veränderung der Nährstoff- und Feuchtezahl in höheren Lagen ausgeprägter als in niedrigeren Lagen (Tab. 2, Abb. 3, 4). Die GPS-Ungenauigkeit hatte fast keine Auswirkungen auf die zeitlichen Änderungen der mittleren Zeigerwerte. Einzig die Feuchtezahl stieg mit zunehmender GPS-Ungenauigkeit signifikant an (Tab. 2). Die Fluktuation der Schlüsselarten von der Erst- zur Folgeerhebung lag bei durchschnittlich 34 % und nahm mit zunehmender GPS-Ungenauigkeit zu (Tab. 3, Abb. 5).

Diskussion – Eine Optimumskurve der Artenzahl entlang des Höhengradienten wie hier gefunden, entspricht der allgemein bekannten Artenzahl-Höhe-Beziehung. Dies lässt sich durch die Überschneidung der Verbreitungsgebiete von Arten aus niedrigen und hohen Lagen, sowie weniger extreme Umweltbedingungen in mittleren als in niedrigen und hohen Lagen erklären (MCCAIN & GRYTNES 2010). Die insgesamt höhere Anzahl von Schlüsselarten der Folgeerhebung im Vergleich zur Ersterhebung ist wahrscheinlich auf die Limitierung von 20 Minuten Bearbeitungsdauer pro Untersuchungsfläche zur Erfassung der Schlüsselarten (EGGENBERG et al. 2001) zurückzuführen. Bei der Folgeerhebung wurden rund 60 Minuten pro Untersuchungsfläche aufgewendet. Da der Zeitaufwand eine wichtige Rolle bei der Vollständigkeit von Artenlisten spielt (BORNAND et al. 2014), ist die Zunahme der Schlüsselartenzahl in der Folgeerhebung erklärbar. Auch die stärkere Zunahme der Schlüsselartenzahl in höheren als in niedrigeren Lagen kann auf die zusätzlich investierte Zeit während der Folgeerhebung zurückgeführt werden: Da die mittlere Artenvielfalt pro Untersuchungsfläche mit der Höhe zunahm, steigt bei gleichem Zeitaufwand die Wahrscheinlichkeit Arten mit zunehmender Höhe zu übersehen.

Die steigende Licht-, Feuchte - und Stresszahl bei gleichzeitig sinkender Temperatur-, Nährstoff- und Ruderalitätszahl mit zunehmender Höhe entsprechen den generellen Veränderungen von Umweltbedingungen mit zunehmender Höhe (GÜSEWELL et al. 2012): Mit der Höhe sinkt die mittlere Temperatur, die Vegetationszeit verkürzt sich, die Sonneneinstrahlung ist stärker und die Niederschlagsmenge ist höher. Gleichzeitig sinken Mineralisierungsrate und Stickstoffdeposition mit der Höhe (KÖRNER 2003). Die Ergebnisse spiegeln somit die sinkende Produktivität und den zunehmenden Umweltstress aufgrund härterer Bedingungen mit zunehmender Höhe wider (VONLANTHEN et al. 2006).

Die abnehmende Licht- und Stresszahl und zunehmende Nährstoff- und Ruderalitätszahl von der Erst- zur Folgeerhebung deutet jedoch auf eine abnehmende Lebensraumqualität hin. Dies könnte auf die Degradierung der Habitate aufgrund von Landnutzungsaufgabe und Intensivierung zurückzuführen sein (ALLAN et al. 2014, VALKÓ et al. 2018). Ähnlich wie bei der Nutzungsaufgabe führt auch die Intensivierung der Landnutzung zu einer biotischen Homogenisierung im Grünland, da konkurrenzstarke Arten zu Ungunsten von Spezialisten gefördert werden (ALLAN et al. 2014, GOSSNER et al. 2016, BUSCH et al. 2019).

Bei der Folgeerhebung fanden wir einen stärkeren Anstieg der Feuchtezahl und einen schwächeren Rückgang der Nährstoffzahl in höheren als in niedrigeren Lagen (Abb. 3, 4). Dies könnte auf weniger effektive Schutzmaßnahmen und die Aufgabe der oft arbeitsintensiven Nutzung in höher gelegenen Trockenwiesen und -weiden von nationaler Bedeutung hindeuten (STÖCKLIN et al. 2007). Die Veränderungen der Zeigerwerte zwischen der Erst- und Folgeerhebung waren jedoch weitgehend unabhängig von der GPS-Ungenauigkeit, was die Eignung von quasi-permanenten Untersuchungsflächen für den Vergleich von Zeigerwerten über die Zeit nahelegt.

Im Gegensatz zu den mittleren Zeigerwerten, stieg die Artenfluktuation mit zunehmender GPS-Ungenauigkeit signifikant an. Dies weist darauf hin, dass quasi-permanente Untersuchungsflächen nicht unbedingt für die Analyse von Diversitätsmustern über die Zeit geeignet sind.

Schlussfolgerungen – Obwohl die Trockenrasen von nationaler Bedeutung in der Schweiz relativ gut geschützt sind, deuten unsere Ergebnisse auf eine abnehmende Lebensraumqualität in einem Zeitraum von nur etwa einem Jahrzehnt hin. Dies gilt insbesondere für höher gelegene Flächen. Unsere Ergebnisse unterstreichen daher die Notwendigkeit von Langzeitmonitorings zur Überwachung der Wirksamkeit des Lebensraumschutzes.

Außerdem lassen sich methodische Schlussfolgerungen für Folgeerhebungen von Vegetationsaufnahmen ableiten. Neben der permanenten Markierung der Untersuchungsflächen zur Wiedererhebung der exakt gleichen Fläche, sollten alle Arten (nicht nur bestimmte Taxa), ohne zeitliche Begrenzung der Bearbeitungsdauer aufgenommen werden. Die Ergebnisse unserer Studie unterstreichen weiterhin die Robustheit der mittleren Zeigerwerte zur Untersuchung von Vegetationsveränderungen über die Zeit in quasi-permanenten Untersuchungsflächen. Die steigende Artenfluktuation mit zunehmender GPS-Ungenauigkeit deutet jedoch darauf hin, dass nur permanent markierte Untersuchungsflächen für die Analyse von Diversitätsmustern über die Zeit geeignet sind.

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Author contribution statement

ABerg and RH conceived and designed the monitoring program of the nationally important habitats in Switzerland. KE designed the weighted site and plot selection procedure. AB, ABerg, HK, KE, MK, UG and SB conducted the resurvey of the vegetation plots. SB and ABerg analyzed the data. SB wrote the first draft of the paper. All authors contributed to the final manuscript.

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