

# **Evidence-based mowing recommendations to restore butterfly populations in extensively managed grasslands**

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# **Evidence-based mowing recommendations to restore butterfly populations in extensively managed grasslands**

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## **Abstract**

Since World War II lowland grassland management has been considerably intensified, which had tremendous impacts on biodiversity. Not surprisingly, maintaining and restoring biodiversity in grasslands is a primary objective of today's agri-environment schemes (AES) across Europe, but it represents a considerable conservation challenge. Less detrimental mowing practices might be a solution for preserving biodiversity in meadowland. In this study, the effect of different mowing regimes on butterfly communities and populations has been experimentally investigated at the field-scale in 12 replicated sites across the Swiss lowlands. Expanded from the standard regime prevailing in extensively managed meadows declared under the Swiss AES policy (here used as control (C-meadow; C): first cut not before 15 June), two alternative mowing regimes have been tested: 1) Refuge meadow (R-meadow; R): conditions as for C, but with 10-20% of the area of the meadow left uncut during mowing operations; 2) Delayed meadow (D-meadow; D): conditions as for C, but first cut delayed from 15 June to 15 July. These three mowing regimes were randomly attributed to individual meadows, and yearly applied by farmers since 2010. In 2013, we recorded (line transect distance sampling method) diurnal butterflies at six sessions from April to August, i.e. before and during mowing (total of 1630 individuals; 39 species). We investigated abundance, species richness, diversity (Shannon-Wiener), as well as community composition, distinguishing between different life-history groups (residency, host plant specialisation and voltinism). Preserving an uncut grass refuge while mowing (R-meadows) as well as delaying mowing by a month (D-meadows) both benefit butterflies, boosting in particular species with life-history traits characteristic of specialists (resident, high host plant specialization and low numbers of generations). R- and D-meadows apparently offered prolonged undisturbed resources and shelter in a different but complementary way; we interpret the patterns as follows. Before mowing,

both regimes showed positive cumulative (over the years, as application of these mowing regimes started in 2010) effects on overall butterfly abundance (R and D had about 70% more individuals than C) and abundances of resident species and mono- and oligophagous species (R and D had almost twice as many individuals as C). After the 15 June, the delayed regime showed a highly positive direct effect on overall butterfly abundance and abundance of all life-history groups (D had about five times more individuals than C and R). The Overall species richness did not differ among the regimes, however, it was higher for specialists in R-meadows compared to C-meadows (R had about 60% more specialist species than C). Shannon Wiener diversity was about 25% higher in D- and R- compared to C-meadows. The two alternative mowing regimes investigated here appear to represent promising measures to boost butterfly populations in extensively managed grasslands. They would be easily implemented by adapting AES financial incentives. These measures could be applied among other grassy habitats such as road verges and canal banks.

**Keywords:** Agri-environment schemes, distance sampling, lepidopteran, life-history groups, meadow, specialist.

## 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 fertilizer application and mechanization that allows more rapid harvesting processes over large areas led to the deterioration of habitat quality and stepwise simplification of the landscape (Benton, Vickery & Wilson 2003; Tschamntke *et al.* 2005). These changes have subsequently resulted in widespread population declines of farmland birds and many invertebrate groups across whole Europe (Vickery *et al.* 2001; Ekroos, Heliola & Kuussaari 2010; van Swaay *et al.* 2010).

Butterflies are a typical example as they have especially suffered from the intensification of the management practices in grasslands (van Swaay *et al.* 2010). Many species have experienced severe declines over the last decades, and nowadays almost 20% of all European species are considered threatened or near threatened (van Swaay *et al.* 2010). Specialists with narrow niche-breath and low dispersal ability have been reported to decline most rapidly (Ekroos, Heliola & Kuussaari 2010; Borschig *et al.* 2013). Hence, communities in many of today`s EU lowland grasslands are dominated by few ubiquitous generalists, which are less prone to disturbances (Van Dyck *et al.* 2009; Ekroos, Heliola & Kuussaari 2010).

Although many agri-environment schemes (AES) are specifically targeted to grasslands, so far they have only provided limited benefits for biodiversity (Kleijn *et al.* 2006; Aviron *et al.* 2007). It has been argued that they often provide too little habitat and land-use heterogeneity (Konvicka *et al.* 2008; Cizek *et al.* 2012) and fail to promote high-quality habitats for sensitive, more specialized species (Ekroos, Heliola & Kuussaari 2010). Moreover, a big part of underlying research on grassland management has been targeted on plant assemblages, which are often not limited by the same factors as animals (Littlewood,

Stewart & Woodcock 2012). Hence, finding conservation measures to improve the current state of semi-natural grasslands for invertebrates like butterflies is urgently needed.

The diversification of mowing practices within field and landscape is a promising way to restore heterogeneity and enhance insect diversity (Cizek *et al.* 2012; Buri, Humbert & Arlettaz 2014). Low-intensity mowing has been used as a tool to restore semi-natural grasslands in a nature reserve in the Czech Republic (Konvicka *et al.* 2008) and has been approved because of its beneficial effect on plant diversity by suppressing the growth of shrubs and trees (Erhardt 1985; Öckinger, Eriksson & Smith 2006). However, mowing also causes substantial damage to invertebrates like butterflies by increasing direct caterpillar mortality and rapidly removing nectar sources (Dover *et al.* 2010; Humbert *et al.* 2010). If too indiscriminately applied or poorly timed, mowing can have negative effects on population persistence, especially for species with specialized needs (Johst *et al.* 2006; Konvicka *et al.* 2008).

Several suggestions have been made to mitigate the negative impact of mowing on butterflies. First, late-summer cuts are thought to be less harmful than cuts in early summer (Feber, Smith & Macdonald 1996; Valtonen, Saarinen & Jantunen 2006; Potts *et al.* 2009) – which can be attributed to the smaller amount of juveniles in this period of the season (Walter, Schneider & Gonseth 2007). More evidences come from a recent meta-analysis which concludes that delaying the first mowing date can have positive effects on species richness and abundance of invertebrates (Humbert *et al.* 2012b). The delay extends the temporal availability of resources and lowers the mowing pressure over the whole season by reducing the overall number of cuts. Second, leaving uncut refuges while mowing has often been suggested as a way to reduce animal mortality caused by the harvesting machines (Humbert *et al.* 2010) , as well as to provide continuous shelter and food supply (Weibull, Bengtsson & Nohlgren 2000; Valtonen, Saarinen & Jantunen 2006; Humbert *et al.* 2012a). Additionally, refuges can act as permanent oviposition sites for some butterfly species laying their eggs directly on plants within the meadow (Erhardt 1985). The beneficial effect of

leaving uncut refuges has already been demonstrated for orthopterans and wild bees (Humbert *et al.* 2012a; Buri, Arlettaz & Humbert 2013; Buri, Humbert & Arlettaz 2014). It has also been suggested for butterflies (Kühne *et al.* in prep; Dover *et al.* 2010) but without clear quantitative proof on long-term biodiversity benefits at the population level.

The aim of this study was to experimentally investigate these hypotheses, namely the influence of leaving uncut grass refuges or delaying mowing in lowland extensively managed grasslands under Swiss AES. The ultimate goal was therefore to deliver evidence-based management recommendations to improve the outlook for butterflies. This study is part of an ambitious research program launched in 2010 at the University of Bern with the objectives to better understand the influence of different mowing regimes on field invertebrates, vertebrates and flora communities. Three different mowing regimes were devised in 2010 and distributed randomly to one of three extensively managed meadows in 12 regions of Switzerland. The first mowing regime (and study control) conforms to the standard regulations for extensively managed meadows under Swiss AES, i.e. first cut not earlier than 15 June. For the second regime, a small portion of the meadow (10-20%) was left uncut as a refuge during each mowing event; for the third regime, the first possible cut was delayed by one month to the 15 July. The results of this study can help to further develop current European and Swiss AES measures towards more efficient protection of butterflies and other invertebrate groups in extensively managed grasslands.

## **2. Materials and methods**

### *2.1 Study sites*

In 2010, 35 extensively managed meadows registered under Swiss AES at least since 2004 were selected across the Swiss lowland Plateau. All meadows were located between 390 and 833 m altitude (Appendix S1). They were equally distributed among twelve regions of three meadows each, except for one region (Coffrane, canton of Neuchatel) which contained

only two meadows as one was lost in 2012. While a minimal distance of 5 km was assured between the regions, the three meadow per region were clustered within a 3.5 km radius with a minimum distance of 440 m between each other. Meadows had a minimum size of 0.3 ha (range: 0.3–1.7 ha).

## *2.2 Experimental design*

The experiment has been arranged in a randomized block design, where the three mowing regimes have been randomly applied to one of three meadows in a region (block), resulting in twelve independent replicates of each regime. The following three mowing regimes were applied continuously during the time span of the experiment:

1. Control (C-meadow; C): Extensively managed meadow according to the Swiss AES regulations (i.e. no fertilizer application and earliest cut 15 June).
2. Refuge (R-meadow; R): Extensively managed like C, but with a refuge area of 10-20% left uncut while mowing (no restriction on the shape of the refuge, but the location of the refuge being changed to avoid vegetation succession).
3. Delayed (D-meadow; D): Extensively managed like C, but the earliest possible cut delayed to 15 July.

## *2.3 Butterfly sampling*

In summer 2013, diurnal butterflies were sampled on line transects. Distance sampling method was adopted, which enables the incorporation of detectability by additionally recording the perpendicular distances in meter-intervals from the individuals to the transect line (Buckland *et al.* 2001). Distance sampling is an extended alternative of standard line-transect sampling according to the prescriptions of Pollard & Yates (1993). It has mainly been used for bird sampling in the past (Buckland *et al.* 2001) and has recently been suggested to produce a more reliable estimate of butterfly populations (Pellet *et al.* 2012). In



this study it has mainly been chosen to account for possible differences in detectability among the mowing regimes.

When the shape of the meadow was approximately rectangular, transects were positioned along the longest diagonal line. In other cases, transects were placed alongside the middle of the meadow. Before the first sampling session, the middle line and the 5-meter intervals on both sides were marked with colored flags for better visualization. Transects were followed in a single direction at a continuous, steady pace. All detected individuals and their perpendicular distance to the transect line were recorded. If possible, visual identification was made. In case of identification ambiguity, individuals were caught with a black butterfly net, identified immediately and released afterwards. Butterflies were identified to species level according to the identification guide of Lewington & Tolman (2012) and Bühler-Cortesi (2009).

Six sampling sessions were conducted during the main flight season from end of April to beginning of September. Three surveys were done before 15 June, one between 15 June and 15 July and two after 15 July. Samplings were done between 10:00 and 17:00 on sunny and warm days with a minimal air temperature of 13°C and a maximal wind speed of 3 Beaufort, as suggested by Pollard and Yates (1993) and used by the Biodiversity Monitoring Switzerland for butterflies and the British Butterfly monitoring scheme (Altermatt *et al.* 2008; van Swaay *et al.* 2008). Meadow sampling-order within a region was randomly chosen each day.

#### *2.4 Statistical analysis*

The initial analyses on abundance done with distance sampling models (DSMs), using the *distsamp* function of the *Unmarked* package for R (Chandler & Fiske 2011), showed that there were no significant differences in butterfly detectability among mowing regimes (Appendix S2). In light of this fact, further analyses were made with conventional generalized linear mixed models (GLMMs) using the *lmer* function from the package *lme4* (Bates *et al.*

2012) directly on the raw data (without distances included). An advantage to use GLMMs over DSMs was the option to include the regions as random factor in the models. Response variables were number of individuals in total, per family and per life-history group standardized to an average transect length of 100 m. These variables were analyzed with a Poisson error distribution. The model's fixed effects were composed of the three mowing regimes and the sampling sessions. The first three sessions were pooled in one model because all meadows were in the same unmown stage in these sessions. Any found differences here were due to a cumulative effect from former years. After 15 June the sessions were analysed separately because direct and cumulative effects were interacting and meadows were no longer in the same vegetative stage. For abundance analyses of families and life-history groups, only the sampling sessions with occurrence in minimum six different regions were considered.

Species richness was computed over all sampling sessions. Analyses were done with linear mixed models (LMMs) using the same function as for GLMMs, but with Gaussian error distribution. Response variables were species richness in total, per family and per life-history group. Fixed effects were the mowing regimes and transect length to account for differences due to field sizes. Only families and life-history groups with more than four species and with presence in at least six different regions were analysed.

Shannon-Wiener indices of diversity were additionally analysed (Wilsey *et al.* 2005). The index of each species was calculated from the standardized abundance data summed-up over all sessions using the function *diversity* of the package *Vegan* in R (Oksanen 2013). The index reaches its maximum when all species are equally abundant. Analyses were also done with linear mixed models (LMMs). Response variables were the diversity indices and fixed effects were the mowing regimes. All statistics were performed using R version 3.0.1 (R Core Team 2013).

Life-history groups were the following: (1) narrow feeding niche (mono & oligophagous species); (2) low mobility species (residents) and (3) species being less

mobile, uni- or bivoltine and mono- or oligophagous (specialists). Groups were made after Settele *et al.* (1999) and Lepidopterologen-Arbeitsgruppe (1987) (Table 1).

### 3. Results

A total of 1630 individuals were recorded. Overall, 39 different species out of 7 families were found: Nymphalidae (12); Pieridae (8); Satyridae (7); Lycaenidae (7); Hesperidae (4); Zygaenidae (1); and Papilionidae (1) (Table 1). Satyridae was the most abundant family, having high abundances in July and August. Pieridae was the prevalent family in the first three sessions followed by a decrease in June. Members of Lycaenidae were present at very low abundances until July and then increased in numbers in the fifth and sixth sampling session. Nymphalidae were present across the whole season, but mostly solitary or in low numbers. Hesperidae and Papilionidae were always infrequent and Zygaenidae only emerged in August.

#### 3.1 Butterfly abundance

Mean butterfly abundance ranged from 1 to 20 individuals per 100 m, with clear differences among mowing regimes and sampling sessions (Fig. 1 and Appendix S4). Before mowing (sessions 1–3), butterfly abundance was significantly higher in D and R compared to C (D vs C: Estimate, hereafter abbreviated E,  $\pm$  standard error =  $0.47 \pm 0.20$ ,  $P = 0.017$ ; R vs C: E =  $0.54 \pm 0.19$ ,  $P = 0.005$ ). Note that estimates are on the log scale. R and D did not differ significantly from one another. In session four, the mid-season period between 15 June and 15 July (all meadows cut except D), abundance was significantly higher in D compared to C and R (D vs C: E =  $1.89 \pm 0.32$ ,  $P < 0.001$ ; R vs D: E =  $-1.87 \pm 0.23$ ,  $P < 0.001$ ), while R did not differ from C. In session five (D-meadows cut), C and R had significantly higher abundances than D (C vs D: E =  $2.74 \pm 0.30$ ,  $P < 0.001$ ; R vs D: E =  $0.76 \pm 0.12$ ,  $P < 0.001$ ).

R and C did not differ. In session six there was no longer a significant difference among the regimes.

Regarding family level analyses before mowing, only Pieridae reached the predetermined threshold, but no significant effects were found for neither R nor D compared to C (R vs C:  $E = 0.44 \pm 0.27$ ,  $P = 0.097$ ; D vs C:  $E = 0.37 \pm 0.28$ ,  $P = 0.183$ ). See appendices S3 and S4 for detailed graphical and model outputs. In session four, Nymphalidae abundance was significantly higher in D compared to C and R (C vs D:  $E = -2.27 \pm 0.72$ ,  $P = 0.002$ ; R vs D:  $E = -1.97 \pm 0.63$ ,  $P = 0.002$ ), while C and R did not differ. Satyridae were significantly more abundant in D compared to C and R (D vs C:  $E = 1.36 \pm 0.34$ ,  $P = 0.001$ ; R vs D:  $E = -2.644 \pm 0.38$ ,  $P < 0.001$ ), while C and R did not differ significantly. The other families had too low abundances in this session. In session five, Satyridae were significantly less abundant in D compared to C and R (C vs D:  $E = 0.68 \pm 0.15$ ,  $P < 0.001$ ; R vs D:  $E = 0.815 \pm 0.15$ ,  $P < 0.001$ ). There were significantly less Pieridae in D compared to C and R (C vs D:  $E = 0.75 \pm 0.23$ ,  $P = 0.001$ ; R vs D:  $E = 0.772 \pm 0.23$ ,  $P < 0.001$ ). In both cases, R and C were not significantly different. Both, Nymphalidae and Lycaenidae abundances did not differ among the regimes. In session six, Satyridae were less abundant in D compared to C and R (D vs C:  $E = 1.08 \pm 0.21$ ,  $P < 0.001$ ; R vs D:  $E = 0.738 \pm 0.22$ ,  $P < 0.001$ ). R had as well lower abundances of Satyridae than C ( $E = -0.344 \pm 0.16$ ,  $P = 0.032$ ) in this session. Pieridae abundance did not differ in C compared to D and R, but was higher in R compared to D (R vs D:  $0.43 \pm 0.21$ ,  $P = 0.036$ ). Lycaenidae abundance was significantly higher in D compared to C and R (C vs D:  $E = -1.14 \pm 0.27$ ,  $P < 0.001$ ; R vs D:  $E = -0.815 \pm 0.24$ ,  $P > 0.001$ ). Nymphalidae were not significantly different.

Analyses of life-history groups before mowing showed that resident species were significantly more abundant in D and R compared to C (D vs C:  $E = 0.70 \pm 0.31$ ,  $P = 0.026$ ; R vs C:  $E = 0.63 \pm 0.31$ ,  $P = 0.045$ ; Appendices S3 and S4). Mono- and oligophagous species were more abundant in D and R compared to C (D vs C:  $E = 0.55 \pm 0.27$ ,  $P = 0.046$ ; R vs C:  $E = 0.65 \pm 0.27$ ,  $P = 0.014$ ). Specialist species were too scarce in this period to be modelled

effectively. In session four, resident species were significantly more abundant in D compared to C and R (D vs C:  $E = 1.60 \pm 0.33$ ,  $P < 0.001$ ; R vs D:  $E = -2.26 \pm 0.29$ ,  $P < 0.001$ ). Mono- and oligophagous species were also significantly more abundant in D compared to C and R (D vs C:  $E = 0.56 \pm 0.37$ ,  $P < 0.001$ ; R vs D:  $E = -0.94 \pm 0.35$ ,  $P = 0.007$ ). Specialist species were more abundant in D compared to C and R (D vs C:  $E = -0.09 \pm 0.42$ ,  $P = 0.006$ ; R vs D:  $E = -0.91 \pm 0.46$ ,  $P = 0.047$ ). In session five, resident species were significantly less abundant in D compared to C and R (C vs D:  $E = 0.63 \pm 0.14$ ,  $P < 0.001$ ; R vs D:  $E = 0.76 \pm 0.14$ ,  $P < 0.001$ ). Specialists were not significantly different between the regimes. Mono- and oligophagous species were significantly more abundant in R compared to C (R vs C:  $E = 0.778 \pm 0.34$ ,  $P = 0.027$ ) and not significantly different between D and C. In session six, no differences between mowing regimes were found for any life-history group.

### *3.2 Butterfly species richness and diversity*

39 different species were found. Mean  $\pm$  standard error (SE) for C-meadows was ( $5.46 \pm 2.00$ ), for D ( $7.51 \pm 1.31$ ) and R ( $7.52 \pm 1.24$ ). Differences were not significant (C vs D:  $E = 1.61 \pm 1.27$ ,  $P = 0.219$ ; C vs R:  $E = 2.07 \pm 1.20$ ,  $P = 0.101$ ; D vs R:  $E = 0.01 \pm 1.29$ ,  $P = 0.992$ ; Fig.2a). At the family level, significantly more Pieridae species were found in R compared to C (R vs C:  $E = 1.12 \pm 0.46$ ,  $P = 0.013$ ), while D and C did not differ. Significantly more Lycaenidae were found in D compared to C (D vs C:  $E = 1.20 \pm 0.48$ ,  $P = 0.021$ ), while R and C did not differ. For Nymphalidae and Satyridae, no differences among the regimes were found. Regarding life-history groups, significantly more specialists were found in R compared to C (R vs C:  $E = 0.63 \pm 0.29$ ,  $P = 0.047$ ), whereas for mono & oligophagous species and residents, no differences were detected (Appendices S5 and S6). Butterfly diversity (Shannon indices) was significantly higher in D and R compared to C (D vs C:  $E = 0.40 \pm 0.15$ ,  $P = 0.015$ ; R vs C:  $E = 0.35 \pm 0.14$ ,  $P = 0.027$ ; Fig. 2b) D and R did not differ significantly.

## 4. Discussion

This study shows that delaying the first possible cut by one month (i.e. to 15 July, D-meadows) or leaving an uncut refuge while mowing on 15 June onward (R-meadows) has positive effects on butterfly diversity, specialist species and overall abundance compared to meadows mown on 15 June onward without refuge left (C-meadows). It is, to our knowledge, the first study that has experimentally tested the effects of new mowing regimes on butterfly populations at the field-scale in extensively managed meadows. It assesses for the first time the effects of changes in mowing regimes on different lepidopteran families and guilds and provides evidence-based management recommendations for their conservation. Four red-listed species have been found (*Melitaea parthenoides*, *Melitaea cinxia*, *Boloria Boloria dia* and *Cupido argiades*), as well as more demanding species such as *Lycaena tityrus*, *Erynnis tages* and *Brenthis daphne* (Wermeille, Chittaro & Gonseth 2014), indicating an adequate habitat quality for sensitive species. Because of harsh weather conditions occurring in spring 2013 (MeteoSchweiz 2013), abundances were low in the period before mowing. This may have limited the probability of detecting a difference between mowing regimes, and has to be considered when interpreting the results of the study.

### 4.1 Butterfly abundance

Higher densities of butterflies were observed in both alternative regimes prior to any mowing action (sampling sessions 1–3). This indicates that the alternative mowing regimes had positive effects on butterfly populations the previous years (experiment implemented in 2010) that carried-over to spring 2013. Many of the species observed during that period have two or more generations per year and likely benefited from higher survival and reproductive success in the former year. This so-called “cumulative” effect has also been observed for orthopterans (Buri, Arlettaz & Humbert 2013) and wild bees (Buri, Humbert & Arlettaz 2014) in the same project. The results indicate that this is especially important for resident species

and species with narrow feeding niches, as they are highly prone to disturbances (Reinhardt *et al.* 2005; Borschig *et al.* 2013).

The immediate positive effect of the D-regime became more obvious in the mid-season period (4<sup>th</sup> session), where D-meadows supported on average five times higher butterfly densities than C and R-meadows. At that time, all but D-meadows were cut. Therefore it is uncertain how many of the observed butterflies were local and how many were emigrants that were attracted by the unmown site in a time when resources were depleted (Valtonen, Saarinen & Jantunen 2006). In both cases, D-meadows played, at least temporally, a crucial role for the survival and fecundity of the occurring butterflies (WallisdeVries, Van Swaay & Plate 2012). Satyridae were by far the most abundant family in this session, showing high preference for the unmown D-meadows. This confirms that this family is very sensitive to mowing (Dover *et al.* 2010) and relies on swards with a high proportion of grasses (Lepidopterologen-Arbeitsgruppe 1987). Nymphalidae also preferred D-meadows, potentially due to newly emerged fritillary species (*M. athalia* and *M. parthenoides*). They are known to be highly dependent on low-intensity mowing with less than two cuts per year (Settele *et al.* 2009). It is worth noting that by delaying the first mowing date, the number of cuts per year could be reduced (Buri, Arlettaz & Humbert 2013). Similar positive effects of D were found for all life-history groups, suggesting that all species benefited equally from the prolonged availability of resources. In this context, R-meadows were suggested to provide comparable benefits, as they also offer a patch of permanent nectar. Surprisingly, after mowing R-meadows had neither a direct effect on total butterflies, nor single families or life-history groups in this session. The advantage of R-regime for butterflies could more explicitly involve protection of resident juveniles against direct damage resulting from the harvesting process and the provision of diverse host plants (Humbert *et al.* 2010), than in the offer of nectar flowers for adults. The comparatively small sizes of the refuges seem to limit their ability to attract significantly more adults from surrounding habitats (Öckinger & Smith 2006). Alternatively, adult butterflies may have aggregated in the uncut

refuges leading to an uneven distribution of the populations within the R-meadows. As uncut refuges were typically placed along an edge of the meadows, our mid-meadow-line-transect surveys may have underestimated overall abundances. In fact, this hypothesis was confirmed by Kühne et al. (2013) who found triple the butterfly density within uncut grass refuges compared to the surrounding cut matrices.

In the fifth sampling session, while D-meadows were freshly cut, the vegetation in C- and R-meadows had already regrown and relative densities reversed with significantly lower numbers of butterflies in D- than C- and R-meadows. Satyridae abundances peaked in this session and were remarkably lower in D- compared to R- and C-meadows, probably due to their high sensitivity to mowing (Dover *et al.* 2010). Note, however, that most of Satyridae species have their abundance-peak in June (Lepidopterologen-Arbeitsgruppe 1987). The unfavorable weather conditions in spring 2013 could have retarded their phenology in such a way that peak emergence more negatively interfered with the delayed cut than it typically would (Sparks & Yates 1997). Similarly, and in line with the after mowing population breakdowns observed by Dover *et al.* (2010), resident species, dominated by the very common species *Maniola jurtina*, were less abundant in delayed compared to the other two regimes. Pieridae and Lycaenidae abundances increased in all three regimes, mainly due to subsequent generations of polyphagous species like *Polyommatus icarus* or *Colias croceus* feeding mostly on early regrown Fabaceae (Lepidopterologen-Arbeitsgruppe 1987). Species with narrow feeding-niches and specialists did not significantly differ between D- and C-meadows, possibly demonstrating that the time of the mow in D-regime does not conflict with the phenology of these species. Meadows with a refuge were significantly preferred by species with narrow feeding-niches. This strengthens the hypothesis that R-meadows might offer more heterogeneous swards with a wider variety of plants considered essential for butterfly abundance and species richness (Potts *et al.* 2009; Woodcock *et al.* 2009).

In the sixth session, D-meadows apparently became more suitable again, and mean butterfly abundances were the same across all mowing regimes. As there was no restriction



on the timing of the second cut in any of the mowing regimes at this time of the season, meadow development was fairly heterogeneous within and among mowing regimes. I.e., in all regimes some meadows harbored regrown flowering plants while others harbored short freshly cut swards.

#### *4.2 Butterfly species richness and diversity*

No significant effect on overall species richness was found, although a positive tendency was apparent with about 37% more species in D- (mean  $\pm$  SE =  $7.51 \pm 1.31$ ) and R- ( $7.52 \pm 1.24$ ) compared to C-meadows ( $5.46 \pm 2.00$ ). Similar results were found in the Netherlands by Valtonen, Saarinen & Jantunen (2006), where mid-summer mown road verges had lower species richness of butterflies and diurnal moths compared to late summer and partially mown verges. They also suggested that environmental factors have stronger influences on butterfly species richness than the management of the investigated road verges. In our study, environmental factors did not cause any bias towards one regime or another, thanks to the random allocation of the experimental mowing treatments. Nevertheless, environmental factors were a source of noise, which reduced our ability to detect a signal in the data. Closer investigations of life-history groups revealed that specialist species preferred R- over C-meadows, further confirming the importance of nectar sources, shelter and diverse host plant assemblages for sensitive species (Borschig *et al.* 2013). Butterfly diversity came out to be significantly higher in D- and R-meadows compared to C-meadows. Suggesting that species were more evenly distributed in D- and R-meadows, what led to a more pronounced difference in diversity compared to species richness alone.

Meadow restoration is a relatively slow process, colonization by new species is not only limited by local factor, but also the presence, distance and connection to source populations (Öckinger & Smith 2006). In this regard, four years (2010-2013 included) is considered brief (Walker *et al.* 2004), thus observed positive effects of the alternative regimes are expected to further increase with time.

#### 4.3 Conclusions and management recommendations

The alternative mowing regimes investigated in this study demonstrated remarkable effects on butterfly diversity, abundances and species richness, especially for species with specialist traits. The benefit of the delayed regime was clearly a result of the prolonged availability of rich feeding sources in a period (mid-June to mid-July) when resources were generally scarce across the landscape. In addition to delaying the first mowing event, this treatment also decreases the total number of cuts per season and can be therefore especially beneficial for species depending on a low level of disturbance. The benefit of the refuge regime was primarily based on the provision of a continuous undisturbed vegetated area preferentially protecting low-mobility stages and species with restricted dispersal and feeding flexibility from direct mortality caused by the harvesting process. The underlying experimental approach used makes it possible to derive evidence-based management recommendations for the conservation of butterflies in European farmlands. Moreover, as butterflies are considered good indicators for invertebrate biodiversity, results can be readily extrapolated to other groups (Thomas *et al.* 2004; Van Swaay, Warren & Lois 2006).

In conclusion, it can be stated that both alternative mowing regimes enhance butterfly abundance and diversity in differing and complementary ways. Based on this, the implementation of both regimes into the agricultural matrix is recommended. The overall required minimum quantity and spatial distribution of these meadows cannot be determined from this study and would require further large scale empirical studies. However, it is likely that the necessary financial resources available to encourage the effective implementation of these mowing regimes will limit the “quantity” before a minimum upper threshold is reached. In light of the present conclusion, these measures constitute promising options to increase the effectiveness of Swiss and European AES compared to current situation (Kleijn *et al.* 2006; Batary *et al.* 2011). They also apply to other grassland structures such as road verges and grassland nature sites where conservation of biodiversity is of concern.

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We thank our colleagues at the Division of Conservation Biology and the members of the accompanying group for their valuable input on the project. Special thanks to Pierrick Buri and Isabel Kühne for their support with methods and help in the field, and to Davide De Masi for his careful reading of the manuscript. We also thank the farmers for their participation and collaboration in this project. We are grateful to the Swiss National Science Foundation (grants no. 31003A 125398/1 and 31003A 149656/1 to R. Arlettaz), the Federal Offices for Agriculture and the Environment, and several Swiss cantons (Aargau, Bern, Basel-Landschaft, Fribourg, Graubünden, Neuchâtel, Valais and Vaud) for their financial support.

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**Table 1:** List of species with number of individual found per mowing regimes (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 refuge of 10-20% area left uncut while mowing) and per region (RE). Red list-status (RL) after Swiss red list of butterflies of Wermeille, Chittaro & Gonseth (2014). Red-list status abbreviations are: LC: least concern; NT: nearly threatened; VU: vulnerable. Other columns provide information on the diet (m = monophagous, o = oligophagous, p = polyphagous, residency with yes = resident and no = nonresident), and voltinism of the species (m = multivoltine, b = bivoltine, u = univoltine). The last column state if species were classified as specialist or not. Life-history classifications are derived from (Settele, Feldmann & Reinhardt 1999).

Species	Family	RL	C	D	R	RE	Diet	Residency	Voltinism	Specialist
<i>Aglais urticae</i>	Nymphalidae	LC	1	4	5	5	m	no	m	no
<i>Araschnia levana</i>	Nymphalidae	LC	1	0	1	1	m	no	b	no
<i>Brenthis daphne</i>	Nymphalidae	LC	0	2	0	1	m	yes	u	yes
<i>Boloria dia</i>	Nymphalidae	NT	1	0	1	2	m	yes	b	yes
<i>Inachis io</i>	Nymphalidae	LC	2	1	4	5	p	no	m	no
<i>Issoria lathonia</i>	Nymphalidae	LC	0	4	2	2	p	no	m	no
<i>Melitaea athalia</i>	Nymphalidae	LC	0	12	0	2	o	yes	u	yes
<i>Melitaea parthenoides</i>	Nymphalidae	VU	0	2	0	1	m	yes	b	yes
<i>Melitaea cinxia</i>	Nymphalidae	VU	1	0	0	1	m	yes	u	yes
<i>Vanessa athalanta</i>	Nymphalidae	LC	0	3	1	4	p	no	m	no
<i>Vanessa cardui</i>	Nymphalidae	LC	20	7	12	9	p	no	m	no
<i>Polygonia c-album</i>	Nymphalidae	LC	0	1	0	1	p	no	m	no
<i>Anthocharis cardamines</i>	Pieridae	LC	2	1	2	3	p	yes	u	yes
<i>Colias crocea</i>	Pieridae	LC	43	19	41	11	p	no	m	no
<i>Colias hyale</i>	Pieridae	LC	7	2	16	9	p	no	m	no
<i>Gonepteryx rhamni</i>	Pieridae	LC	0	1	3	4	p	no	b	no
<i>Pieris brassicae</i>	Pieridae	LC	10	15	20	9	p	no	m	no
<i>Pieris napi</i>	Pieridae	LC	65	61	64	12	p	no	m	no
<i>Pieris rapae</i>	Pieridae	LC	17	17	38	12	p	no	m	no
<i>Leptidea sinapis</i>	Pieridae	LC	5	5	1	2	p	yes	b	no
<i>Celastrina argiolus</i>	Lycaenidae	LC	0	2	1	2	p	no	b	no
<i>Cupido argiades</i>	Lycaenidae	NT	7	10	6	7	o	yes	m	yes
<i>Lycaena phlaeas</i>	Lycaenidae	LC	0	1	1	2	p	yes	m	no
<i>Lycaena tityrus</i>	Lycaenidae	LC	2	1	2	3	m	yes	b	yes
<i>Polyammatus icarus</i>	Lycaenidae	LC	16	53	34	11	o	yes	m	no
<i>Cyaniris semiargus</i>	Lycaenidae	LC	5	33	8	10	m	yes	m	no
<i>Aricia aegestis</i>	Lycaenidae	LC	1	0	0	1	p	yes	m	no
<i>Aphantopus hyperantus</i>	Satyridae	LC	1	3	0	2	p	yes	u	no
<i>Coenonympha pamphilus</i>	Satyridae	LC	22	20	32	11	p	yes	m	no
<i>Lasiommata megera</i>	Satyridae	LC	3	3	1	4	p	yes	m	no
<i>Maniolata jurtina</i>	Satyridae	LC	253	206	210	12	p	no	u	no
<i>Melanargia galathea</i>	Satyridae	LC	26	13	39	8	o	yes	u	yes
<i>Pararge aegeria</i>	Satyridae	LC	0	2	0	1	m	yes	b	no
<i>Erynnis tages</i>	Hesperiidae	LC	0	3	0	2	m	yes	b	yes
<i>Ochlodes venata</i>	Hesperiidae	LC	0	1	1	2	o	yes	u	no
<i>Thymelicus lineola</i>	Hesperiidae	LC	7	1	8	2	o	yes	u	yes
<i>Thymelicus sylvestris</i>	Hesperiidae	LC	0	0	3	2	o	yes	u	yes
<i>Papilio machaon</i>	Papilionidae	LC	3	6	3	9	o	no	b	no
<i>Zygaena filipendulae</i>	Zygaenidae	LC	6	2	24	4	p	yes	u	no

## Figure legends

**Figure 1.** Seasonal abundance (May-August 2013) of butterflies (mean  $\pm$  SE) in response to the three mowing regimes. Each sampling session is represented by a single date that corresponds to the average of the 2–7 days needed to complete the sessions. For regime descriptions see legend of Table 1.

**Figure 2.** Butterfly species richness **(a)** and diversity **(b)** per mowing regime. Species richness corresponds to the number of species found over the whole season and diversity equals to the related Shannon-Wiener indices. For regime descriptions see legend of Table 1. Median: bold line; mean: cross; first and third quartiles: box borders; interquartile distance multiplied by 1.5: whiskers; open circles: outliers. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05.

**Figure 3.** Number of butterfly specialist species per mowing regime. For specialist species and regime description see Table 1. For detailed information on box-plot features and significance codes see legend of Fig. 2.

Fig.1:

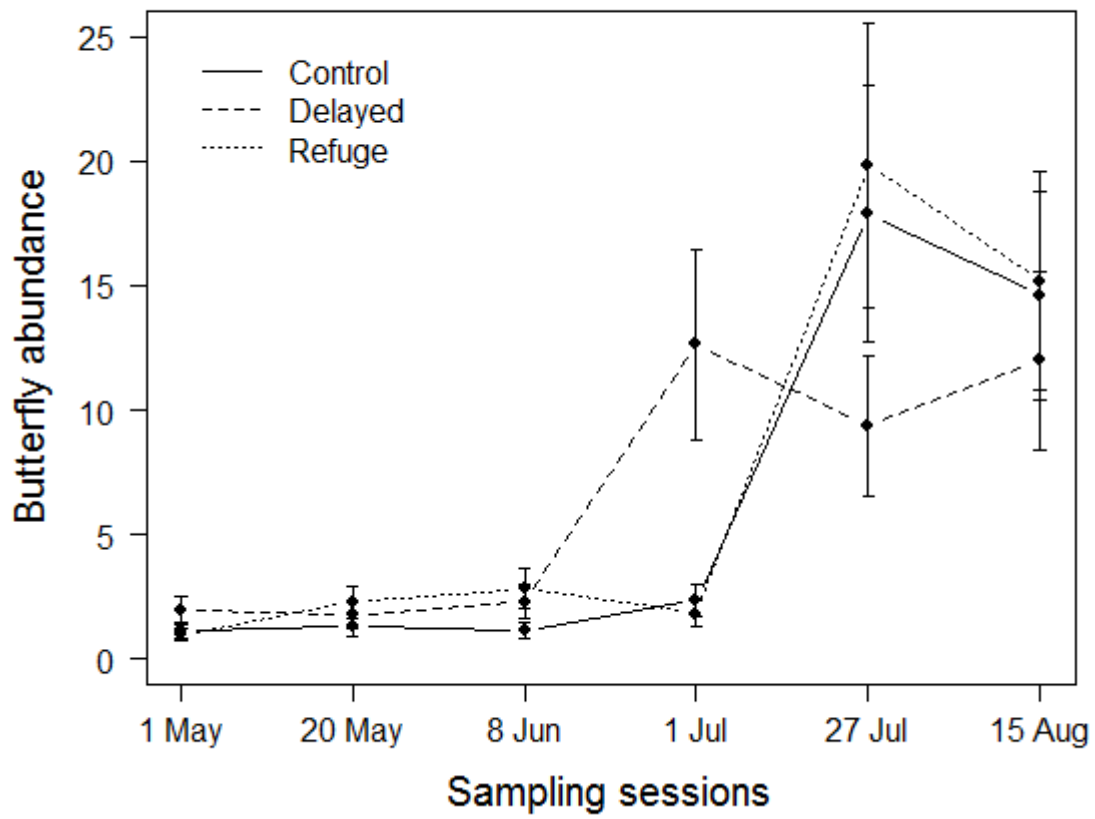


Fig.2:

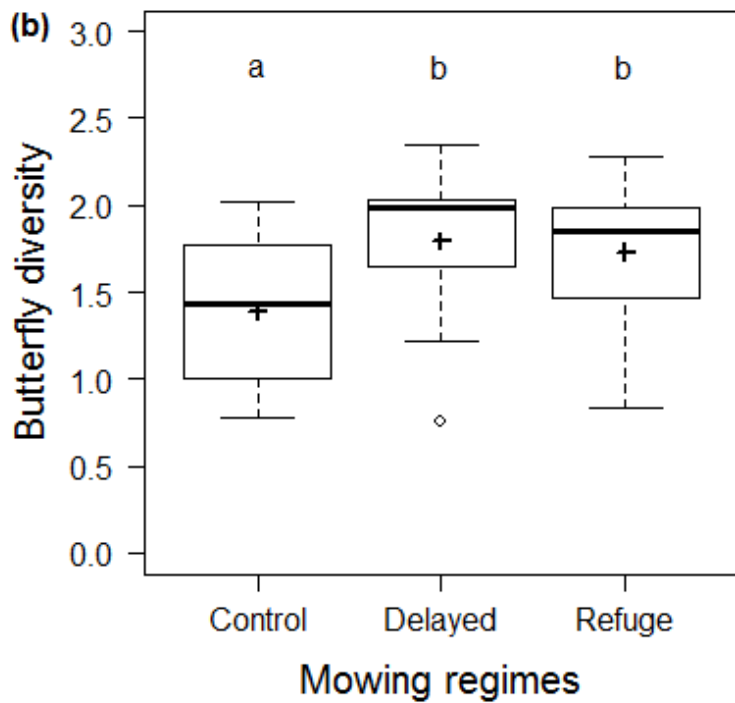
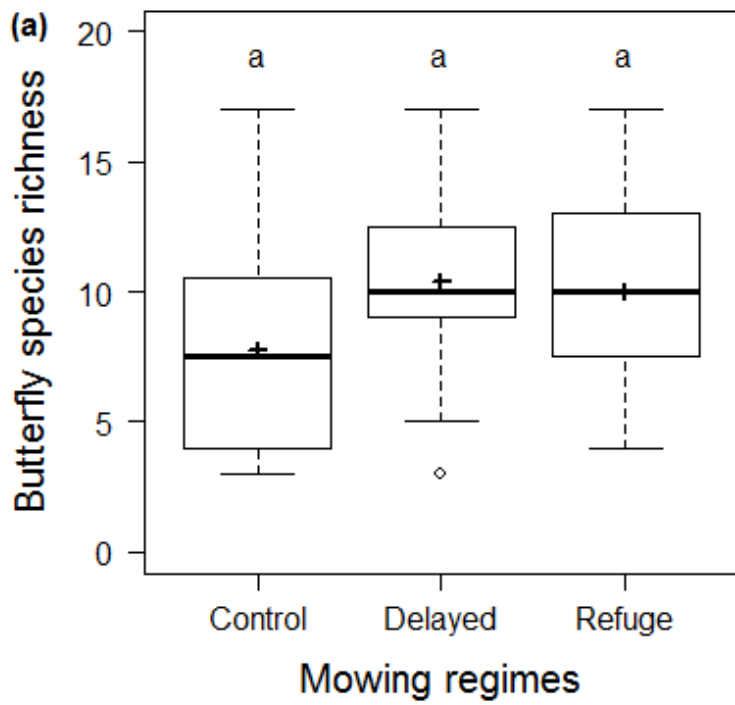
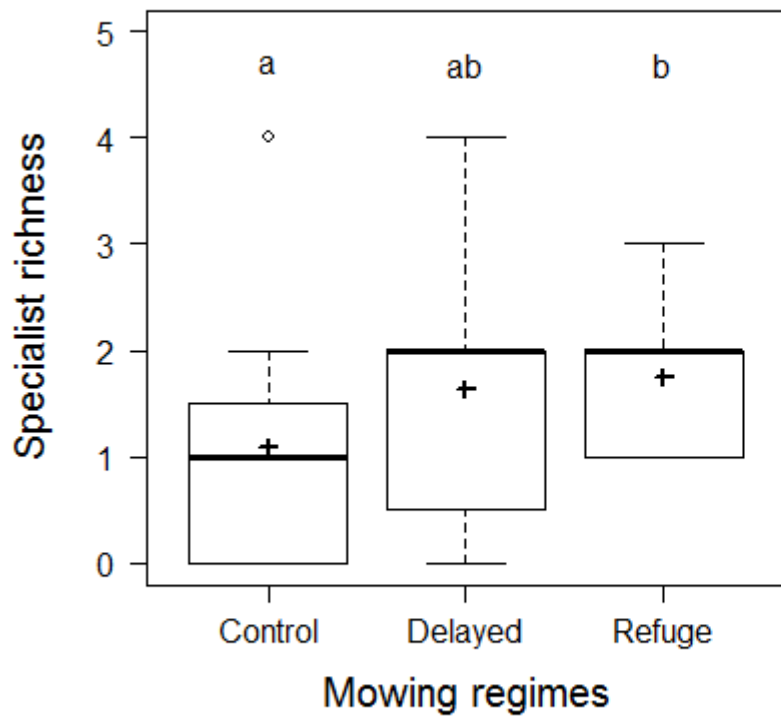


Fig.3:



## **Appendices:**

**Appendix S1.** Summary list of butterfly species and study sites (Excel file)

**Appendix S2.** Distance sampling analyses and model outputs

**Appendix S3.** Group-wise butterfly abundances

**Appendix S4.** Model comparison for butterfly abundance (Excel file)

**Appendix S5.** Group-wise butterfly species richness

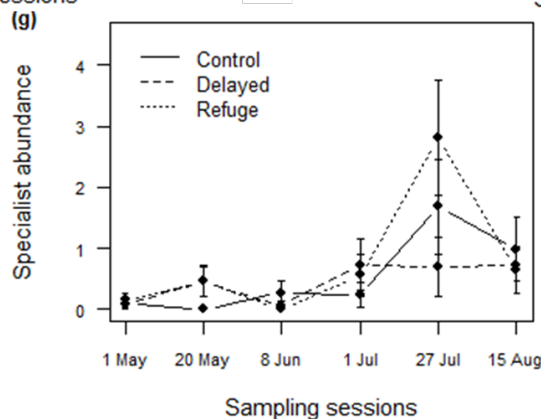
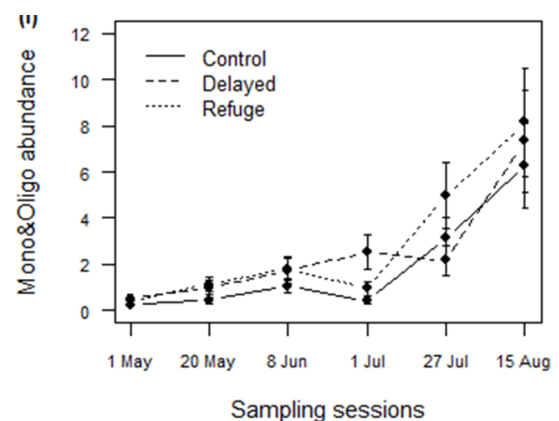
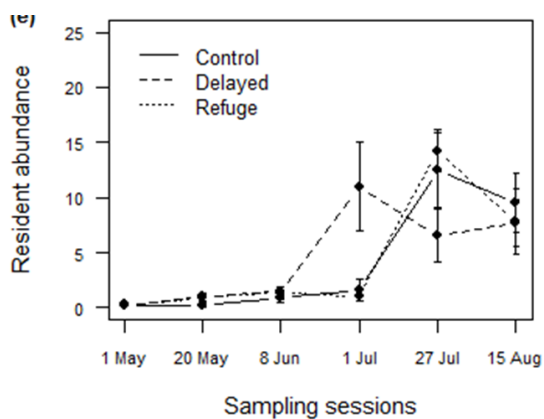
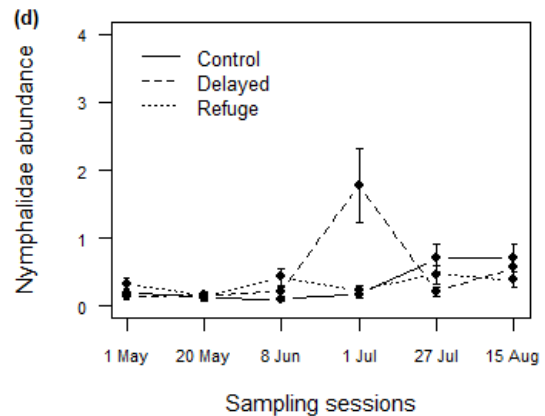
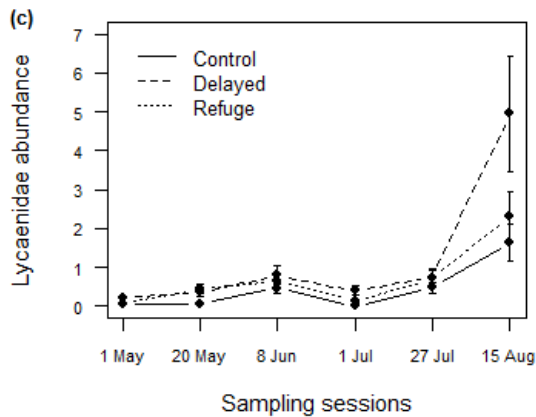
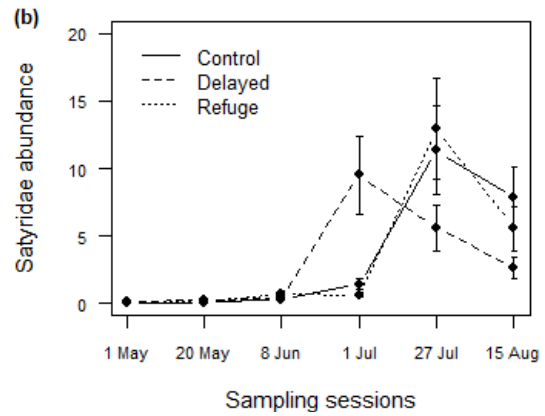
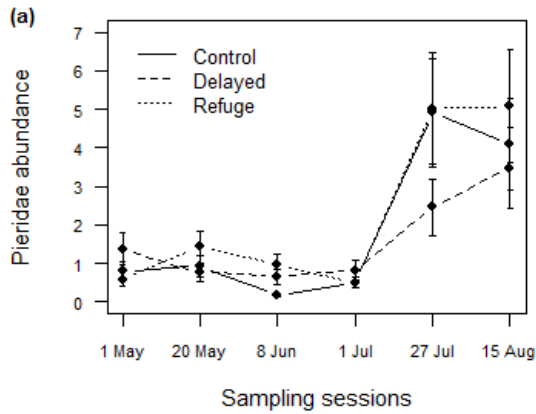
**Appendix S6.** Model comparison for butterfly species richness (Excel file)



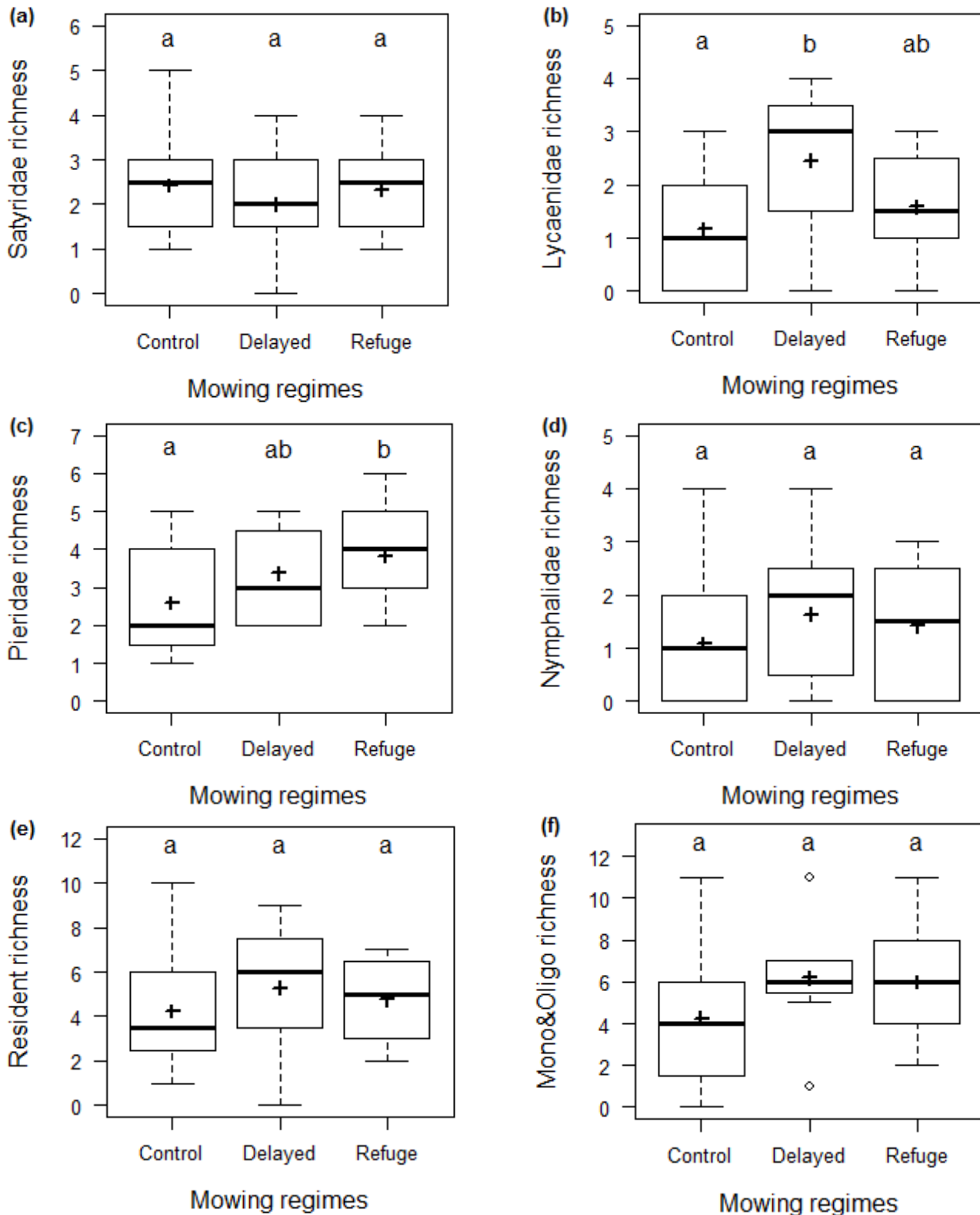
**Appendix S2:** Distance sampling analyses. Detection probabilities are calculated of the perpendicular distances to the transect line. The function *distsamp* from the package *Unmarked* for Software R version 3.0.1 has been used. Response variable was the standardized total number of butterflies and fixed effects were mowing regimes and session. Detection probabilities never differ among mowing regimes.

<b>Session 1,2,3:</b>					
<u>Density:</u>					
	Estimate	SE	z	P(> z )	
Control	1.579	0.268	5.89	<0.001	
Delayed	0.374	0.322	1.16	0.246	
Refuge	0.69	0.293	2.36	0.018	
Session	0.411	0.264	1.56	0.119	
Session	0.565	0.256	2.21	0.027	
<u>Detection:</u>					
	Estimate	SE	z	P(> z )	
Control	5.97	73.6	0.08	0.935	
Delayed	-4.67	73.6	-0.06	0.949	
Refuge	-4.4	73.6	-0.06	0.952	
<b>Session 4:</b>					
<u>Density:</u>					
	Estimate	SE	z	P(> z )	
Control	3.115	0.306	10.2	<0.001	
Delayed	1.969	0.328	6.01	<0.001	
Refuge	-0.361	0.476	-0.76	<0.001	
<u>Detection:</u>					
	Estimate	SE	z	P(> z )	
Control	1.448	0.574	2.52	0.0116	
Delayed	-0.623	0.581	-1.07	0.2837	
Refuge	-0.359	0.693	-0.52	0.6039	
<b>Session 5:</b>					
<u>Density:</u>					
	Estimate	SE	z	P(> z )	
Control	5.41	0.1	53.9	0	
Delayed	-1.091	0.187	-5.84	<0.001	
Refuge	0.157	0.136	1.16	0.248	
<u>Detection:</u>					
	Estimate	SE	z	P(> z )	
Control	1.159	0.118	9.81	<0.001	
Delayed	0.295	0.321	0.92	0.359	
Refuge	-0.208	0.144	-1.45	0.148	
<b>Session 6:</b>					
<u>Density:</u>					
	Estimate	SE	z	P(> z )	
Control	5.238	0.11	47.5	0	
Delayed	-0.437	0.171	-2.56	0.015	
Refuge	-0.131	0.156	-0.84	0.401	
<u>Detection:</u>					
	Estimate	SE	z	P(> z )	
Control	1.1076	0.12	9.19	<0.001	
Delayed	-0.0708	0.177	-0.4	0.689	
Refuge	0.1352	0.191	0.71	0.478	

**Appendix S3: Group-wise butterfly abundances.** For more detailed explanation see Fig. 1 and Table 1 in the main document. The figure is divided in seven parts according to butterfly families and life-history groups: (a) Pieridae; (b) Satyridae; (c) Lycaenidae; (d) Nymphalidae; (e) Resident species; (f) Mono- and oligophagous species; (g) Specialist species.



**Appendix S5:** Group-wise butterfly species richness. For more detailed explanation see Fig. 2 in the main document. The figure is divided in six parts according to butterfly families and life-history groups: (a) Satyridae species; (b) Lycaenidae species; (c) Pieridae species; (d) Nymphalidae species; (e) Resident species; (f) Mono- and oligophagous species.



# Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: .....

Matrikelnummer: .....

Studiengang: .....

Bachelor       Master       Dissertation

Titel der Arbeit: .....

.....

.....

LeiterIn der Arbeit: .....

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetzes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

Ich gewähre hiermit Einsicht in diese Arbeit.

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