



# No detrimental effects of delayed mowing or uncut grass refuges on plant and bryophyte community structure and phytomass production in low-intensity hay meadows

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## Abstract

To maintain European semi-natural grasslands, agri-environment schemes (AES) have been established in many countries but their biodiversity benefits have remained limited. We tested the effects of three new mowing regimes designed to benefit biodiversity in extensively managed meadows across the Swiss lowlands. Our experimental treatments mimicked easily implementable farming practices. We previously showed that invertebrates benefit from delayed mowing and leaving an uncut grass refuge. Here we focus on the effects on plant and bryophyte communities.

We compared the standard AES practice (earliest mowing on June 15, no fertilizer input, but no restriction on number of cuts) to three alternative mowing regimes: (i) earliest mowing delayed by one month, (ii) maximum of two cuts per year with at least eight weeks in between, and (iii) leaving an uncut refuge on 10–20% of the meadow area in 12 study areas in the Swiss lowlands. We also tested for the interactive effects of ambient temperature, precipitation, elevation, meadow size, local forest cover, time since AES registration, and phytomass production.

After five years of application, we found no difference in the effects of mowing regimes on vascular plant or bryophyte species richness, community composition, phytomass, flowering phenology or average plant height (the latter two indices were derived from the literature). However, cutting frequency and hay nutritional quality (C:N and Ca:P ratios) were lower under delayed mowing. Vascular plant and bryophyte species richness as well as forage quality were negatively related to phytomass, while the latter was positively related to mean summer temperature and negatively to time since AES registration.

We conclude that supporting invertebrate biodiversity with alternative mowing regimes has no detrimental effects on the vascular plants and mosses, while the reduced forage quality calls for additional financial compensation of the farmers adopting these agri-environment schemes.

## Zusammenfassung

In Europa wurden Agrarumweltprogramme zur Förderung und zum Erhalt von Dauergrünländern etabliert. In den grundsätzlichen Richtlinien des Vertragsnaturschutzes fehlen jedoch meist konkrete Bewirtschaftungsempfehlungen. Auch die Wirkung

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der nutzungsgebundenen Instrumente zur Erreichung von Umweltzielen und dem Biodiversitätsschutz bleiben weitgehend unerforscht. Am Beispiel von extensiv genutzten Wiesen des Schweizer Mittellandes untersuchten wir deshalb drei alternative Mahdregime, die zur Förderung der Biodiversität konzipiert wurden und in der landwirtschaftlichen Praxis einfach umsetzbar sind. Eine frühere Studie auf diesen Wiesen zeigte bereits positive Auswirkungen einer späten Mahd sowie von temporär ungemähten Streifen auf die Diversität von Invertebraten. In der vorliegenden Studie untersuchten wir Gefäßpflanzen und Moose auf extensiven Wiesen in 12 Regionen des Schweizer Mittellandes, die nach der Standard-Nutzungsaufgabe bewirtschaftet wurden (Mahd ab 15. Juni, keine Düngung, keine Beschränkung Anzahl Schnitte) mit jenen auf Wiesen, die (1) einen Monat später, (2) höchstens zweimal, jedoch zeitlich mindestens acht Wochen versetzt und (3) die auf einer Fläche von 10 bis 20% der Wiesen temporär nicht gemäht wurden. Fünf Jahre nach Beginn des Experiments unterschieden sich die Wiesen nicht bezüglich ihrer Gefäßpflanzen- und Moosvielfalt und –zusammensetzung, Biomasseproduktion, Phänologie und mittlerer Pflanzenhöhe. Die Biomassequalität (C:N- und Ca:P-Verhältnis) war jedoch signifikant niedriger in den einen Monat später gemähten, als in den übrigen Wiesen. Die Gefäßpflanzen- und Moosvielfalt, sowie die Biomassequalität zeigten eine negative Beziehung zur Produktivität. Unsere Ergebnisse zeigen, dass die alternativen, für Invertebraten förderlichen Mahdregime Gefäßpflanzen und Moose nicht beeinträchtigen. Aufgrund der reduzierten Biomassequalität von später gemähten Wiesen sollten Landwirte, die dieses Mahdregime anwenden, zusätzliche finanzielle Anreize erhalten.

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## Introduction

European semi-natural grasslands under traditional, low intensity management harbor an extremely high diversity of plants (Wilson, Peet, Dengler, & Pärtel 2012) and animals (Tucker & Evans 1997; WallisDeVries & Van Swaay 2009). Traditional mowing can maintain a high plant species richness by suppression of tall-statured plant species, thereby decreasing light competition, and allowing short-statured species to persist (Grime 1973; Hautier, Niklaus, & Hector 2009). Grassland biodiversity in Western Europe has strongly declined over the past century due to agricultural intensification (Benton, Bryant, Cole, & Crick 2002; Kleijn et al. 2009). To counteract this negative trend, agri-environment schemes (AES) have been implemented in many countries (see Kleijn & Sutherland 2003 for an historic overview), but their efficacy in protecting or enhancing biodiversity has, so far, been limited (e.g. Kleijn et al. 2006; Aviron et al. 2009). There is thus an urgent need for alternative management systems that not only enhance biodiversity within AES but are also easily implementable and accepted by local stakeholders.

In the Swiss lowlands, the most popular AES for grasslands is the so called ‘extensively managed hay meadow’. This scheme allows an earliest cut on June 15 (without limiting the number and frequency of subsequent cuts) and prohibits the application of fertilizers and pesticides. It is currently implemented on 6.9% of the Swiss lowland agricultural area (BLW 2015). Generally, mowing here takes place on the earliest permitted date, or shortly thereafter, leading to a strong spatio-temporal homogenization of the grassland landscape throughout the Swiss Plateau.

To enhance the effectiveness of the AES for meadow biodiversity, several simple changes of management regime

might be envisioned, such as delayed mowing, leaving an uncut grass refuge, or limiting the cutting frequency. Earlier it was shown that several invertebrate groups benefit from both delaying mowing (reviewed by Humbert, Pellet, Buri, & Arlettaz (2012)) and leaving an uncut refuge (Nentwig 1988; Humbert, Ghazoul, Richner, & Walter 2012; Buri, Arlettaz, & Humbert 2013), but impacts on vegetation are more ambiguous. A meta-analysis has established that plant species richness tends to increase when mowing is delayed from spring to summer, but decreases when mowing is delayed from spring or early summer to fall (Humbert, Pellet et al. 2012).

Delayed mowing can affect plant diversity through several mechanisms. On the one hand, more plant species can potentially reach reproductive maturity before mowing (Jantunen, Saarinen, Valtonen, & Saarnio 2007; Smith & Jones 1991), leading to increases in plant species richness (Humbert, Pellet et al. 2012). On the other hand, tall-statured plant species could gain dominance with negative consequences for short-statured vascular plant species and bryophytes, leading to an overall decline in species numbers (Bobbink & Willems 1991; Aude & Ejrnaes 2005). Hence, the effects of delayed mowing, as well as leaving an uncut refuge, may critically depend on competition for light and the timing of seed set. Delayed mowing can thus be expected to cause a shift in community composition, where tall-statured species and/or species with a later phenology would increase in abundance.

However, the effects of agricultural management practices on plant communities are not independent of the local and regional environmental context, and may thus also depend on differences in local biotic and abiotic site conditions (Socher et al. 2012), landscape context (e.g. Tscharrnke, Klein, Kruess, Steffan-Dewenter, & Thies 2005) or climate

(de Bello, Lepš, & Sebastià 2006). Such variables may therefore interact with the mowing regime in shaping plant community and functional composition.

Here, we present the results of a five-year field experiment testing the effects of three alternative mowing regimes on plant and bryophyte community composition. Aiming at promoting biodiversity in extensively managed hay-meadows, the regimes were designed in collaboration with local stakeholders and represent a compromise between potential applicability over large scales, realistic implementation by agricultural practice and easy integration into AES. More specifically, we compare the standard Swiss AES implementation for extensively managed hay meadows (mowing after 15 June, no fertilizer) to (i) mowing delayed by one month (to 15 July earliest), (ii) maximum mowing frequency of two cuts per year with a minimum eight weeks interval, and (iii) leaving an uncut refuge on 10–20% of the area of a meadow each time it is mown. We evaluate the effects of these alternative mowing regimes, as well as interactive effects with environmental variables, on plants and bryophytes (species richness, community and functional composition), and agronomic aspects (cutting frequency, phytomass and hay nutritional quality). Overall, we hypothesize that tall-statured species and vascular plant species with a late phenology will become more abundant under delayed mowing, which may increase species richness.

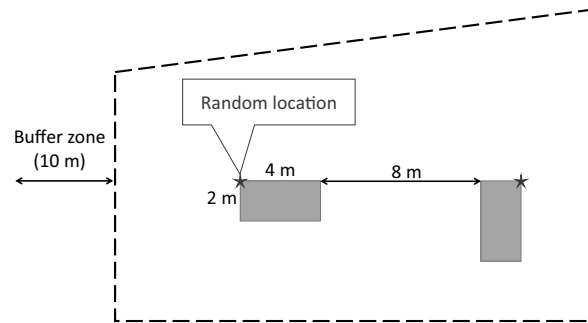
## Material and methods

### Study sites and experimental design

The study was performed in extensively managed hay meadows located in the Swiss lowlands, the so called Plateau, situated between the Jura Mountains and the Alps. The Swiss Plateau represents a typical case of Western-/Central-European agricultural landscape. It is a densely populated region, where high-intensity agriculture is interspersed with forest stands (<20% of the total land area).

All investigated meadows were registered as biodiversity promotion areas (BPA) within the Swiss AES since 2004 or earlier. The elevation of the sites ranged from 390 to 826 m a.s.l., annual precipitation ranged from 845 to 1148 mm, and mean annual temperature from 13.7 to 16.3 °C. The meadows belonged to the *Molinio-Arrhenatheretea* class.

A randomized block design experiment was applied to a total of 48 meadows from 2010 onwards, where in each of 12 study areas four AES meadows with a minimum size of 0.3 ha (mean 0.8 ha, max 1.7 ha) were selected. The study areas were spaced at least 5 km apart, with a maximum distance of 195 km between the most distant meadows (Supplementary Appendix A: Fig. A1). Within each study area, the four meadows were located within a radius of 3.5 km and spaced minimum 440 m apart. One of four mowing regimes was



**Fig. 1.** Schematic example of the location of the two permanent vegetation plots in an experimental meadow.

randomly allocated to each of the four extensively managed meadows within a study area:

- 1) Control regime (C): standard regime for meadows declared as BPA within the Swiss AES, i.e. first cut not before June 15 without restrictions on the number and frequency of subsequent cuts; no application of pesticide and fertilizer. Aftermath grazing was allowed only between September 1 and November 30 (BPA regulations; [Swiss Federal Council 1998](#)), hence dung could have been present.
- 2) Delayed mowing (D): as C-regime, but with first cut delayed by one month, i.e. not before July 15, and no restriction on the number and frequency of subsequent cuts; again, no pesticide or fertilizer application.
- 3) Eight weeks between cuts (8W): as C-regime, but with a maximum of two cuts per year, and at least eight weeks between the cuts.
- 4) Refuge apportioning (R): leaving 10–20% of a meadow in the form of an uncut grass refuge, each time the meadow was mown. Farmers were free to choose where to leave the refuge, though the location of the refuge had to change at each cut to avoid vegetation succession; otherwise first cut not before June 15.

### Sampling

In each meadow, two permanent vegetation plots (PP) of 2 m × 4 m were defined before the start of the experiment and marked with metal pins. The location of the PP was determined randomly in each meadow, excluding a 10-m buffer zone around the meadow (Fig. 1). In the R-meadows we had no prior knowledge of the positioning of the uncut refuge. The pin-heads (diameter 7 cm) were flush with the soil surface to avoid interference with agricultural practice, and subsequently found back using a metal detector. The first random point marked the corner of the first PP. The corner of the second PP was set at 14 m from the first point in a random direction, excluding a possible overlap with the buffer zone. Two such plots were installed per meadow to capture the small-scale heterogeneity of vegetation patterns.

In 2010, before the first cut, the composition of the vascular plant community was assessed by visually estimating the percentage area of the PP covered by any given species in order to obtain baseline data. After this, one experimental meadow was lost due to a land-use change. Sampling of vascular plants was repeated on the remaining 47 meadows in 2014 and 2015, i.e. four and five years after the onset of the experiment. In 2015, we also recorded bryophyte species and measured phytomass just before the first cut. To measure phytomass production (i.e. hay yield), we clipped two 0.25 m<sup>2</sup> (0.5 × 0.5 m) squares of vegetation to 5 cm height at the edge of each PP. All four samples were pooled, dried at 80 °C for 48 h and weighed. The cutting dates of all meadows were recorded during all years.

The nutritional quality of the phytomass samples was assessed by near-infrared spectroscopy (NIRS) following [Kleinebecker, Klaus, and Hölzel \(2011\)](#). In short, the dried and ground phytomass was scanned at 1 nm intervals over a range from 1250 to 2350 nm using a Spectra Star 2400 (Unity Scientific, Columbia, MD, USA). From this, the concentrations of C, N, P, K, Ca, Mg, as well as fiber components NDF (neutral detergent fiber), ADF (acid detergent fiber) and ADL (acid detergent lignin) were calculated. From these percentages, the C:N and Ca:P ratios were calculated as indicators of nutritional quality ([Tallowin & Jefferson 1999](#)).

## Statistical analysis

For all analyses the data from the two PPs were pooled. Tree and shrub species (i.e. seedlings) were excluded from the analysis. All analyses were performed using R 3.2.5 ([R Core Team 2016](#)), using the packages *lme4* ([Bates, Maechler, Bolker, & Walker 2014](#)) for generalized linear mixed models (GLMM), *vegan* ([Oksanen et al. 2014](#)) for multivariate analyses and *FD* ([Laliberté, Legendre, & Shipley 2014](#)) for functional diversity measures.

A trait-based approach was used to investigate if tall-statured plant species and/or species with a later phenology were more abundant in the meadows with the alternative mowing regimes (particularly D-meadows). The mean plant height values of all species were obtained from the LEDA trait database ([Kleyer et al. 2008](#)), and for three species that were not available in LEDA, the values were obtained from the TRY database ([Kattge et al. 2011](#)). Phenological data (first month of flowering) were extracted from Flora Helvetica ([Lauber, Wagner, & Gygax 2012](#)). The community-weighted mean (CWM) of plant height and flowering phenology was calculated by multiplying the trait value of each species by its relative abundance.

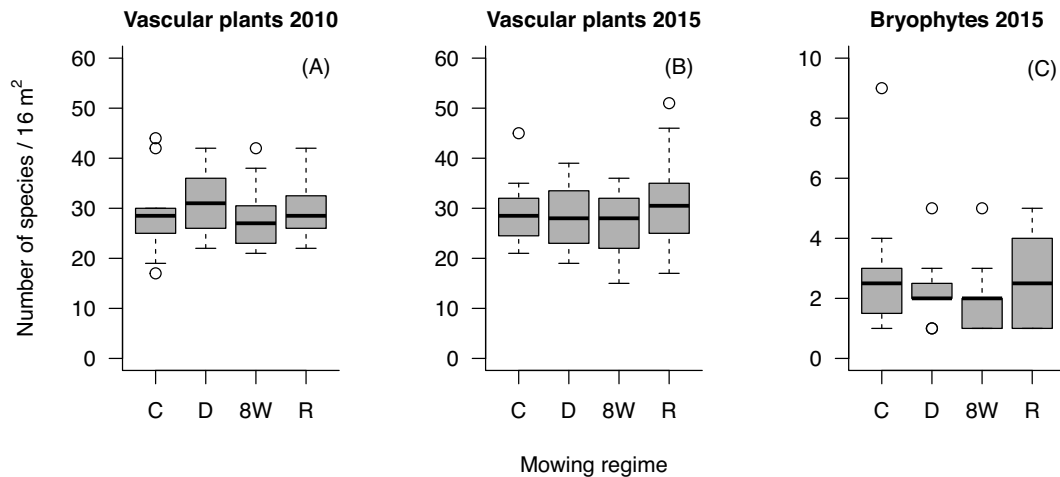
The GLMMs used for the analyses of differences in the response variables (vascular plant and bryophyte species richness, CWM plant height, CWM phenology, phytomass, and hay nutritional quality) included mowing regime as

fixed effect (factorial variable, four levels) and study area as random effects (12 levels). The error structure was set to follow a Poisson distribution for vascular plant and bryophyte species richness and a Gaussian distribution for phytomass, CWM and nutritional quality. *P*-values for the models with a Gaussian error distribution were obtained using the *lmerTest* package ([Kuznetsova, Brockhoff, & Christensen 2014](#)). Model assumptions (normality of the residuals distribution and homoscedasticity) were checked and met for each analysis.

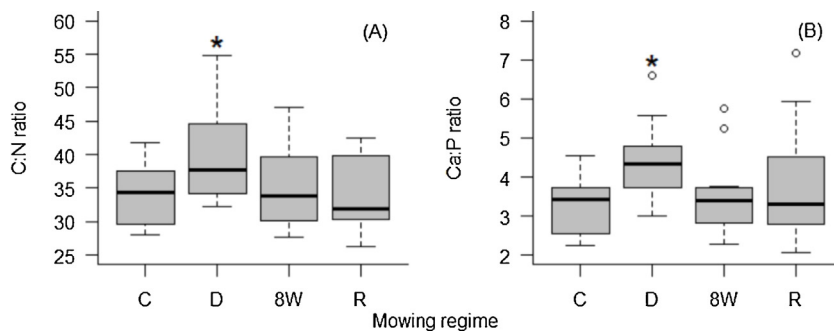
We tested for differences in vascular plant community composition between the mowing regimes using permutational multivariate ANOVA (adonis in the *vegan* package) and visualized this by non-metric multidimensional scaling (NMDS). In order to account for the block design, permutations were only allowed within the study areas by setting strata. The local and landscape variables were then correlated to the NMDS axes.

To test if local or landscape variables interacted with the mowing regimes in shaping the vascular plant communities, the following variables were obtained for each meadow: total annual precipitation, mean summer temperature (April–September), elevation, meadow size, percentage of forest in a 500-m radius around the center of the meadow, and the number of years the meadow had been registered as AES. Additionally, vascular plant species richness and phytomass were included in the models to explain bryophyte species richness, CWM plant height, C:N and Ca:P ratios. For explaining vascular plant species richness, phytomass was also included in the model. Meadow size, elevation and forest cover were extracted from the Vector 25 database of the Swiss Federal Office of Topography ([Swisstopo 2014](#)). Temperature and precipitation data were obtained from the Federal Office of Meteorology and Climatology MeteoSwiss for the period 1981–2010. The year of AES registration was obtained directly from the farmers.

The most important environmental descriptors for each of our response variables were obtained using GLMM, with the same random structure and error distribution as mentioned above. Since there was no a priori reason to assume interactive effects between the variables, no interactions were included in the models. Mean summer temperature and elevation were strongly correlated ( $r = -0.7$ ), therefore only temperature was used in the models. Because of strongly differing scales of the variables, the data of precipitation, temperature, forest cover, time since AES registration and phytomass were standardized (i.e. scaled to the mean, with standard deviation of 1). In all these models, study area was again used as a random factor. Backward model selection was applied to obtain the minimum adequate model. A new set of GLMMs was then constructed, which included mowing regime in interaction with each of the significant explanatory variables for each response variable. Study area was here again included as a random effect.



**Fig. 2.** Vascular plant species richness in 2010 (A) and 2015 (B), and bryophyte species richness in 2015 (C) with respect the mowing regime, abbreviated as follows: C: control (first cut no earlier than June 15); D: mowing delayed by one month; 8W: maximum two cuts a year, with a minimum of 8 weeks in between; R: uncut refuge left during mowing operations over 10–20% of meadow area. The boxes represent the 25% and 75% quartiles from the median (thick line), whiskers represent the maximum and minimum values, excluding outliers, where outliers are defined as points further than 1.5 times the interquartile range.



**Fig. 3.** Delayed mowing decreased forage quality by increasing C:N (A) and Ca:P ratios (B). Asterisks denote significant differences from the C-regime ( $P < 0.05$ ). Abbreviations and box-plot features as in Fig. 2; see also Supplementary Fig. A.5 for more information about minerals and nutrients.

## Results

Overall, 129 vascular plant species were recorded in 2010, and 134 vascular plant and 21 bryophyte species in 2015 (see Supplementary Appendix B for the species list). The average number of species per 16 m<sup>2</sup> was 29.4 (range 17–44) and 29.0 (range 15–51), in 2010 and 2015, respectively. There were no differences in vascular plant species richness between the mowing regimes before the onset of the experiment (GLMM:  $\chi^2 = 1.92$ ,  $P = 0.59$ ; Fig. 2A). Species richness of vascular plants did not differ among the mowing regimes in 2014 (see Supplementary Appendix A: Fig. A.2), nor in 2015 (GLMM:  $\chi^2 = 4.06$ ,  $P = 0.26$ , Fig. 2B). Also bryophyte species richness (GLMM:  $\chi^2 = 2.43$ ;  $P = 0.49$ , Fig. 2C), CWM plant height ( $\chi^2 = 2.34$ ,  $P = 0.51$ ) and CWM flowering phenology ( $\chi^2 = 1.04$ ,  $P = 0.79$ , Fig. A.3) did not differ between the mowing regimes. There was also no consistent difference in vascular plant species composition detectable according to the permutational multivariate ANOVA (*adonis*:  $F_{3,43} = 0.77$ ,  $P = 0.68$ , Supplementary Fig. A.4).

In the D-meadows, cutting frequency was reduced to an average of 1.52 cuts per year, with 52% of the meadows cut only once per year (annual average over five years 2010–2014). In contrast, the C- and 8W-meadows were cut, on average, 1.9 times per year, while only 20% of C-meadows and 14% of 8W-meadows were cut only once annually. The R-meadows were cut 2.1 times per year, on average, and in only 2% of the cases only once.

We found no significant differences in phytomass production between the mowing regimes (GLMM:  $\chi^2 = 1.48$ ,  $P = 0.69$ , Supplementary Fig. A.5). Under delayed mowing, the C:N ratio of the phytomass was increased by 17% ( $t = 2.72$ ;  $P = 0.01$ ) and the Ca:P ratio by 35% ( $t = 2.62$ ;  $P = 0.01$ ), indicating a decrease in forage quality (Fig. 3). Of the fiber fractions and raw elements measured, the phytomass from the D-meadows contained a significantly lower fraction of N and P, and a higher concentration of NDF, and elemental C than the phytomass of the control meadows. No differences among regimes were found for ADL, NDF, Ca, K, or Mg (Supplementary Fig. A.6).

The variables measured at the local and landscape scales showed various relations with the plant community properties (Table 1): vascular plant- and bryophyte species richness were negatively related to phytomass (Fig. 4), but C:N ratio showed a positive relation. The Ca:P ratio was positively related to phytomass, which was driven by variation in Ca concentration, but not in P-concentration (Supplementary Fig. A.7). Phytomass itself showed a weak negative relationship with time since BPA registration, and a positive relationship with mean summer temperature. CWM plant height and CWM flowering phenology showed a negative relationship with forest cover. Meadow size had no significant effect on any of the measured variables. Testing for interactive effects between mowing regime and the significant local and landscape variables on any of our response variables yielded no significant interactions.

## Discussion

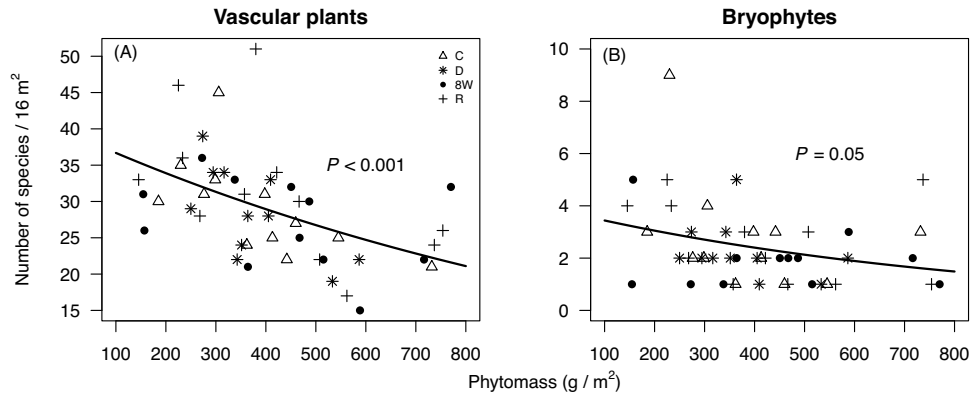
We found no evidence that the tested alternative mowing regimes affected vascular plant or bryophyte species richness, species composition, functional composition or phytomass, in contrast to our hypotheses. However, delayed mowing caused a decrease in forage quality, and led to a decrease in cutting frequency. Although several variables influenced plant community properties, we found no evidence for interactive effects between the mowing regimes and other environmental variables.

Among all mowing regimes, delayed mowing was expected to cause the strongest impacts on the vegetation, in line with our previous findings on invertebrates within the same experimental set up (Buri et al. 2013; Bruppacher, Pellet, Arlettaz, & Humbert 2016; Buri et al. 2016). The absence of effects on any of the plant community properties is possibly due to a too short duration of the experiment (5 years) to cause significant changes in the plant community (Humbert, Pellet et al. 2012). Alternatively, the slight changes in the mowing regimes may also have been too shallow to influence the vegetation. This corroborates previous studies that have found no or only small differences in plant species richness in response to slight variations mowing date (Čop, Vidrih, & Hacin 2009; Parr & Way 1988; Smith, Buckingham, Bullard, Shiel, & Younger 1996; Smith, Shiel, Millward, & Corkhill 2000).

Although we cannot prove that the alternative mowing regimes tested have no effect on vascular plant species richness, the effect size might well be below detectability given the great inter-plot variability in our data. Indeed, a simulation-based power analysis (following Johnson, Barry, Ferguson, & Müller 2014) showed that, given our experimental setup (observed mean, variance of random effects, and nested random structure), a mean difference of almost five species in one of the regimes would be required to obtain a significant difference at  $\alpha = 0.05$ ; this represents 17% of the average number of species recorded per meadow (see Sup-

**Table 1.** Relationships between vegetation properties (first column) and several explanatory variables, as well as GLMM model fit (last column). Results are only shown for those variables retained from modelling; CWM = community weighted mean, BPA: biodiversity promotion area, S: species richness. Meadow size (ha) was not significant in any model, and therefore omitted. Effects on vascular plant species richness, and bryophyte species richness were tested using GLMM with Poisson error distributions, all other variables were tested with Gaussian error distributions.

	Precipitation		Temperature		BPA age		Forest cover		Phytomass		Vascular plant S		Model fit	
	$z$	$P$	$t$	$P$	$t$	$P$	$t$	$P$	$z/t$	$P$	$t$	$P$	$\chi^2$	$P$
Vascular plant S	-3.11	0.002							$z = -4.84$	<0.001	-	-	25.72	<0.001
Bryophyte S									$z = -1.94$	0.052	-	-	3.88	0.049
Biomass			2.20	0.033	-2.05	0.046			-	-	-	-	6.63	0.036
CWM plant height							-2.99	0.005					8.46	0.004
CWM phenology							-3.8	<0.001					12.34	<0.001
C:N ratio			3.42	0.001					$t = 2.46$	0.018	2.35	0.023	16.99	<0.001
Ca:P ratio									$t = -2.63$	0.012			20.63	<0.001



**Fig. 4.** Negative relationships between vascular plant (A) and bryophyte (B) species richness and phytomass. The different mowing regimes (for abbreviations of codes see Fig. 2) are represented by different symbols. The regression line is drawn from GLM with a Poisson error distribution.

plementary Appendix A: Fig. A.8). Our observed effect size of on average only one species difference between D- and C meadows was clearly below this detectability threshold (for more details see Supplementary Appendix A).

Overall, we found a general negative relationship between total phytomass and vascular plant and bryophyte species richness. A hump-shaped relationship between phytomass and species richness has long been hypothesized based on the balance between competition and abiotic stress (Grime 1973). Since the productivity of all our meadows is relatively high ( $>200 \text{ g m}^{-2}$ ), a negative relationship between phytomass and species richness would be expected (see Fraser et al. 2015). Our results are thus in agreement with a large number of case studies from relatively productive grasslands in central and northern Europe, which have all established that both vascular plant (Peintinger & Bergamini 2006; Pärtel, Laanisto, & Zobel 2007; Klaus et al. 2013) and bryophyte species richness (Aude & Ejrnaes 2005; Peintinger & Bergamini 2006; Müller et al. 2012) decline with increasing phytomass. This would confirm that competition for light is one of the major forces limiting species richness in European grasslands. Any management change that increases phytomass production, notably higher fertilizer input, would thus cause a decrease in plant species richness. Under the current AES prescriptions, however, soil nutrients are gradually removed from the system with the harvested hay since any fertilizer input is prohibited, which explains the observed decrease in phytomass production with increasing age since AES registration.

Few of the environmental and landscape covariables tested in addition to mowing regimes had marked effects on plant community properties. One surprising finding, however, was the strength of the negative relationship between regional forest cover and both plant height and flowering phenology. This finding corresponds to the patterns in the multivariate analysis, where both CWM flowering phenology and CWM are directed oppositely to forest cover and elevation. This indicates that the plant species composition is similar in areas with high regional forest cover and higher elevations, and

that at these locations plant communities consist of small-statured plants with an earlier phenology. This may be related to light competition with trees, a cooler microclimate, or to unmeasured confounding factors that drive both regional forest cover and community functional structure.

Delayed mowing led to a decrease in hay nutritional quality, in line with conventional knowledge (Tallowin & Jefferson 1999). The percentages of P in the hay from all regimes seemed to be on average around the minimum required for growing livestock (0.15%), while the percentages of K, Mg and Ca were more than adequate (Tallowin & Jefferson 1999). The Ca:P ratios found were within tolerable ranges of 1–7, although Ca uptake will be suboptimal (NRC 2001). The percentage ADF, however, was with over 35% generally too high for optimal livestock performance. The percentage N was low under all regimes, but particularly under delayed mowing. In many of the D-meadows cutting frequency was reduced to only once per year, indicating that this regime led to a change in agricultural practice.

We could not find evidence for any positive or negative effects of delayed mowing or leaving an uncut refuge on hay meadow plant and bryophyte communities. This contrasts with our previous findings on several invertebrate taxa investigated in the same experimental set up, which showed positive responses to these two alternative mowing regimes (butterflies: Bruppacher et al. 2016; spiders and leafhoppers: Buri et al. 2016, orthopterans: Buri et al. 2013; wild bees: Buri, Humbert, & Arlettaz 2014). Since they overall offer good options for promoting grassland biodiversity, we suggest that such alternative mowing regimes are recognized as new valuable options within European agri-environmental schemes. The advantage of these options is that they are easy to implement by agricultural practice, i.e. would be readily adopted by farmers.

However, because of the decrease in nutritional quality, and cutting frequency (i.e. overall annual productivity), financial compensation for delayed mowing should be higher than for the standard AES implementation. This compensation should take into account the losses due to the decrease in nutritional

quality in comparison to both the quality of a cut in June (which is already of poorer quality than earlier cuts), and the conventional cutting in May. Additionally, the loss of the more nutrient-rich additional cuts should be considered in cases where cutting frequency is decreased. A comparison between the agronomy of conventional meadow use and the delayed mowing in terms of phytomass and nutritional quality is thus required to determine the financial compensations for such AES.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2017.02.003>.

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