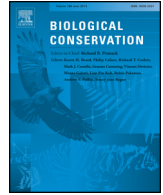




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Simple modifications of mowing regime promote butterflies in extensively managed meadows: Evidence from field-scale experiments



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ABSTRACT

Restoring biodiversity-rich grasslands within cultivated matrices represents a real conservation challenge. One set of options consists in adopting less disruptive mowing regimes, as mowing impacts on invertebrates can be considerable. We experimentally tested the effect on butterfly populations of a spatio-temporal modification of mowing regimes within extensively managed meadows. The control regime (C) followed the standard Swiss agri-environment schemes (AES) regulation: no cutting before 15 June and no fertilisation. The second regime consisted of delaying (D) the first possible cut by one month (to 15 July). The third regime consisted in maintaining a 10–20% uncut grass refuge (R) during mowing operations. This experiment was replicated at 12 study sites across the Swiss lowlands, and applied yearly since 2010. Butterflies were sampled in 2013. Butterflies generally benefitted from D- and R-regimes. Before the onset of mowing operations, both D- and R-regimes yielded higher butterfly densities (+70%) compared to the C-regime, demonstrating positive cumulative effects (i.e. carry-over effects from one year to the next), not only for the whole butterfly community, but also for resident, multivoltine, mono- and oligophagous species. After 15 June, densities were about six times higher in D- than in C- and R-meadows until D-meadows were cut mid-July. Species richness of specialist butterflies was significantly higher in R-meadows (+60%) compared to C-meadows. This study is the first that demonstrates positive and cumulative effects of delaying the first cut or leaving a refuge on butterfly populations. It would be easy to implement these measures within European and Swiss AES regulations.

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1. Introduction

Extensively managed grasslands are among the most biodiversity-rich ecosystems in Europe and indispensable habitats for many plants and animals (Veen et al., 2009). However, changes in their management, such as increased fertiliser application and improved mechanisation of the harvesting process have led to a massive deterioration of habitat quality and a progressive homogenization of the landscape (Tscharntke et al., 2005). These changes have caused a widespread decline of farmland wildlife across the continent, dramatically impacting birds and arthropods (van Swaay et al., 2010; Vickery et al., 2001). Butterflies, have, for instance, experienced acute declines over recent decades, so that nowadays almost 20% of all European species are considered to be threatened or near threatened (van Swaay et al., 2010). In western European countries the figures are often worse: for example in Switzerland 35% (78 species) of all butterflies appear on the country's Red List as threatened, and 19.5% (44 species) as

near threatened (Wermeille et al., 2014), while in Great Britain, only 28 species (45%) of butterflies are considered to be not threatened (Fox et al., 2010). Specialists with narrow niche-breadth (i.e. few host plants) and low dispersal ability have been reported to decline most rapidly (Börschig et al., 2013; Ekroos et al., 2010; Heer et al., 2013). Hence, communities in many of today's EU lowland grasslands are dominated by a few ubiquitous generalists that are less prone to disturbances (Ekroos et al., 2010; van Dyck et al., 2009).

Although many agri-environment schemes (AES) are specifically targeted to grasslands, they have so far provided only limited benefits for biodiversity (Kleijn et al., 2006; Princé et al., 2012). It has been argued that they are mostly too small in size and offer too little spatio-temporal heterogeneity in terms of both habitat types and land-uses (Botham et al., 2015; Cizek et al., 2012; Konvicka et al., 2008), thus failing to promote habitats of sufficient quality for sensitive, more specialised species (Ekroos et al., 2010). Moreover, a great deal of research on the effects of management upon grassland biodiversity has been targeted at plant assemblages, which are typically moulded by other limiting factors than animal communities (Andrey et al., 2014; Hudewenz et al., 2012; Littlewood et al., 2012). Defining efficient conservation and restoration measures to improve arthropod biodiversity in semi-natural grasslands is therefore urgently needed.

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Diversifying the mode and timing of mowing operations enables some spatio-temporal heterogeneity to be restored among farmland habitats, at both field and landscape scales, which, in turn, can benefit arthropod communities and boost population density (e.g. Buri et al., 2013, 2014; Cizek et al., 2012; Noordijk et al., 2009). Even so, mowing can also cause substantial immediate damage to butterflies, notably because caterpillars are destroyed by the grass harvesting process, while nectar sources for imagines are suddenly annihilated (Dover et al., 2010; Humbert et al., 2010b). If applied indiscriminately or badly timed, mowing can have long-term negative effects on butterfly population survival, especially for species with a flying period in late summer, low dispersal ability and/or highly specific resource requirements (Humbert et al., 2012b; Johst et al., 2006; Konvicka et al., 2008; Walter et al., 2007).

A recommendation that has been repeatedly framed to avoid the negative impact of mowing on butterflies is to delay the first mowing date (Humbert et al., 2012b; Potts et al., 2009; Valtonen et al., 2006), but it has never been experimentally tested at the field scale. Late-summer cuts are in effect less harmful to butterflies than early summer cuts because they enable most species to accomplish their reproductive cycle (Walter et al., 2007). In addition to extending the temporal availability of crucial resources, delaying mowing diminishes the overall seasonal pressure exerted by mowing activities, notably via a reduction in the number of annual cuts (Buri et al., 2013). Leaving an uncut grass refuge on a fraction of the meadow is another grassland management option that contributes to a lower mortality of field invertebrates that are otherwise decimated by the mowing process (e.g. on orthopterans Humbert et al., 2012a). Such grass refuges provide continuous shelter and food supply (Valtonen et al., 2006; Weibull et al., 2000) and can offer permanent oviposition sites to insects that lay their eggs directly on meadow plants (Erhardt, 1985). The tremendously beneficial effect of maintaining a grass refuge within a meadow has recently been demonstrated for orthopterans (Buri et al., 2013; Humbert et al., 2012a). This measure has been suggested for butterflies as well (Dover et al., 2010; Kühne et al., 2015; Lebeau et al., 2015), but we lack quantitative evidence about its effects on butterfly populations.

The aim of this study was to experimentally test, at the field scale, whether leaving uncut grass refuges and delaying mowing within extensively managed lowland grasslands declared under Swiss AES can enhance butterfly communities and populations. The ultimate goal was to deliver evidence-based management recommendations in order to improve habitat conditions for farmland butterflies.

2. Materials and methods

2.1. Study sites

In 2010, 35 extensively managed hay meadows declared under Swiss AES since at least 2004 were selected across the Swiss lowlands (Plateau). The Swiss Plateau can be characterised mainly as a simple landscape where non-farmland semi-natural habitats (e.g. hedges and forest patches) are still present, but constitute usually only 1–20% of the matrix. All meadows were located between 390 and 826 m altitude (Appendix S1). The majority of the meadows could be assigned to *Arrhenatherum elatius* or *Alopecurus pratensis* grassland types, harbouring between 25 and 35 species per 16 m² (unpublished data). They were equally distributed among twelve geographic sites, all but one harbouring three meadows (one site had only two meadows as one had been converted into a gravel pit in 2012). While there was a minimal distance of 5 km between study sites, the three meadows per site were clustered within a 3.5 km radius with a minimum distance of 440 m between each other. While butterflies can easily migrate several km, average daily movement rates rarely exceed 200 m (e.g. Debinski et al., 2001; Schneider et al., 2003). Meadows had a minimum size of 0.3 ha (range: 0.3–1.7 ha).

2.2. Experimental design

The experiment was arranged in a randomised block design, in which three mowing regimes were randomly applied to one of the three meadows at a site (block), resulting in twelve independent replications of each regime (except the D-regime, see below, that had only eleven replicates). The following three mowing regimes were applied continuously during the entire duration of the experiment:

1. The first mowing regime, which corresponded to our control (hereafter called C-meadows), conforms to the standard regulations for extensively managed meadows as declared under Swiss AES: no fertiliser application and first cut not before 15 June, but with no restriction on the number and frequency of subsequent cuts.
2. In the second mowing regime, the first possible cut of an extensively managed meadow as declared under Swiss AES was delayed (D-meadows) by one month to the 15 July at the earliest.
3. The third mowing regime was again applied to an extensively managed meadow in conformity with Swiss AES, but here a small fraction (10–20%) was left uncut as a refuge (R-meadows) at each mowing operation. There was no restriction regarding the shape of the refuge, but its location within the meadow had to be changed at each mowing.

2.3. Butterfly sampling

In summer 2013, butterflies and Zygaenidae were sampled along line transects. A distance sampling method was adopted, which enabled the incorporation of detectability by additionally recording the perpendicular distances, in m-intervals, between the observed butterfly and the transect line (Buckland et al., 2001). Distance sampling is an extension of classic line-transect sampling techniques (see prescriptions by Pollard and Yates, 1993). Although so far mainly used for bird sampling, it has recently been suggested that it would lead to more reliable estimates of butterfly population abundance (Pellet et al., 2012). It was selected here mainly to account for possible differences in detectability due to the distinct vegetation structures generated by various mowing regimes.

Sampling transects were positioned along the longest diagonal line cutting through the centre of the meadow; average length was 111 m (range 65–215 m). Before each survey, the start, middle and end points of transect lines as well as the 5-m intervals on both sides of the transect were marked with coloured flags to ensure better visibility. Transects were walked in a single direction at a continuous, steady pace, alternating start points between surveys. All detected butterflies as well as their perpendicular distance to the transect line were recorded. Visual identification was performed, as far as feasible. In cases of identification ambiguity, individuals were caught with a butterfly net, immediately identified and released. For identification we referred to the guides by Tolman and Lewington (2012).

Six surveys were conducted during the main butterfly flight season, from the end of April to the beginning of September. Three surveys were carried out before 15 June, one between 15 June and 15 July and two after 15 July, these threshold dates corresponding to the timing of mowing operations. Surveys were conducted between 10:00 and 17:00 on sunny, warm days with a minimal air temperature of 13 °C and a maximal wind speed of 3 Beaufort, as suggested by Pollard and Yates (Pollard and Yates, 1993). The chronological order of meadow surveys was randomised within a region on a given sampling day.

2.4. Data analysis

Initial analyses of abundance performed with distance sampling models (DSMs), using the *distsamp* function of the *Unmarked* package for R (Fiske and Chandler, 2011), showed that there were no significant differences in butterfly detectability among mowing regimes (Appendix

S2). Further analyses were thus performed with conventional generalised linear mixed models (GLMMs) applied to the raw data, i.e. without accounting for sampling distances, using the *lmer* function from the package *lme4* (Bates et al., 2011). An advantage of using GLMMs instead of DSMs resided in the possible inclusion of the study sites as a random factor in the models. Response variables were the number of individuals in total, per family and per life-history group; numbers were standardised to an average transect length of 100 m (Dover et al., 2011). They were modelled with a Poisson error distribution. The fixed effects in the model were the three mowing regimes and, when necessary, the sampling survey. The first three surveys (before 15 June) were pooled in a single model because all meadows were then in the same unmown stage (and sampling survey was added as a fixed effect). Any statistical differences obtained here would reflect cumulative effects (i.e. carry-over effects over three years) induced by the application of the experimental mowing regimes since 2010. After 15 June, surveys were analysed separately because direct immediate (i.e. within-year) and cumulative effects were interacting, while meadows were no longer in the same vegetative stage. To better appraise the influence of the mowing regimes on the butterfly assemblage, the same statistical analyses were then performed separately on the abundance of different groups based on their life-history traits. For these analyses, only the groups occurring in at least six out of twelve different study sites were considered. Three categories of life-history traits were distinguished: 1) residency, with sedentary species with low vagility defined as resident (dispersion classes 1–4 in Settele and Reinhardt, 1999), versus non-resident (dispersion classes 5–9 in Settele and Reinhardt, 1999); 2) diet, with species defined as being monophagous (caterpillars feed on a single plant genus), oligophagous (caterpillars feed on a single plant family) or polyphagous (caterpillars feed on two or more plant families); and 3) voltinism, i.e. number of generations per year (univoltine, bivoltine, or multivoltine). Accordingly, species were further classified as either specialist or generalist, with specialists being resident species with a mono- or oligophagous diet and a maximum of two generations per year. Life-history traits were derived from Settele and Reinhardt (1999) and Geiger (1987).

Analyses of species richness (total and per life-history group) were performed with linear mixed models (LMMs) using the same function as for abundance, but assuming a Gaussian error distribution. While the length of the transects differed among meadows, mean transect lengths did not differ among the mowing regimes (mixed models ANOVA: $F_{2,32} = 1.468$, $P = 0.246$), which indicates that any differences between two mowing regimes are unlikely to be biased due to transect length. In addition, species rarefaction curves showed that species number – according to transect length – reached the asymptote in all three mowing regimes (Appendix S2). For these reasons, species richness LMMs were run on the raw data without any “correction” for transect length. Only life-history groups composed of more than four species, and occurring in at least six out of the twelve study sites were analysed.

Pielou's evenness indices (J) were also analysed with LMMs. $J = H / \ln(S)$, where H = the Shannon–Wiener index and S = number of species. This index, which peaks when all species are equally abundant has the advantage to be independent from the total number of species and thus comparable across studies. H (the Shannon–Wiener index) was calculated from the abundance data summed-up over all surveys using the function *diversity* of the package *Vegan* in R (Oksanen, 2014). The response variable was the index J , while fixed effects were the mowing regimes. All statistics were performed using R version 3.2.2 (R Core Team, 2015).

3. Results

A total of 1630 individuals of 39 butterfly species and 7 families were found: Nymphalidae ($n = 12$ species); Pieridae (8); Lycaenidae (7); Satyridae (7); Hesperidae (4); Papilionidae (1) and Zygaenidae (1) (Table 1). Satyridae was the most abundant family, with peak

abundance in July and August. Pieridae prevailed during the first three surveys, but decreased in June. Members of Lycaenidae were always present at a very low density until July but then dramatically increased in numbers during the penultimate and ultimate surveys. Nymphalidae were present across the whole season, but occurred mostly singly or at very low density. Hesperidae and Papilionidae were always scarce while Zygaenidae only emerged in August. Note that Satyridae have recently been grouped within Nymphalidae, though here they were kept separated as in the referred guide (Tolman and Lewington, 2012). C- and R-meadows were both cut on average 2.0 ± 0.3 (mean 2010–2013 \pm standard deviation) times per year, with the first cut occurring on average on 20 June ± 3.5 days. D-meadows were cut on average 1.5 ± 0.5 times a year, with the first cut occurring on average on 21 July ± 6.8 days.

3.1. Butterfly abundance

Mean butterfly abundance ranged from 1 to 20 individuals per 100 m of transect segment, with clear differences among mowing regimes and survey dates (Fig. 1; and Appendix S3 for detailed model outputs). Before mowing (surveys 1–3), butterfly abundance was significantly higher in D- and R- compared to C-meadows (D vs C: estimate, hereafter abbreviated as E, \pm standard error = 0.47 ± 0.20 , $P = 0.017$; R vs C: $E = 0.54 \pm 0.19$, $P = 0.005$; note that estimates are on the log scale). R- and D-meadows, however, did not differ significantly from one another. At the fourth survey (mid-season, between 15 June and 15 July, i.e. when all but D-meadows had been cut) abundance was significantly higher in D- compared to C- and R-meadows (D vs C: $E = 1.62 \pm 0.21$, $P < 0.001$; R vs D: $E = -1.87 \pm 0.23$, $P < 0.001$), while R did not differ from C. At survey five (when also D-meadows had eventually been cut), C- and R- had significantly higher butterfly abundances than D-meadows (D vs C: $E = -0.66 \pm 0.12$, $P < 0.001$; R vs D: $E = 0.76 \pm 0.12$, $P < 0.001$), while R- and C-meadows did not differ from each other. Finally, at survey six, there were no longer any significant differences among the three mowing regimes.

Results of the analyses of each life-history group are presented in detail in Appendix S3 (model outputs) and Appendix S4 (graphical outputs). In brief, densities of generalist species showed exactly the same qualitative responses as the total mean butterfly densities throughout the flight season. Before the onset of mowing operations, resident species were significantly more abundant in D- and R- compared to C-meadows whereas non-residents did not show any differences. Similarly mono- and oligophagous species were also more abundant than in D- and R- compared to C-meadows, while specialists were still too scarce to be modelled. Densities of polyphagous species did not differ among mowing regimes, whereas multivoltine species were more abundant in R- than C-meadows. At survey four, all groups, except the non-resident species, were significantly more abundant in D- compared to C- and R-meadows. Additionally, polyphagous densities were higher in C- than in R-meadows. At survey five, all groups were less abundant in D- compared to C- and R-meadows, but differences were not statistically significant for mono- and oligophagous species or for specialist species regarding abundance in D- vs C-meadows. At survey six, polyphagous and univoltine densities were higher in C- vs D-meadows, and univoltine and generalist densities were higher in R- vs D-meadows. No differences among mowing regimes were found in the other groups. Note that the occurrence of bivoltine species was always too scarce to be analysed.

3.2. Butterfly species richness and diversity

Mean (\pm standard error SE) species richness was 7.75 (± 1.23), 10.36 (± 1.22) and 10.00 (± 1.10), for C-, D- and R-meadows, respectively, but differences were not significant (Fig. 2a). Similarly, butterfly evenness (Pielou's index) did not differ statistically among mowing regimes (Fig. 2b). Regarding life-history groups, significantly more

Table 1

List of species with the number of individuals found per mowing regime (C, control regime: first cut not before 15 June; D, delayed regime: first cut delayed to 15 July; and R, refuge regime: as C, but with uncut refuge left over 10–20% of meadow area). Red-list status (RL) based on the Swiss red list of butterflies (Wermeille et al., 2014), referring to IUCN status criteria (LC: least concern; NT: nearly threatened; VU: vulnerable). Information is also provided on the diet (m = monophagous, o = oligophagous, p = polyphagous), residency (resident indicated with yes), and voltinism (u = univoltine, b = bivoltine, m = multivoltine). The last column states if a species has been classified as a specialist (yes) or a generalist (no) overall in the present study. Life-history traits were derived from Settele and Reinhardt (1999) and Geiger (1987).

Species	Family	RL	Mowing regime			Diet	Residency	Voltinism	Specialist
			C	D	R				
<i>Aglais urticae</i>	Nymphalidae	LC	1	4	5	m	no	m	no
<i>Araschnia levana</i>	Nymphalidae	LC	1	0	1	m	no	b	no
<i>Brenthis daphne</i>	Nymphalidae	LC	0	2	0	m	yes	u	yes
<i>Boloria dia</i>	Nymphalidae	NT	1	0	1	m	yes	b	yes
<i>Inachis io</i>	Nymphalidae	LC	2	1	4	p	no	m	no
<i>Issoria lathonia</i>	Nymphalidae	LC	0	4	2	p	no	m	no
<i>Melitaea athalia</i>	Nymphalidae	LC	0	12	0	o	yes	u	yes
<i>Melitaea parthenoides</i>	Nymphalidae	VU	0	2	0	m	yes	b	yes
<i>Melitaea cinxia</i>	Nymphalidae	VU	1	0	0	m	yes	u	yes
<i>Vanessa atalanta</i>	Nymphalidae	LC	0	3	1	p	no	m	no
<i>Vanessa cardui</i>	Nymphalidae	LC	20	7	12	p	no	m	no
<i>Polignonia c-album</i>	Nymphalidae	LC	0	1	0	p	no	m	no
<i>Anthocharis cardamines</i>	Pieridae	LC	2	1	2	p	yes	u	yes
<i>Colias crocea</i>	Pieridae	LC	43	19	41	p	no	m	no
<i>Colias hyale</i>	Pieridae	LC	7	2	16	p	no	m	no
<i>Gonepteryx rhamni</i>	Pieridae	LC	0	1	3	p	no	b	no
<i>Pieris brassicae</i>	Pieridae	LC	10	15	20	p	no	m	no
<i>Pieris napi</i>	Pieridae	LC	65	61	64	p	no	m	no
<i>Pieris rapae</i>	Pieridae	LC	17	17	38	p	no	m	no
<i>Leptidea sinapis</i>	Pieridae	LC	5	5	1	p	yes	b	no
<i>Celastrina argiolus</i>	Lycaenidae	LC	0	2	1	p	no	b	no
<i>Cupido argiades</i>	Lycaenidae	NT	7	10	6	o	yes	m	yes
<i>Lycaena phlaeas</i>	Lycaenidae	LC	0	1	1	p	yes	m	no
<i>Lycaena tityrus</i>	Lycaenidae	LC	2	1	2	m	yes	b	yes
<i>Polyommatus icarus</i>	Lycaenidae	LC	16	53	34	o	yes	m	no
<i>Cyaniris semiargus</i>	Lycaenidae	LC	5	33	8	m	yes	m	no
<i>Aricia aegestis</i>	Lycaenidae	LC	1	0	0	p	yes	m	no
<i>Aphantopus hyperantus</i>	Satyridae	LC	1	3	0	p	yes	u	no
<i>Coenonympha pamphilus</i>	Satyridae	LC	22	20	32	p	yes	m	no
<i>Lasiommata megera</i>	Satyridae	LC	3	3	1	p	yes	m	no
<i>Maniola jurtina</i>	Satyridae	LC	253	206	210	p	no	u	no
<i>Melanargia galathea</i>	Satyridae	LC	26	13	39	o	yes	u	yes
<i>Pararge aegeria</i>	Satyridae	LC	0	2	0	m	yes	b	no
<i>Erynnis tages</i>	Hesperiidae	LC	0	3	0	m	yes	b	yes
<i>Ochlodes venata</i>	Hesperiidae	LC	0	1	1	o	yes	u	no
<i>Thymelicus lineola</i>	Hesperiidae	LC	7	1	8	o	yes	u	yes
<i>Thymelicus sylvestris</i>	Hesperiidae	LC	0	0	3	o	yes	u	yes
<i>Papilio machaon</i>	Papilionidae	LC	3	6	3	o	no	b	no
<i>Zygaena filipendulae</i>	Zygaenidae	LC	6	2	24	p	yes	u	no

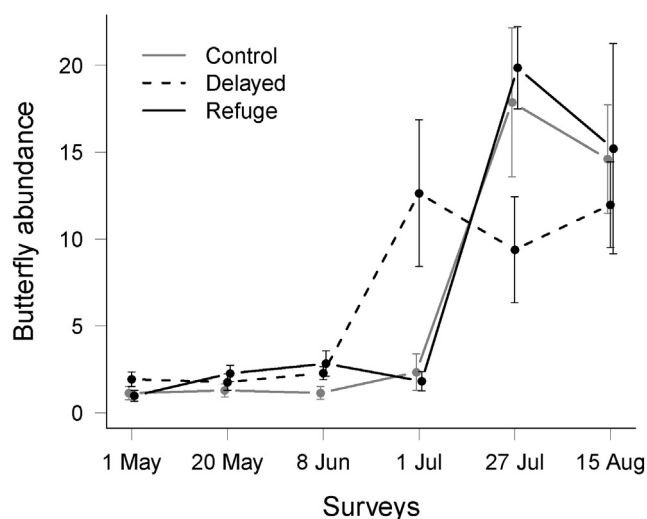


Fig. 1. Seasonal (May–August 2013) abundance (mean numbers per 100 m of transect segment \pm SE) of butterflies in response to the three different mowing regimes (control, delayed and refuge; see legend of Table 1 for more details). Each survey (1 to 6) is represented by a single date that corresponds to the average of the 2–7 days needed to complete a full survey at all study sites.

specialist (Fig. 3), non-resident and multivoltine species were recorded in R- compared to C-meadows, whereas significantly more mono- and oligophagous species were found in D- compared to C-meadows (see Appendices S5 and S6 for detailed model and graphical outputs). For all other groups (i.e. residents, polyphagous, univoltine and generalists), no differences were detected.

4. Discussion

This study shows that two simple modifications of mowing regimes in extensively managed grasslands, namely delaying the first possible cut by one month (i.e. until 15 July) or leaving an uncut refuge while mowing, had positive effects on butterfly abundance and number of specialist species. To the best of our knowledge, this is the first study that has experimentally tested at the field-scale the effects of alternative mowing regimes, with a given regime being randomly attributed to a meadow, on butterfly populations. The major advantage of such an experimental approach, over a traditional observational study (where management regimes are not randomly applied to study sites), is that it better accounts for confounding factors, such as the influence of surrounding landscape features or the fact that AES are systematically applied in more marginal, i.e. less optimal agricultural land. Therefore, conclusions provide evidence-based management recommendations (Sutherland et al., 2004) for effective butterfly conservation actions

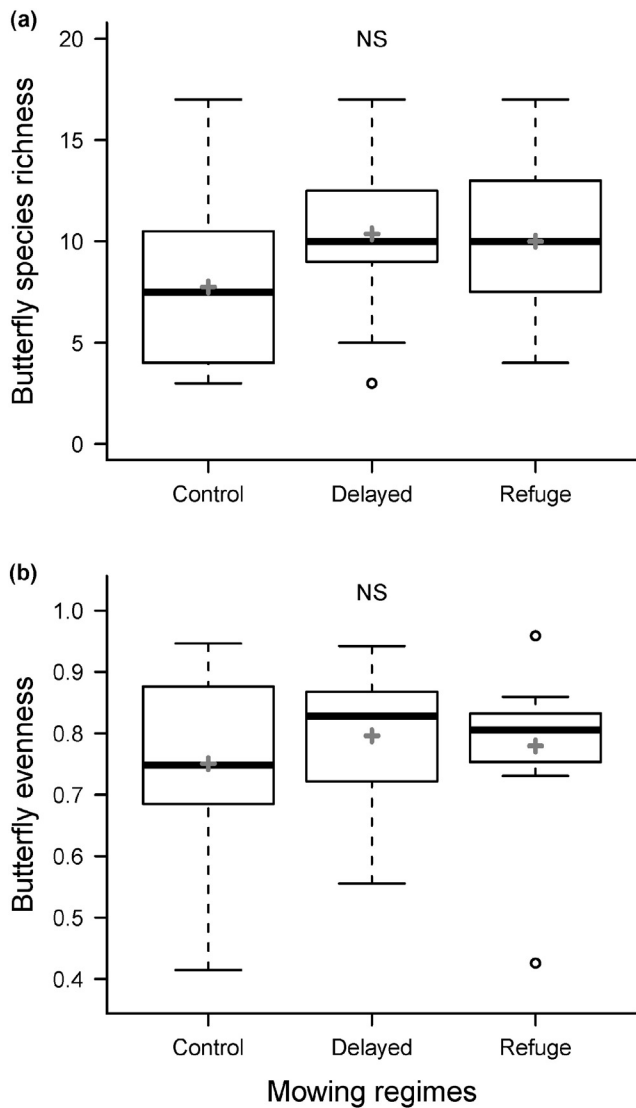


Fig. 2. Response of butterflies to mowing regimes: (a) butterfly species richness; and (b) butterfly evenness (Pielou's index). Box-plot median: bold line; mean: grey cross; first and third quartiles: box borders; interquartile distance multiplied by 1.5: whiskers; open circles: outliers. NS means no significant differences among regimes at an alpha-rejection level of 0.05. For mowing regime description, see legend of Table 1.

that are urgently needed. The study was carried out on the Swiss low-land Plateau, which has a similar climate and land-use pattern as western and central European countries. In addition, most of the sampled species have European-wide distributions. Hence, these findings have clear implications beyond Switzerland.

4.1. Butterfly abundance

Densities of butterflies were about 70% higher in D- and R-meadows prior to any mowing operations (surveys 1–3) compared to C-meadows. This demonstrates that measures implemented in 2010–2012 had positive cumulative effects (carry-over from one year to the next years) discernible in spring 2013. It is likely that these two alternative mowing regimes enhanced survival and reproductive success during the previous seasons. A similar cumulative phenomenon has also been evidenced for orthopterans (Buri et al., 2013), wild bees (Buri et al., 2014) and spiders subjected to the same experimental design. Interestingly, resident and specialist butterflies, which are more sensitive to disturbance (Börschig et al., 2013), benefited more from these measures than generalists.

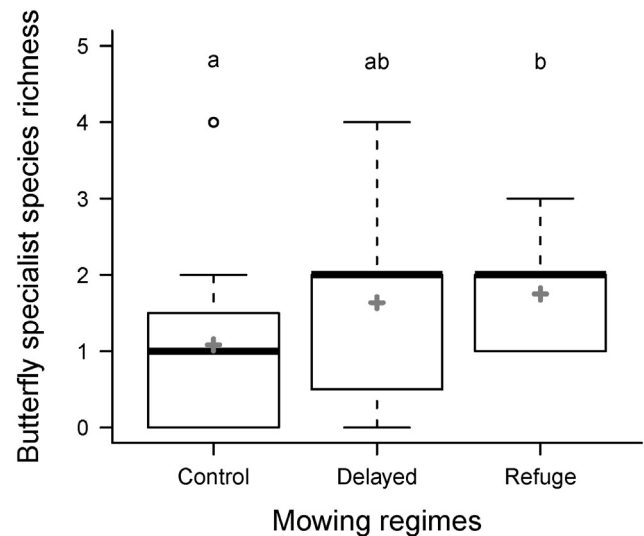


Fig. 3. Species richness of specialist butterflies in response to mowing regimes. For mowing regime description, see legend of Table 1. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05. Box-plot features as shown in Fig. 2.

During the fourth survey, i.e. when all but D-meadows had been mown and R-meadows harboured an uncut refuge, the delayed mowing regime led to, on average, five times higher butterfly densities in D- than in C- and R-meadows. This reflects a combination of immediate, within season, and cumulative effects on the populations. The question remains, however, whether these butterflies stemmed from the same D-meadow or whether they immigrated from nearby mown meadows (Valtonen et al., 2006). Whatever the mechanism, D-meadows were likely to enhance butterfly survival and fecundity, at least temporarily (WallisDeVries et al., 2012). Satyridae, which were by far the most abundant family in this survey, and Nymphalidae, dominated by the newly emerged fritillaries species *Melitaea athalia* and *Melitaea parthenoides*, were more abundant in D- compared to C- and R-meadows (results not shown), which is not surprising as these butterflies are well known for their dependency on very low-intensity mowing regimes, usually tolerating only one to two grass cuts a year (Dover et al., 2010; Settele and Reinhardt, 1999). Indeed, our delayed regime resulted in an overall reduction of the number of cuts per year. Similar positive or neutral effects of the D-regime were observed for all life-history groups investigated, suggesting that most species benefited to some extent from prolonged resource availability. R-meadows were expected to provide benefits of the same kind as D-meadows at the fourth survey, because they also offered prolonged availability of resources such as nectar, although over a much smaller area. Surprisingly, however, we found no evidence of such an effect, neither for the entire butterfly community, nor for life-history groups. The problem might be methodological since the study by Kühne et al. (2015) conducted within the same research programme has established that butterfly density was, on average, three times higher within uncut grass refuges compared to the mown fraction of the same R-meadow (see also Lebeau et al., 2015). Our surveys were carried out along transect lines traversing the middle of a meadow, i.e. somewhat distant from the grass refuges that had typically been installed along the meadow edge (L. Bruppacher personal observation). Because butterflies had aggregated in the uncut grass refuges they remained largely undetected during our surveys, underestimating abundances in R-meadows (Kühne et al., 2015). Additionally, the advantage of an R-meadow for butterflies detected during surveys 1–3 might lie more in the protection of caterpillars and pupae against the direct damage caused by the harvesting machinery (Humbert et al., 2010a) than in the presence of nectar sources for adults.

In the fifth sampling survey, i.e. after D-meadows had eventually been cut, relative butterfly abundances were inverted compared to the situation in previous surveys, with significantly lower densities in D- than in C- and R-meadows. This can be attributed to an advanced vegetation regrowth in the latter two meadows that had been mown around mid-June. Resident species, dominated by the very common species *Maniola jurtina*, increased in abundance in this survey, but were less numerous in D-meadows compared to the other two regimes, confirming the post-mowing population breakdowns described by Dover et al. (2010). Overall butterfly densities with narrow feeding-niches (mono- and oligophagous species) slightly increased in the fifth survey, but by then R-meadows harboured higher densities than C- and D-meadows. This supports the hypothesis that uncut grass refuges offer a greater variety of plants and more heterogeneous swards, both of which are essential for butterflies with narrow feeding-niches (Potts et al., 2009; Woodcock et al., 2009). In contrast, densities did not significantly differ between D- and C-meadows, suggesting that a late mowing, here represented by the D-regime, would not constitute a handicap for these species. Densities of specialist species culminated during the fifth survey, with higher abundance in R- than D-meadows, but no difference in abundance between C- and R- or C- and D-meadows was detected.

At the sixth survey, D-meadows had apparently once again become attractive for butterflies. Actually, mean butterfly abundance was by then comparable across all mowing regimes. As there were no restrictions regarding the timing of the second cut in our experimental setting, meadow development was fairly heterogeneous around mid-August, both within and among mowing regimes.

4.2. Butterfly species richness and diversity

Overall species richness did not differ statistically among mowing regimes despite an apparent trend. D- and R-meadows harboured, on average (\pm SE), 10.36 (\pm 1.22) and 10.00 (\pm 1.10) species, respectively, compared to 7.75 (\pm 1.23) in C-meadows. In other words, mean species richness was 32% higher in D- and R-meadows than in C-meadows. In Finland, Valtonen et al. (2006) recorded lower species richness of butterflies and diurnal moths in mid-summer mown road verges than in late summer- and partially mown verges. They suggested, however, that environmental factors other than mowing regimes strongly influence butterfly species richness along road verges (see also Perović et al., 2015). In our fully-controlled experimental setting, environmental factors might well have been a source of noise, reducing the strength of ecological signals, but could not have caused any bias, thanks to a random allocation of experimental treatments to meadows. The analysis of life-history groups revealed that specialist species were more frequent in R- than in C-meadows, confirming the importance of nectar sources and shelter sites that a diverse host plant assemblage offers to sensitive species (Börschig et al., 2013). Butterfly diversity showed a similar trend as species richness.

Meadow restoration is a relatively slow process, in which colonisation by new species is not only limited by local vegetation conditions, but is also affected by the presence, distance and connection to source populations (Öckinger and Smith, 2006; Woodcock et al., 2012). The positive effects on butterfly communities of the alternative regimes tested here can be expected to further increase with the duration of the experiment, as well as the probability of colonisation events augmenting with time (Collinge, 2000). Patches of woodland in the immediate surrounding landscape (\leq 250 m) have also been shown to have positive effect on butterfly species richness and abundance within grasslands (Villemey et al., 2015). Nevertheless, the local quality of the habitat, and thus its management, is usually the most important factor for the butterfly community, in particular for specialist species (e.g. Curtis et al., 2015; Krämer et al., 2012; Thomas et al., 2001).

4.3. Conclusions and management recommendations

The alternative mowing regimes experimentally tested in this study significantly benefited grassland butterfly communities, in particular species with specialised life-history traits. The delayed mowing regime prolongs the availability of feeding sources at a period when mowing causes a sudden and widespread collapse of vital resources across the landscape. Another collateral effect of the delayed mowing regime is a reduction in the number of cuts per season from an average of 2 cuts/year to 1.5 cuts/year, which favours species that naturally have a low resilience to habitat disturbance (Hudewenz et al., 2012; Konvicka et al., 2008). The refuge regime provides a continuous vegetation cover throughout the season for caterpillars and pupae, as well as for species with restricted dispersal and feeding potential, notably those which are typically impacted by the mowing process (Humbert et al., 2010b; Johst et al., 2006).

These results provide guidance for the development of new evidence-based recommendations for butterfly restoration in European farmlands that could be integrated into current and future AES policies. As the two alternative mowing regimes favour butterflies in different but complementary ways, we recommend implementing them in parallel in the agricultural matrix. This study yields no information about the optimal spatial arrangement of these measures at the landscape scale. However, in this respect, our field-scale experiment demonstrates that even localized implementation can contribute to increasing the effectiveness of AES (Batary et al., 2011; Ekroos et al., 2014). An uncut grass refuge within AES extensively managed hay meadows has already been implemented in some Swiss cantons as a voluntary measure, and the uptake was high. For example in 2015, 37% (representing 2139 ha) of all lowland AES hay meadows in canton Aargau and respectively 81% (representing 5301 ha) in canton Bern, harboured a refuge. Since butterflies are recognized as being good bioindicators (Thomas, 2005), delaying mowing and keeping uncut grass refuges among meadowland would also favour other groups of arthropods that depend on a similar spatio-temporal heterogeneity of farmland habitats. Finally, these alternative mowing regimes would also readily apply to other managed grasslands such as road verges, grassland nature reserves and canal banks where biodiversity conservation is also of concern.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.02.018>.

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