Effects of altered mowing regimes in extensively managed meadows on ground and rove beetles

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Effects of altered mowing regimes in extensively managed meadows on ground and rove beetles

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Abstract

1. The agri-environment schemes (AES) that were launched in Western Europe two decades ago have failed to increase biodiversity in grasslands, which have suffered from massive farmland conversion and intensification since World War II. New AES regulations are thus needed to improve the status of grassland biodiversity.
2. We tested the effects of experimentally altered mowing regimes on ground (Carabidae) and rove (Staphylinidae) beetle communities of extensively managed meadows (EMM) declared as AES measures in 12 replicated areas across the Swiss Plateau. In each area, four different mowing regimes were randomly applied to four meadows, with one treatment per meadow: 1) control EMM (hereafter C-meadow), with first cut not before 15 June, no fertilisation and no restriction on number and frequency of subsequent cuts (in line with the standard Swiss AES regulation); 2) delayed mowing EMM (D-meadow), with first cut not before 15 July; 3) 8 weeks EMM (8w-meadow), like C-meadows but with maximum two cuts per year and a minimum of 8 weeks in between; and 4) refuge EMM (R-meadow), like C-meadows but with a rotational uncut refuge on 10–20% of the meadow area. Ground and rove beetles were sampled by means of pitfall traps in 2015, twice in each meadow: once before 15 June and once after (after C-, 8w and R-meadows were mown, but before the mowing of the D-meadows). Ground beetles were identified to species level whereas rove beetles were only counted. To investigate the effect of the applied mowing regimes on the different ground beetle species, the three following species traits were considered, referring to the extant literature: 1) body size: mean species size; 2) habitat strictness: eurytopic species that live in more than one habitat or stenotopic species that live in only one habitat (e.g. grassland, forest, arable land); and 3) humidity preference: hygrophilous (wet habitat), mesophilic (medium humidity habitat) or xerophilous (xeric habitat) species.

3. No difference in total abundance was observed between treatments before any mowing for either taxonomic group. There is thus no indication of long-term, cumulative effects from the altered mowing regimes compared to the control regime on ground and rove beetle abundances. After the 15 June, ground beetle abundance did not differ among mowing regimes whereas rove beetle abundance was significantly greater in C- (+42%), 8w- (+26%) and R-meadows (+31%) than in D-meadows (the latter were still unmown at this time). Species richness of stenotopic and xerophilous ground beetles was significantly greater in 8w- (+70%) and R-meadows (+70%) than in D-meadows (sum of the samples before and after 15 June).
4. *Synthesis and applications*. The D-regime hence did not promote either of the taxa, contrary to expectations. This might be due to activity-catchability issues that originated from a comparison between cut and uncut meadows. In effects, in the unmown meadows, the sward is complex, providing denser foraging opportunities for these beetles that then move little, which is likely to reduce their catchability. Although no mowing regime benefitted ground and rove beetles, C-, 8W- and R-meadows performed equally well. Altogether, these two taxa respond differently from wild bees, orthopterans, butterflies and parasitic wasps sampled in the same experimental set up, which all benefitted from the uncut refuge (R-meadows). Our results don't provide any argumentation against the promotion of unmown refuges among meadowland.

Key-words: grassland, ground beetles (Carabidae), mowing, rove beetles (Staphylinidae)

1. Introduction

Extensively managed grasslands in Europe are hotspots of biodiversity that are inhabited by many endangered species, be it plant or animal (Veen *et al*. 2009). The agricultural intensification that started in the 1960s severely impacted those biodiversity-rich habitats (Robinson & Sutherland 2002; Stoate *et al*. 2009; Wesche *et al*. 2012). Up to today, many of them were converted into arable land or experienced a tremendous intensification, which negatively impacted a variety of grassland plants and animals (Matson *et al*. 1997; Geiger *et al*. 2010; Wesche *et al*. 2012). To counteract this adverse trend, agri-environment schemes (AES) were launched in many European countries in the 1990s (Kleijn & Sutherland 2003). Similarly, in Switzerland, farmers must manage at least 7% of their farmland as biodiversity promoting areas (BPAs). In spite of the CHF 270 million annually dedicated to the BPAs in Switzerland, the biodiversity benefits of these schemes are marginal (Herzog, Richner & Walter 2006; Kleijn *et al*. 2006; Knop *et al*. 2006; Aviron *et al*. 2009). Among the different types of BPAs that are possible in Switzerland (e.g. extensively managed meadows, hedges, wildflower strips, high-stem orchards, stone heaps), extensively managed meadows made up 52% (73'263 hectares) of the total BPA areas in 2013 which made them the BPA-type with by far the biggest surface in the country (BLW 2014). The regulations of these BPA meadows include a late first cut and banned fertilizer application.

The aim of this study was to test the impact of three altered mowing regimes for extensively managed meadows (EMM) registered as BPA in 12 study regions across the Swiss plateau on ground (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae). In each region, four different mowing regimes were randomly applied to four meadows. Ground and rove beetles are two diverse beetle families with 523 respectively 1'414 (excl. Pselaphinae) species in Switzerland (Marggi & Luka 2001; Luka *et al*. 2009b). The ecology of the two families is multifarious and well documented (Marggi 1992; Marggi & Luka 2001; Luka *et al*. 2009b). For example, some ground beetle species have very broad habitat requirements such as the eurytopic *Anisodactylus binotatus* (Fabricius, 1787) (Luka *et al*. 2009a). Other species have very specific habitat requirements such as the critically endangered hygrophilous ground beetle *Agonum viridicupreum* (Goeze, 1777) that only lives in wet meadows (Luka *et al*. 2009a). Due to the species specific knowledge that is available for ground and rove beetles and because their sampling is easy and cheap (Spence & Niemelä 1994), these two beetle families are predestined as useful bioindicators (Luff 1996; Bohac 1999; Zimmermann & Büchs 1999; Rainio & Niemelä 2003; Luka 2004). Furthermore, they are important predators of pest species (Bohac 1999; Pfiffner & Luka 2003; Luka *et al*. 2009b) and act as important food source for higher trophic levels (Zahn, Rottenwallner & Güttinger 2006).

The three altered mowing regimes that are introduced in this study are designed to act contrary to the structural and ecological impoverishment in farmland. Through application of these regimes, increased habitat heterogeneity and a wider range of microclimates and habitats are present, which might favour the diversity of arthropods such as the ground-dwelling ground and rove beetles. Previous studies of our research group on wild bees, orthopterans, butterflies and parasitic wasps showed a positive impact of the R-regime on abundance and / or species richness of the tested groups (Humbert *et al*. 2012a; Humbert *et al*. 2012b; Buri, Arlettaz & Humbert 2013; Buri, Humbert & Arlettaz 2014; Kühne *et al*. 2015; Szikora 2015). In contrast to these already investigated groups that live mainly in the vegetation layer (e.g. orthopterans and butterfly caterpillars) or depend on pollen or nectar as food resource (like bees and butterflies), the mainly ground dwelling ground and rove beetles are probably less affected by the applied mowing regimes (Cizek *et al*. 2012; Buri, Arlettaz & Humbert 2013; Buri, Humbert & Arlettaz 2014; Bruppacher *et al*. 2016). Before mowing, the climatic conditions within the four different mowing regimes are the same. Therefore we do not expect differences in the ground beetle abundance and species richness or rove beetle abundance between the regimes for the first sampling period (i. e. before any mowing event).

In the second sampling period (after the mowing of the C-, 8w- and R-meadows) we expect differing responses of the ground beetle abundance and species richness and rove beetle abundance when compared to C-meadows, which are EMM with the first cut not before 15 June and no restriction on the number and frequency of subsequent cuts. For the 8w-meadows, which are the same as the C-meadows but with maximum two cuts per year and minimum 8 weeks between the cuts, we expect no differing effect from the C-meadows for ground beetle abundance and species richness and rove beetle abundance. This is because the two regimes are very similar to each other and thus there are no differences in habitat conditions that could be reflected by ground or rove beetles. For the R-meadows which are the same as the C-meadows but with a rotational uncut refuge (location of refuge changes at each mowing event) on 10-20% of the meadow area (R for refuge) we do not expect differences in the cut R area of these meadows since again the habitat conditions are as in the C-meadows. For the D-meadows which are the same as the C-meadows but with the first cut not before 15 July (D for delayed) we expect a higher abundance and richness of ground beetles and abundance of rove beetles than in the C-meadows since the habitat with the uncut sward is more complex and thus provides more possible prey for these groups. In accordance with this expectation lies Cameron & Leather (2012), which stated that ground beetle abundance and species richness on a heathland, were positively correlated with invertebrate abundance and order richness. In another study, Cizek et al. (2012) found, that the biggest proportion of the ground beetle species was more abundant in traps that are located in uncut compared to cut sward. For rove beetles, contrary, Hofmann & Mason (2006) found higher abundances in cut compared to uncut plots. In order to interpret these contrasting results, we should have a close look on the specific species traits of the ground and rove beetles that occurred in these studies. If the grass is mown, the sunlight reaches the soil and thus the temperatures are higher. This causes a drier microclimate, which favours species that prefer to live in dry (xerophilous) habitats (Cizek *et al.* 2012). This is why we expect a higher proportion of xerophilous ground beetle species in the cut C-, 8w- and R-meadows compared to the uncut D-meadows and Ruc-area of the R-meadows. For the species trait body size we do not expect differences between the mowing regimes, since this trait is linked to disturbance (e.g. mowing intensity), which is almost the same in all our mowing regimes (Humbert *et al.* 2010; Venn & Kotze 2014).

2. Material and Methods

2.1 Study sites

In 2010, 48 extensively managed meadows (EMM) that were registered as BPA since at least 2004 were selected. The meadows were spread across 12 study regions on the Swiss Plateau (lowlands between the Jura and the Alps) in the cantons of Vaud, Fribourg, Neuchâtel, Bern, Aargau and Basel-Land (study sites coordinates are provided in appendices 1 & 2 and a map in appendix 4). They ranged from 390 to 833 m a.s.l. and the average size of a meadow was 0.8 ha (range: 0.3-1.7 ha). The minimal distance between two study regions was 5 km and the four meadows of a region were within a 3.5 km radius with at least 440 m distance from border to border.

2.2 Experimental design

A randomized block design was adopted; i.e. the four mowing regimes were randomly assigned to the four meadows within each region (the block). Consequently, each mowing regime was represented once in each study region and the number of replicates n = 12. The four applied mowing regimes (experimental treatments) were as follows:

1. C-meadows: EMM with first cut not before 15 June, no restriction on the number and frequency of subsequent cuts; these meadows constitute our baseline controls (C for control).
2. D-meadows: EMM, but first cut not before 15 July (D for delayed).

3. 8w-meadows: EMM with first cut not before 15 June, but maximum two cuts per year and minimum 8 weeks between them (8w for eight weeks).
4. R-meadows: EMM with first cut not before 15 June, but with rotational uncut refuge (location of refuge changes at each mowing event) on 10-20% of the meadow area (R for refuge).

In 2012, the D-meadow in Coffrane was converted into a gravel pit, reducing the total number of meadows by one to thenceforth 47.

2.3 Sampling design

Ground beetles (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae) were sampled using four white pitfall traps of 90 mm in diameter and a capacity of 500 ml in each meadow. The pitfall traps were placed so that the upper rim flushed with the ground. They were placed at the four corners of a 10 m x 10 m quadrat and protected against rainfall with 20 x 20 cm transparent covers that were installed 5 cm above them. As killing and preserving agent, 0.25 l of propylene glycol diluted with water (ratio 2:1) were poured into the cups, as it has been shown to be a valid alternative to the environmentally hazardous ethylene glycol previously used in similar studies (Weeks R.D. Jr. & McIntyre 1997). Additionally, we added a few drops of detergent to reduce surface tension (Topping & Luff 1995). Sampling was conducted in two periods where the traps remained in each case open for two weeks: the first sampling period was in May before any mowing event. The content was removed after the first week and replaced with fresh traps. The second sampling period was end of June-beginning of July after C-, 8w and R-meadows were mown, but before the mowing of the D-meadows. The sampling design of this second period was as for the first one, except that in the R-meadows, we set up four pitfall traps in the mown part and another four traps in the uncut refuge area of the meadows (Ruc for refuge uncut). The catches were divided by taxonomic groups and the ground and rove beetles counted and stored in 99.8% ethanol (denatured with 2% butanone). The ground beetles were then mounted and identified to species level (Müller-Motzfeld 2004).

2.4 Data analysis

To describe the effect of mowing regimes on the abundance of ground and rove beetles, the mean abundance per trap was calculated. For the analysis, the data of the two weeks of the first sampling period were pooled as well as the data of the two weeks of the second sampling period. Generalized linear mixed-effects models (GLMMs, package lme4) using a Poisson distribution and with site as random factor were conducted in R version 3.1.1 (Bates *et al.* 2014; R Core Team 2014) with ground and rove beetle abundance per trap as response variable and mowing regime (8w, C, D, R for the first sampling period and additionally Ruc for the second period) as explanatory variables. Mean abundance per trap was used because some traps contaminated with mice and shrews – that lured ground and rove beetles –, had to be discarded.

To describe the effect of mowing regimes on the species richness and diversity of ground beetles, the data of the first and the second sampling period were pooled and richness and diversity (Shannon index) per trap were calculated. Though the traps set within the uncut refuge area (Ruc) within the R regime were not included as well as the traps contaminated with small mammals. Similarly to abundances, GLMMs were conducted in R using a Poisson distribution, site as random factor and ground beetle richness or diversity per trap as response variable and mowing regime (8w, C, D, R) as explanatory variable.

In addition, the same statistical analyses were then performed separately on different groups of ground beetles based on three species traits:

1) Body size: mean species size according to Müller-Motzfeld (2004).

2) Habitat strictness: eurytopic species that live in more than one habitat or stenotopic species that live in only one habitat (e.g. grassland, forest, arable land, classification according to Luka et al. (2009a)).

3) Humidity preference: hygrophilous, mesophilic or xerophilous species (classification according to Luka et al. (2009a)).

The mean body size per trap was obtained by multiplication of the species data sheet by the literature mean species value. Then, the obtained figures were weighted according to the number of individuals. To describe the effect of mowing regimes on the body size, habitat strictness and humidity preference of ground beetles, the same analysis as for the one of the overall ground beetle richness and diversity was conducted.

As an additional method to test whether the mowing regimes affect ground beetle species richness, species accumulation curves (package vegan) with the method exact for the mowing regimes 8w, C, D and R were calculated in R version 3.1.1 (R Core Team 2014; Oksanen *et al*. 2015). With this method the expected (mean) species richness in response to the mowing regimes and according to the number of traps is estimated. Differences between the species accumulation curves of the different mowing regimes were assessed according to the overlap of their confidence intervals. The data from the Ruc were not included.

3. Results

After the exclusion of the 112 traps with mice or shrews, 752 traps that contained 4'553 ground and 7'460 rove beetles remained. For ground beetles, a total of 87 species were found with the most abundant species *Poecilus versicolor* (Sturm, 1824) making up 8.5 % (387 individuals) and the ten most abundant species making up 60.6 % (2759 individuals) of the whole catch (Appendix 3). Of the caught species, *Agonum viridicupreum* (Goeze, 1777) (3 individuals; critically endangered), *Amara fulvipes* (Audinet-Serville, 1821) (186 ind.), *Amara kulti* Fassati, 1947 (187 ind.), *Anisodactylus nemorivagus* (Duftschmid, 1812) (24 ind.), *Brachinus elegans* Chaudoir, 1842 (1 ind.; vulnerable), *Harpalus subcylindricus* Dejean, 1829 (89 ind.), *Licinus hoffmanseggi* (Panzer, 1803) (1 ind.) and *Ophonus puncticollis* (Paykull, 1798) (1 ind.), are notable (Appendix 3).

3.1 Ground and rove beetle abundance

In the first sampling (in May, before mowing), the mean abundance ± SE (standard error) per trap was 7.08 ± 8.50 for ground beetles and 9.69 ± 9.83 for rove beetles. No alternative mowing regime showed significant differences in ground (Fig.1a) or rove beetle abundances (Fig.1b) when compared with the C-meadows. During the second sampling period (after mowing), the mean abundance per trap was 5.17 ± 6.98 for ground beetles and 10.12 ± 13.90 for rove beetles. In this second sampling period, none of the mowing regimes showed a significant difference in ground beetle abundances when compared with the C-meadows (Fig.1c). Though, rove beetle abundances in the second sampling period where significantly lower in the D-meadows when compared with the C- (Estimate = -0.58 ± 0.26, t = -2.24, P = 0.030), the 8w- (Estimate = -0.74 ± 0.26, t = -2.86, P = 0.007) and the R-meadows (Estimate = -0.69 ± 0.26, t = -2.68, P = 0.010; Fig.1d; Table 1). In addition, the Ruc-area of the R-meadows showed significantly lower rove beetle abundances than the 8w-meadows (Estimate = -0.54 ± 0.25, t = -2.14, P = 0.038; Fig.1d; Table 1).

3.2 Ground beetle species richness, diversity, size and species accumulation curves

Neither for the ground beetle species richness (Fig.2a), nor for the diversity (Fig.2b) or the species trait size (Fig.2c) any significant differences were found. Species accumulation curves with the method exact were calculated in order to find the expected (mean) species richness in response to the different mowing regimes and according to the number of traps. The total number of traps per mowing regime was 192 (12 study regions * 4 meadows per region * 4 taps per meadow). They did not show any significant differences for the mowing regimes (Fig.2d).

3.3 Ground beetle habitat and humidity preferences

The species trait habitat strictness did not show any significant differences regarding the eurytopic species (Fig.3a), whereas a significantly lower number of stenotopic species was found in D-meadows when compared to 8w- (Estimate = -0.293 ± 0.112, t = -2.619, *P* = 0.013) and R-meadows (Estimate = -0.300 ± 0.112, t = -2.679, *P* = 0.012; Fig.3a; Table 3). Regarding humidity preference, no significant differences were found for the hygrophilous and the mesophilic species. For xerophilous species, however, significantly lower ground beetle species richness was found for the D-meadows when compared to the 8w- (Estimate = -0.307 ± 0.116, t = -2.656, *P* = 0.012) and R-meadows (Estimate = -0.280 ± 0.116, t = -2.421, *P* = 0.021; Fig.3b; Table 4). Between the C- and D-meadows, however, no significant differences for stenotopic and xerophilous ground beetle species were found. Between the R- and Ruc-meadows (only after mowing), no significant differences were found in the analysed variables. Additionally, species accumulation curves of stenotopic (Fig.3c) and xerophilous (Fig.3d) ground beetles did not show any significant differences for the mowing regimes.

4. Discussion

In this study we show that even within one group, the different preferences of the species cause differing reactions to changed mowing regimes among them which is also shown in Batáry et al. (2011). Rove beetle abundances are lower if the mowing of extensively managed meadows (EMM) is delayed by one month (i.e. until 15 July) when compared to regular EMM. Furthermore, stenotopic and xerophilous ground beetles were more diverse when leaving an uncut refuge while mowing when compared to delaying the mowing by one month (i.e. until 15 July). These results show that even with slight management changes, the effectiveness of the AES could be improved.

4.1 Ground and rove beetle abundance

Before 15 June (i.e. before any mowing intervention), ground and rove beetle abundances were similar in all investigated meadows (C-meadows: EMM with first cut not before 15 June, no restriction on the number and frequency of subsequent cuts; these meadows constitute our baseline controls (C for control). D-meadows: EMM, but first cut not before 15 July (D for delayed). 8w-meadows: EMM with first cut not before 15 June, but maximum two cuts per year and minimum 8 weeks between them (8w for eight weeks). R-meadows: EMM with first cut not before 15 June, but with rotational uncut refuge (Ruc, location of refuge changes at each mowing event) on 10-20% of the meadow area (R for refuge)). These findings are in line with our predictions and underline the conjecture that there is a too small difference between the mowing regimes in order to have an effect on these ground dwelling beetle families. In the first sampling period, the meadows were not already mown and thus there were no direct differences between the mowing regimes at this stage. Only indirect, so-called cumulative or long-term effects that are due to the application of the mowing regimes since the beginning of the experimental treatments in 2010, could have had an influence (Buri, Arlettaz & Humbert 2013; Buri, Humbert & Arlettaz 2014). This means that for ground and rove beetles there were no long-term differences (so-called cumulative effects in Buri, Arlettaz & Humbert (2013)) of the altered mowing regimes compared to the C-regime (C-meadows with first cut not before 15 June) on the population sizes of these two ground dwelling beetle families detected. Later in season, end of June–beginning of July, ground beetle abundances were still similar across all meadows. However, rove beetle abundances were significantly lower in the uncut D-meadows (mowing regime with first cut not before 15 July) compared to the cut C-, 8w- (similar management as C-meadows but with maximum two cuts per year and 8 weeks in between) and R-meadows (similar as C-meadows but with rotational uncut refuge on 10-20% of the meadow area). In the Ruc-area of the R-meadows, rove beetle abundances were lower than in the 8w-meadows. This higher number of catches in mown meadows might be because hunting is facilitated in the mown areas and thus, more rove beetles are hunting there (Chiverton 1984). Another explanation might be that due to the dramatic direct (mortality) and indirect (habitat changes) effects of the mowing event prey densities were reduced which forced the rove beetles to cover bigger distances for their hunt and thus makes it more probable that they fall into the pitfall traps (Holland & Luff 2000; Symondson, Sunderland & Greenstone 2002; Haysom *et al.* 2004). In line with our result of higher rove beetle abundances in mown areas, Hofmann & Mason (2006) found higher rove beetle abundances in cut plots and could explain it with an increase of two dominant species that showed preferences for short vegetation.

4.2 Ground beetle species richness, diversity, size and species accumulation curves

Ground beetle species richness, diversity and the species trait size were similar in all investigated meadows. The similarity of richness and diversity between the meadows might be, because the major part of the caught species (71 %) are species that live in more than one habitat (eurytopic) and are thus less sensitive to habitat changes or disturbance (Cizek *et al.* 2012). The body size did not differ between the mowing regimes which lies in line with our expectation, since the level of disturbance through the mowing was almost the same for all our mowing regimes and thus did not differently affect body size (Humbert *et al.* 2010; Venn & Kotze 2014). Species accumulation curves were similar in all investigated meadows (Fig.3d). This means that the expected (mean) species richness in the meadows was the same irrespective of the mowing regime. We expected to find a higher ground beetle species richness in the D-meadows, since the habitat with the uncut sward is more complex and thus provides more possible prey for them. Since the habitat type extensively managed hay meadow was the same for all our meadows, we think that despite the difference in sward height, the species pool and thus the expected (mean) species richness was the same in all meadows. The data from the Ruc were not included.

4.3 Ground beetle habitat and humidity preferences

Eurytopic species richness (i.e. generalist species) did not show significant differences between the mowing regimes, which might be explained by the fact that this group makes up the biggest proportion (71 %) of the total caught ground beetles, where we did not find any effect either. The C- and D-meadows were similar in eurytopic ground beetle species numbers. Whether this reflects the actual situation is difficult to answer, since there might be a possible bias in sampling mown and uncut areas with pitfall traps. The stenotopic species in the D-meadows, however, had a significantly lower richness when compared to the 8w- (more than two times lower) and R-meadows (more than two times lower for richness). The C- and D-meadows had similar stenotopic ground beetle richness. Similarly to the stenotopic ground beetle species, the xerophilous species in the D-meadows had a lower richness when compared to the 8w- (more than two times lower) and R-meadows (more than two times lower). The C- and D-meadows had similar xerophilous ground beetle species richness. This congruent finding for stenotopic and xerophilous species might be explained by the fact that ten of the 22 (45.5 %) stenotopic species are also xerophilous. On mown areas the sunlight reaches the soil and thus higher temperatures and a drier microclimate prevails. Because of that, xerophilous ground beetle species show a preference for mown areas (Cizek *et al.* 2012). The species accumulation curves of the stenotopic and xerophilous ground beetles were similar. This is contrary to the results we obtained in our models but probably due the big confidence intervals.

4.4 Conclusions and management recommendations

Lower rove beetle abundances were found in uncut areas (D-meadows and Ruc-areas of the R-meadows) after mowing. However, the reason for this finding is probably induced by their higher activity and detectability in these areas and not by a negative effect of the uncut areas (Chiverton 1984; Holland & Luff 2000; Symondson, Sunderland & Greenstone 2002; Haysom *et al.* 2004). Ground beetle abundances were similar between the mowing regimes before and after mowing. This might reflect the assumption that the ecological differences between the mowing regimes are too small to affect ground and rove beetle abundances. Species richness of stenotopic and xerophilous ground beetles was higher in mown areas (C-, 8W- and R-meadows). This reflects the fact that through the mowing a drier microclimate is formed (Cizek *et al.* 2012).

Based on our results C-, 8W- and R-meadows are all equally fine for ground and rove beetles. Therefore no evidence for a best mowing regime can be drawn from our results. In accord with previous studies on arthropod groups such as wild bees, orthopterans, butterflies and parasitic wasps that were conducted at the same study sites and within the same experimental design, we recommend the R-regime as AES EMM management regulation because it is ok for ground and rove beetles and was shown to have positive effects on other arthropod groups. We hope that through this regulation, the effectiveness of the AES will be improved.

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Table 1. Output of linear mixed-effects models for ground and rove beetle abundances per trap in relation to mowing regimes. The first sampling period took place before any mowing event and the second sampling period took place after the first cut of the 8w-, C- and R-meadows. For mowing regime abbreviations see legend of Figure 1.

	Estimate	SE	P-value
a) Ground beetles abundance first period			
8w vs. C	-0.318	0.285	0.272
D vs. C	0.012	0.292	0.969
R vs. C	-0.521	0.285	0.076
D vs. 8w	0.330	0.292	0.267
R vs. 8w	-0.203	0.285	0.481
R vs. D	-0.533	0.292	0.078
b) Rove beetles abundance first period			
8w vs. C	0.145	0.315	0.649
D vs. C	-0.240	0.323	0.463
R vs. C	0.046	0.315	0.884
D vs. 8w	-0.384	0.323	0.243
R vs. 8w	-0.098	0.315	0.757
R vs. D	0.286	0.323	0.382
c) Ground beetles abundance second period			
8w vs. C	-0.297	0.278	0.291
D vs. C	-0.285	0.285	0.323
R vs. C	-0.346	0.278	0.220
Ruc vs. C	-0.468	0.278	0.100
D vs. 8w	0.012	0.285	0.966
R vs. 8w	-0.049	0.278	0.861
Ruc vs. 8w	-0.171	0.278	0.542
R vs. D	-0.061	0.285	0.831
Ruc vs. D	-0.183	0.285	0.524
R vs. Ruc	0.122	0.278	0.664
d) Rove beetles abundance second period			
8w vs. C	-0.160	0.251	0.528
D vs. C	0.578	0.258	**0.030**
R vs. C	-0.114	0.251	0.653
Ruc vs. C	0.377	0.251	0.140
D vs. 8w	0.738	0.258	**0.007**
R vs. 8w	0.046	0.251	0.856
Ruc vs. 8w	0.537	0.251	**0.038**
R vs. D	-0.692	0.258	**0.010**
Ruc vs. D	-0.201	0.258	0.440
R vs. Ruc	-0.491	0.251	0.057

Table 2. Output of linear mixed-effects models for ground beetle species richness, diversity and mean size in relation to mowing regimes. The data of the first sampling period which took place before any mowing event and the second sampling period which took place after the first cut of the 8w-, C- and R-meadows were pooled, since there were the same species present. For mowing regime abbreviations see legend of Figure 1.

	Estimate	SE	P-value
a) Ground beetle richness overall			
8w vs. C	-0.220	0.152	0.156
D vs. C	-0.067	0.155	0.669
R vs. C	-0.246	0.152	0.115
D vs. 8w	0.153	0.155	0.332
R vs. 8w	-0.026	0.152	0.867
R vs. D	-0.179	0.155	0.258
b) Ground beetle diversity overall			
8w vs. C	-0.179	0.159	0.270
D vs. C	-0.017	0.163	0.920
R vs. C	-0.207	0.159	0.202
D vs. 8w	0.162	0.163	0.328
R vs. 8w	-0.029	0.159	0.858
R vs. D	-0.191	0.163	0.251
c) Ground beetle richness only RRuc			
Ruc vs. R	-0.106	0.490	0.833
d) Ground beelte diversity only RRuc			
Ruc vs. R	0.038	0.116	0.747
e) Ground beetle mean size overall			
8w vs. C	0.178	0.487	0.717
D vs. C	0.322	0.501	0.524
R vs. C	0.334	0.487	0.497
D vs. 8w	0.145	0.501	0.775
R vs. 8w	0.157	0.487	0.750
R vs. D	0.012	0.501	0.981
f) Ground beetle mean size only RRuc			
Ruc vs. R	-0.464	0.674	0.506

Table 3. Output of linear mixed-effects models for stenotopic and eurytopic ground beetle species richness in relation to mowing regimes. For mowing regime abbreviations see legend of Figure 1.

	Estimate	SE	P-value
a) Stenotopic species richness overall			
8w vs. C	-0.208	0.109	0.066
D vs. C	0.086	0.112	0.450
R vs. C	-0.214	0.109	0.058
D vs. 8w	0.293	0.112	**0.013**
R vs. 8w	-0.007	0.109	0.952
R vs. D	-0.300	0.112	**0.012**
b) Stenotopic species richness only RRuc			
Ruc vs. R	0.148	0.122	0.251
c) Eurytopic species richness overall			
8w vs. C	-0.316	0.480	0.515
D vs. C	-0.114	0.492	0.819
R vs. C	-0.352	0.480	0.468
D vs. 8w	0.202	0.492	0.684
R vs. 8w	-0.036	0.480	0.940
R vs. D	-0.239	0.492	0.631
d) Eurytopic species richness only RRuc			
Ruc vs. R	-0.399	0.376	0.312

Table 4. Output of linear mixed-effects models for hygrophilous, mesophilic and xerophilous ground beetle species richness in relation to mowing regimes. For mowing regime abbreviations see legend of Figure 1.

	Estimate	SE	P-value
a) Hygrophilous species richness overall			
8w vs. C	0.081	0.050	0.112
D vs. C	0.046	0.051	0.375
R vs. C	0.044	0.050	0.382
D vs. 8w	-0.036	0.051	0.489
R vs. 8w	-0.037	0.050	0.458
R vs. D	-0.002	0.051	0.974
b) Hygrophilous species richness only RRuc			
Ruc vs. R	-0.020	0.457	0.671
c) Mesophilic species richness overall			
8w vs. C	-0.569	0.491	0.254
D vs. C	-0.298	0.503	0.558
R vs. C	-0.644	0.491	0.199
D vs. 8w	0.272	0.503	0.592
R vs. 8w	-0.075	0.491	0.880
R vs. D	-0.347	0.503	0.495
d) Mesophilic species richness only RRuc			
Ruc vs. R	-0.170	0.486	0.733
e) Xerophilous species richness overall			
8w vs. C	-0.150	0.113	0.194
D vs. C	0.157	0.116	0.183
R vs. C	-0.122	0.113	0.286
D vs. 8w	0.307	0.116	**0.012**
R vs. 8w	0.027	0.113	0.811
R vs. D	-0.280	0.116	**0.021**
f) Xerophilous species richness only RRuc			
Ruc vs. R	0.015	0.118	0.903

Figure legends

Fig.1. Ground beetle and rove beetle abundance per trap in response to the four different mowing regimes. The figure has four graphs: (a) ground beetle abundance in the first sampling period (i.e. in May), (b) rove beetle abundance in the first sampling period, (c) ground beetle abundance in the second sampling period (i.e. end of June-beginning of July), (d) rove beetle abundance in the second sampling period. The four applied mowing regimes (experimental treatments) were as follows: C-meadows: first cut not before 15 June, no restriction on the number and frequency of subsequent cuts; D-meadows: first cut not before 15 July; 8w-meadows: first cut not before 15 June, but maximum two cuts per year and minimum 8 weeks between them; R-meadows: first cut not before 15 June, but with rotational uncut refuge (Ruc, location of refuge changes at each mowing event) on 10-20% of the meadow area. Bold transversal bars represent medians; + the means; box boundaries the first and last quartiles; whiskers the inter-quartile distance multiplied by 1.5; and open dots the outliers. In (a) in the mowing regime R an outlier at 43.63 is cut out. In (b) in the mowing regime 8w an outlier at 32.0 is cut out. In (d) in the mowing regime 8w two outliers at 38.86 and 58.86 are cut out. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05. See Table 1 for statistical analyses.

Fig.2. Ground beetle species richness (a), diversity (b), mean size (c) per trap and species accumulation curves (d) in response to the four different mowing regimes and according to the number of traps. The lightblue lines indicate confidence intervals. For mowing regime abbreviations and statistical symbols, see legend of Fig. 1. See Table 2 for statistical analyses.

Fig.3. Stenotopic (a) and xerophilous (b) ground beetle species richness per trap and stenotopic (c) and xerophilous (d) species accumulation curves in response to the four different mowing regimes and according to the number of traps. The lightblue lines indicate

confidence intervals. In (a) in the mowing regime R an outlier at 3.81 is cut out. In (b) in the mowing regime R an outlier at 3.19 is cut out. For mowing regime abbreviations and statistical symbols, see legend of Fig. 1. See Tables 3 and 4 for statistical analyses.

Fig.1.

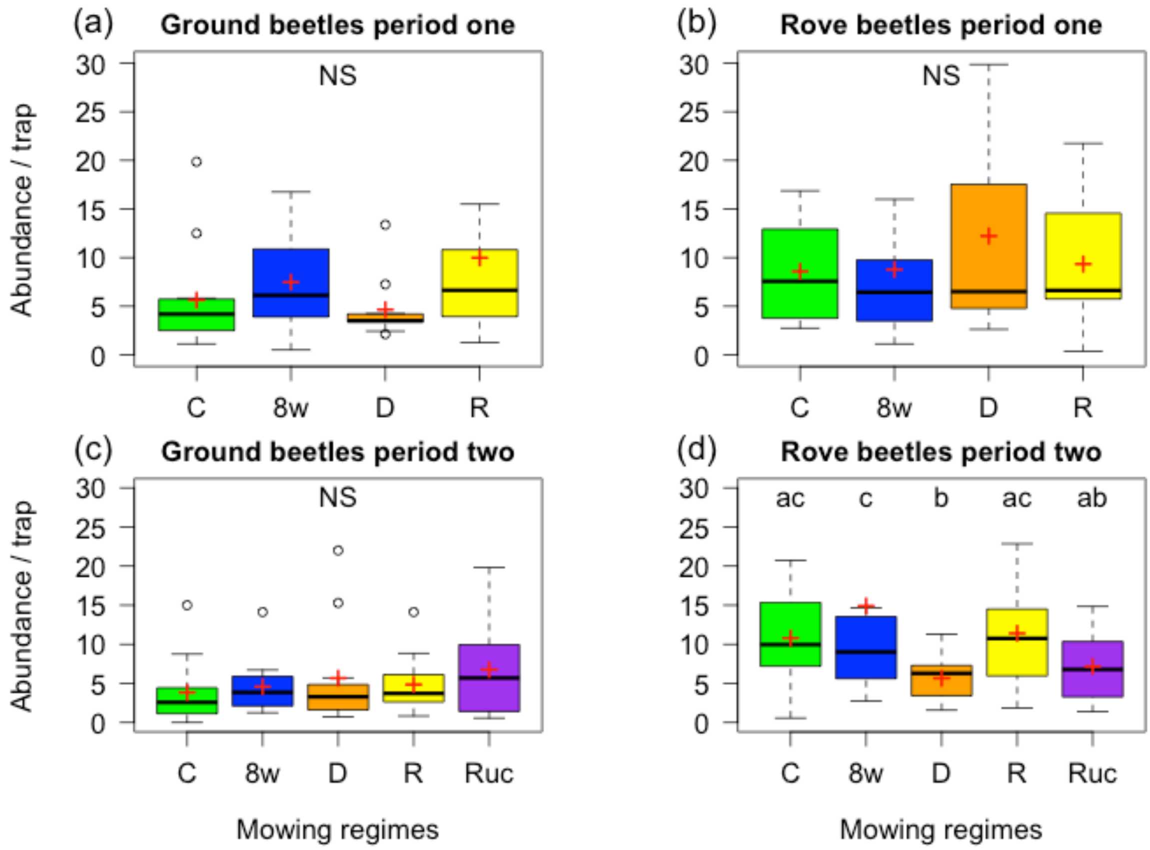
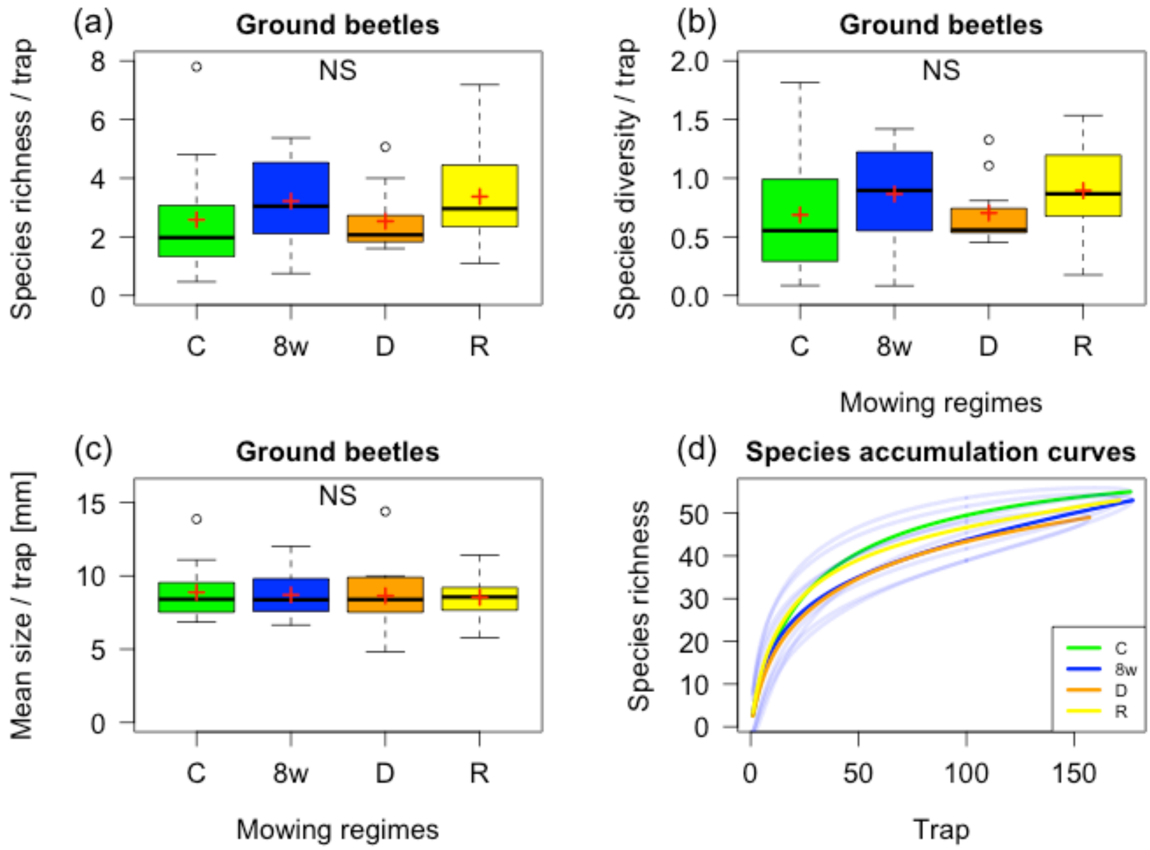
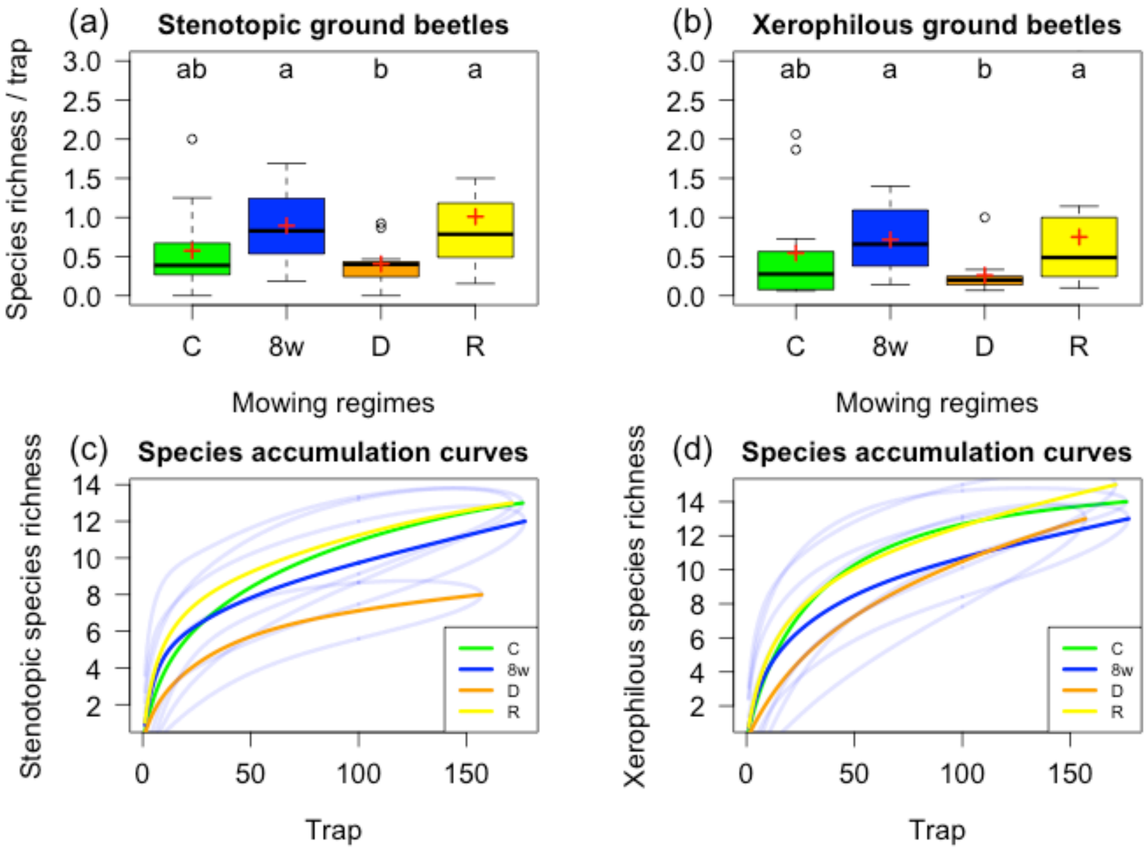

(a)
Ground beetles period one
NS
Abundance / trap
30
25
20
15
10
5
0
C
8w
D
R
(b)
Rove beetles period one
NS
30
25
20
15
10
5
0
C
8w
D
R
(c)
Ground beetles period two
NS
Abundance / trap
30
25
20
15
10
5
0
C
8w
D
R
Ruc
Mowing regimes
(d)
Rove beetles period two
ac
c
b
ac
ab
30
25
20
15
10
5
0
C
8w
D
R
Ruc
Mowing regimes

Fig.2.



(a)
Ground beetles
NS
Species richness / trap
8
6
4
2
0
C
8w
D
R
(b)
Ground beetles
NS
Species diversity / trap
2.0
1.5
1.0
0.5
0.0
C
8w
D
R
Mowing regimes
(c)
Ground beetles
NS
Mean size / trap [mm]
15
10
5
0
C
8w
D
R
Mowing regimes
(d)
Species accumulation curves
Species richness
50
40
30
20
10
0
0
50
100
150
Trap
C
8w
D
R

Fig.3.


(a)
Stenotopic ground beetles
Species richness / trap
3.0
2.5
2.0
1.5
1.0
0.5
0.0
ab
a
b
a
C
8w
D
R
Mowing regimes
(b)
Xerophilous ground beetles
3.0
2.5
2.0
1.5
1.0
0.5
0.0
ab
a
b
a
C
8w
D
R
Mowing regimes
(c)
Species accumulation curves
Stenotopic species richness
14
12
10
8
6
4
2
0
50
100
150
Trap
C
8w
D
R
(d)
Species accumulation curves
Xerophilous species richness
14
12
10
8
6
4
2
0
50
100
150
Trap
C
8w
D
R

Appendix 1. List of meadows with their respective mowing regime, geographic coordinates and abundance of sampled rove beetles (Coleoptera: Staphylinidae) and ground beetles (Coleoptera: Carabidae) per meadow during the first sampling period (before mowing).

Site	Canton	Mowing regime	GPS coordinates E [CH1903]	GPS coordinates N [CH1903]	Rove beetle abundance	Ground beetle abundance
Avenches	VD	C	567193	197127	109	29
Belp	BE	C	605487	192366	25	35
Coffrane	NE	C	556126	205774	23	22
Cousset	FR	C	565063	185881	24	19
Diegten	BL	C	628587	252768	27	9
Grossaffoltern	BE	C	595281	212666	98	41
Hindelbank	BE	C	612352	209751	96	17
Huttwil	BE	C	628558	215769	73	10
Lupfig	AG	C	655871	255464	22	45
Nyon	VD	C	506251	141110	73	139
Orbe	VD	C	528474	173673	135	100
Wohlen	BE	C	595389	205416	44	18
Avenches	VD	8w	566771	196996	9	49
Belp	BE	8w	605869	193107	192	79
Coffrane	NE	8w	555499	206934	128	27
Cousset	FR	8w	564696	185503	14	12
Diegten	BL	8w	628895	252035	18	49
Grossaffoltern	BE	8w	592103	214070	69	134
Hindelbank	BE	8w	608282	208143	49	81
Huttwil	BE	8w	630859	216684	37	4
Lupfig	AG	8w	656968	254806	54	45
Nyon	VD	8w	503625	137146	80	79
Orbe	VD	8w	526781	172298	41	31
Wohlen	BE	8w	598193	203540	76	93
Avenches	VD	D	570876	198726	144	23
Belp	BE	D	602699	195929	221	58
Cousset	FR	D	564488	185974	52	28
Diegten	BL	D	629724	254270	21	30
Grossaffoltern	BE	D	595164	213838	35	34
Hindelbank	BE	D	608715	211818	92	29
Huttwil	BE	D	631454	217636	45	17
Lupfig	AG	D	656488	254973	116	28
Nyon	VD	D	504394	137098	33	17
Orbe	VD	D	527588	172614	29	21
Wohlen	BE	D	598952	205162	239	107
Avenches	VD	R	571156	199189	125	85
Belp	BE	R	605992	193887	174	124
Coffrane	NE	R	555200	206511	52	48
Cousset	FR	R	566709	186749	44	51
Diegten	BL	R	628554	251603	3	10
Grossaffoltern	BE	R	593100	212533	83	88
Hindelbank	BE	R	609796	208848	48	28
Huttwil	BE	R	629144	217791	44	35
Lupfig	AG	R	658689	255134	27	23
Nyon	VD	R	508935	140280	21	19
Orbe	VD	R	528116	174457	81	46
Wohlen	BE	R	596265	202101	127	349

Appendix 2. List of meadows with their respective mowing regime, geographic coordinates and abundance of sampled rove beetles (Coleoptera: Staphylinidae) and ground beetles (Coleoptera: Carabidae) per meadow during the second sampling period (after mowing).

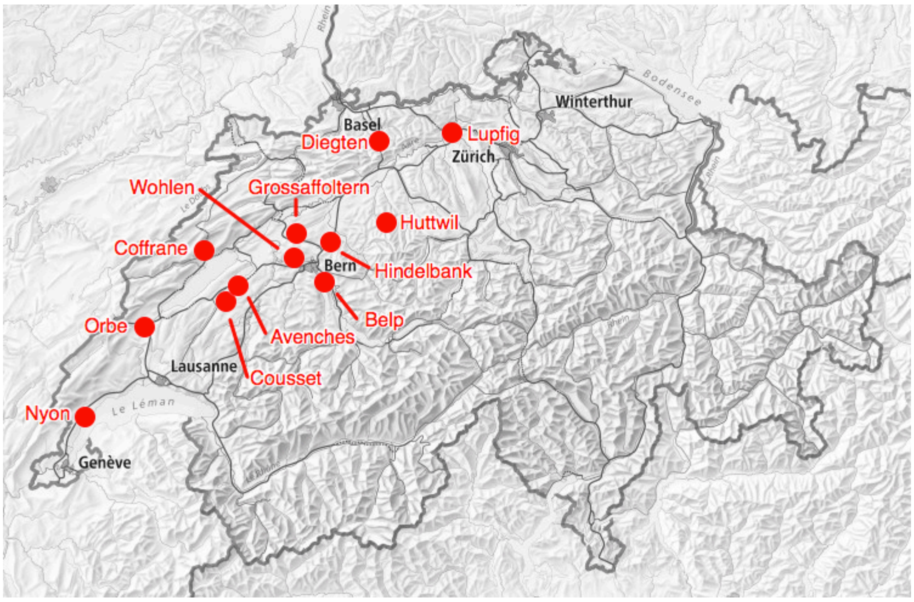
Site	Canton	Mowing regime	GPS coordinates E [CH1903]	GPS coordinates N [CH1903]	Rove beetle abundance	Ground beetle abundance
Avenches	VD	C	567193	197127	77	3
Belp	BE	C	605487	192366	51	9
Coffrane	NE	C	556126	205774	57	36
Cousset	FR	C	565063	185881	117	25
Diegten	BL	C	628587	252768	4	0
Grossaffoltern	BE	C	595281	212666	103	26
Hindelbank	BE	C	612352	209751	72	9
Huttwil	BE	C	628558	215769	102	35
Lupfig	AG	C	655871	255464	36	11
Nyon	VD	C	506251	141110	112	120
Orbe	VD	C	528474	173673	166	70
Wohlen	BE	C	595389	205416	64	8
Avenches	VD	8w	566771	196996	56	38
Belp	BE	8w	605869	193107	272	47
Coffrane	NE	8w	555499	206934	88	11
Cousset	FR	8w	564696	185503	87	36
Diegten	BL	8w	628895	252035	31	20
Grossaffoltern	BE	8w	592103	214070	82	33
Hindelbank	BE	8w	608282	208143	35	113
Huttwil	BE	8w	630859	216684	55	10
Lupfig	AG	8w	656968	254806	19	10
Nyon	VD	8w	503625	137146	77	51
Orbe	VD	8w	526781	172298	42	12
Wohlen	BE	8w	598193	203540	412	25
Avenches	VD	D	570876	198726	55	11
Belp	BE	D	602699	195929	62	107
Cousset	FR	D	564488	185974	27	13
Diegten	BL	D	629724	254270	13	40
Grossaffoltern	BE	D	595164	213838	30	23
Hindelbank	BE	D	608715	211818	40	24
Huttwil	BE	D	631454	217636	54	23
Lupfig	AG	D	656488	254973	79	8
Nyon	VD	D	504394	137098	11	25
Orbe	VD	D	527588	172614	12	3
Wohlen	BE	D	598952	205162	44	154
Avenches	VD	R	571156	199189	90	20
Belp	BE	R	605992	193887	160	39
Coffrane	NE	R	555200	206511	36	30
Cousset	FR	R	566709	186749	156	62
Diegten	BL	R	628554	251603	15	15
Grossaffoltern	BE	R	593100	212533	65	19
Hindelbank	BE	R	609796	208848	74	20
Huttwil	BE	R	629144	217791	78	22
Lupfig	AG	R	658689	255134	34	5
Nyon	VD	R	508935	140280	50	29
Orbe	VD	R	528116	174457	84	40
Wohlen	BE	R	596265	202101	94	113
Avenches	VD	Ruc	571156	199189	68	8
Belp	BE	Ruc	605992	193887	26	47
Coffrane	NE	Ruc	555200	206511	17	28
Cousset	FR	Ruc	566709	186749	14	19
Diegten	BL	Ruc	628554	251603	11	9
Grossaffoltern	BE	Ruc	593100	212533	89	119
Hindelbank	BE	Ruc	609796	208848	46	4
Huttwil	BE	Ruc	629144	217791	75	124
Lupfig	AG	Ruc	658689	255134	26	6
Nyon	VD	Ruc	508935	140280	8	12
Orbe	VD	Ruc	528116	174457	59	52
Wohlen	BE	Ruc	596265	202101	69	57

Appendix 3. List of ground beetle species (Coleoptera: Carabidae), with number of individuals sampled (abundance), mean size, habitat strictness and humidity preference based on literature values (Müller-Motzfeld 2004; Luka *et al*. 2009a).

Species	Abundance	Size [mm]	Habitat strictness	Humidity preference
Abax ovalis	1	13.00	eurytopic	hygrophilous
Agonum emarginatum	1	8.25	eurytopic	hygrophilous
Agonum muelleri	33	8.00	eurytopic	mesophilic
Agonum viridicupreum	3	9.00	stenotopic	hygrophilous
Amara aenea	312	7.50	eurytopic	xerophilous
Amara aulica	2	12.75	eurytopic	mesophilic
Amara bifrons	1	6.50	stenotopic	xerophilous
Amara communis	72	7.00	eurytopic	mesophilic
Amara convexior	170	8.00	eurytopic	mesophilic
Amara familiaris	15	6.50	eurytopic	mesophilic
Amara fulvipes	186	10.50	stenotopic	xerophilous
Amara kulti	187	9.50	stenotopic	mesophilic
Amara lucida	3	5.75	stenotopic	mesophilic
Amara lunicollis	301	7.50	eurytopic	mesophilic
Amara montivaga	109	8.50	eurytopic	xerophilous
Amara nitida	5	8.00	eurytopic	mesophilic
Amara ovata	5	8.75	eurytopic	mesophilic
Amara plebeja	6	7.00	eurytopic	mesophilic
Anchomenus dorsalis	57	6.80	eurytopic	mesophilic
Anisodactylus binotatus	325	11.00	eurytopic	mesophilic
Anisodactylus nemorivagus	24	9.00	stenotopic	xerophilous
Anisodactylus signatus	2	11.75	eurytopic	mesophilic
Asaphidion austriacum	2	4.50	stenotopic	hygrophilous
Badister bullatus	17	5.65	eurytopic	mesophilic
Badister sodalis	3	4.25	eurytopic	mesophilic
Bembidion lampros	185	3.40	eurytopic	mesophilic
Bembidion lunulatum	9	3.65	eurytopic	hygrophilous
Bembidion obtusum	7	3.20	eurytopic	mesophilic
Bembidion properans	386	3.95	eurytopic	mesophilic
Bembidion quadrimaculatum	25	3.05	eurytopic	xerophilous
Brachinus crepitans	1	8.25	eurytopic	xerophilous
Brachinus elegans	1	7.75	stenotopic	mesophilic
Brachinus explodens	17	6.00	eurytopic	xerophilous
Calathus fuscipes	24	12.25	eurytopic	mesophilic
Calathus melanocephalus	18	7.50	stenotopic	xerophilous
Callistus lunatus	5	5.60	eurytopic	xerophilous
Carabus auratus	3	23.50	eurytopic	mesophilic
Carabus granulatus	8	19.50	eurytopic	hygrophilous
Carabus monilis	205	24.50	eurytopic	mesophilic
Carabus nemoralis	1	23.00	eurytopic	hygrophilous
Carabus violaceus	1	30.00	eurytopic	mesophilic
Chlaenius nigricornis	1	11.00	stenotopic	hygrophilous
Cicindela campestris	1	12.50	eurytopic	xerophilous
Clivina collaris	1	5.25	eurytopic	hygrophilous
Clivina fossor	54	6.25	eurytopic	mesophilic
Diachromus germanus	56	8.45	eurytopic	mesophilic
Dyschirius globosus	13	2.75	eurytopic	hygrophilous
Harpalus affinis	128	10.50	stenotopic	mesophilic
Harpalus dimidiatus	74	12.50	eurytopic	xerophilous
Harpalus griseus	3	10.00	eurytopic	xerophilous
Harpalus latus	15	9.50	eurytopic	mesophilic
Harpalus luteicornis	78	6.75	eurytopic	mesophilic
Harpalus rubripes	46	10.00	eurytopic	mesophilic
Harpalus rufipes	116	13.50	eurytopic	mesophilic
Harpalus serripes	5	10.50	eurytopic	xerophilous
Harpalus subcylindricus	89	6.75	stenotopic	xerophilous
Harpalus tardus	16	9.45	eurytopic	xerophilous
Licinus hoffmanseggii	1	12.00	eurytopic	mesophilic
Loricera pilicornis	16	7.50	eurytopic	hygrophilous
Microlestes minutulus	1	3.10	eurytopic	xerophilous
Nebria brevicollis	12	12.00	eurytopic	hygrophilous
Ophonus ardosiacus	20	12.00	stenotopic	xerophilous
Ophonus azureus	5	7.50	stenotopic	xerophilous
Ophonus laticollis	1	9.75	eurytopic	xerophilous
Ophonus puncticeps	5	8.25	stenotopic	xerophilous
Ophonus puncticollis	1	8.25	stenotopic	xerophilous
Ophonus rufibarbis	3	7.55	eurytopic	xerophilous

Panagaeus bipustulatus	1	7.25	stenotopic	xerophilous
Panagaeus cruxmajor	3	8.25	eurytopic	hygrophilous
Parophonus maculicornis	253	6.65	stenotopic	mesophilic
Poecilus cupreus	217	11.00	eurytopic	mesophilic
Poecilus versicolor	387	9.75	stenotopic	mesophilic
Pterostichus anthracinus	2	10.75	eurytopic	hygrophilous
Pterostichus madidus	1	15.50	eurytopic	mesophilic
Pterostichus melanarius	10	15.00	eurytopic	hygrophilous
Pterostichus niger	2	18.00	eurytopic	hygrophilous
Pterostichus nigrita	9	10.25	eurytopic	hygrophilous
Pterostichus oblongopunctatus	1	10.50	eurytopic	hygrophilous
Pterostichus ovoideus	2	6.75	eurytopic	hygrophilous
Pterostichus vernalis	53	6.85	eurytopic	mesophilic
Stenolophus teutonus	3	6.25	stenotopic	mesophilic
Stomis pumicatus	1	7.40	eurytopic	mesophilic
Syntomus truncatellus	101	3.15	eurytopic	mesophilic
Synuchus vivalis	1	7.40	eurytopic	mesophilic
Tachys bistriatus	3	2.20	eurytopic	mesophilic
Trechoblemus micros	1	4.50	stenotopic	hygrophilous
Trechus quadristriatus	3	4.00	stenotopic	mesophilic

Appendix 4. Map of Switzerland with the 12 study regions indicated as red dots.



Erklärung

gemäss Art. 28 Abs. 2 RSL 05

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Studiengang: Master of Science in Ecology and Evolution with special qualification in Animal Ecology and Conservation, Universität Bern

Bachelor ☐ Master ☒ Dissertation ☐

Titel der Arbeit: Effects of altered mowing regimes in extensively managed meadows on ground and rove beetles

Leiter der Arbeit: Dr Jean-Yves Humbert, Dr Roel van Klink und Prof Dr Raphaël Arlettaz

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.

Ort/Datum Unterschrift

Marbach, 20.05.16 Lukas Lischer