Determinants of invertebrate presence in extensively managed grasslands in the Swiss lowland

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Determinants of invertebrate presence in extensively managed grasslands in the Swiss lowland

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Abstract

Semi-natural grasslands have experienced severe degradation in the last 70 years due to agricultural intensification and their biodiversity has diminished dramatically as a consequence. To counteract this decline the Swiss government introduced some environmental-friendly farmland regulations in the 1990s, including the so called biodiversity promotion areas (BPA). Extensively managed hay meadows under BPA regulations have shown to be beneficial for biodiversity, however their floral and faunal diversity are still impoverished compared to reference grasslands from the 1950s.

This study aimed to find the key variables that drive today's invertebrate communities in extensively managed BPA meadows in the Swiss lowlands. From April to August 2018, plant and invertebrates were sampled in 72 BPA meadows. Invertebrate data included abundance of spiders, gastropods, plant- and leafhoppers, weevils, lepidopteran larvae (caterpillars), ground beetles, rove beetles as well as abundance and species richness of orthopterans. Some local abiotic variables were also recorded, and the habitat surrounding of each meadow was mapped.

Out of 36 explanatory variables, only three emerged as statistically significant drivers of biodiversity, with a relatively low conditional R^2. In particular, the cover of unsealed areas (gardens, road verges and ruderal areas) and impervious areas (urban structures and paved areas) within 50-m radius around meadows were found to be an important driver of invertebrate communities. Specifically, after the first mowing event, a 15% increase of unsealed structures in the direct surroundings of a meadow led to a 20% increase in the multi-abundance of herbivores (conditional $R^2 = 0.151$). Similarly, an increase of 0 to 30% of impervious areas led to a loss of two orthopteran species per meadow, on average, which corresponds to 30% of species richness (conditional $R^2 = 0.411$). Multi–abundance of predators showed a negative correlation with the ecological quality of the meadows, as assessed by the vegetation assemblage.

In conclusion, this study highlights that the actual faunal composition of extensively managed meadows in the Swiss lowland is multifaceted as no single or simple combination of variables can explain the observed invertebrate abundance. Yet, working at a finer taxonomic resolution than we did and incorporating species-traits into the analysis might enable more sophisticated analyses with more contrasted outcomes.

Keywords: Invertebrates, communities, semi-natural grasslands, agri-environment schemes

1. Introduction

Even though temperate Europe is seen as relatively species poor compared to the biodiversity hotspots of this earth, it contains several habitats which rank the highest in terms of species richness at local scale, particularly the semi-natural grasslands (Wilson *et al.* 2012). Grassland habitat cover about 21% of Europe's terrestrial surface and is behind woodland and cropland the third most abundant land cover (Eurostat 2018). During the last 50 years grasslands have experienced continuous alteration due to land use change and are nowadays considered the most endangered ecosystems of this planet (IUCN 2016, Foley *et al.* 2005).

In Switzerland grasslands have been dramatically impacted during the green revolution. Grasslands got heavily altered by removing structures that hindered the use of machines, wet sites got drained or filled up, nutrient poor sites got fertilized and dry sites watered (BAFU 2018). *Arrhenatherion* meadows were the most dominant grassland type in the 1920s in Switzerland. These grasslands are characterized by the grass *Arrhentherum elatius* and low intensity use in terms of mowing and fertilized only with dung. In the past 100 years *Arrhenatherion* meadows have declined to about 2% of the agricultural used surface of Switzerland. For example, the canton of Zürich reported a decline of 55 000 ha to only 500 ha today. The remaining 2% of today are still impoverished in terms of botanical and faunal diversity (Bosshard 2015).

To counteract this decline of biodiversity, the Swiss government introduced biodiversity promotion areas, hereafter abbreviated as BPA, in 1993 (Bundesrat 2013). To get the general direct payments (state subsidies) it is compulsory for farmers to set at least 7% of their agricultural used land as BPA. Approximately 50% of the current BPAs in Switzerland are extensively managed hay meadows which have no fertilizer, herbicides or pesticides input and are mown at least once per year but not before 15th June and the cut material must be exported. Grazing is allowed between September and November. The basic requirements are financially supported by the Quality I input-based contributions (hereafter called QI). On top of the QI contributions a farmer can get a bonus known as the Quality II output-based contributions (hereafter called QII). Whether a meadow qualifies as QI or QII is based upon a quality assessment key which contains a list of plant indicator species. A meadow that harbours at least six of the listed species qualifies as QII meadow, i.e. meadows with higher ecological quality (BLW 2014).

With the implementation of BPAs, grasslands biodiversity increased locally but today's grasslands are nevertheless nowhere near the quality they have exhibited in the past. Bosshard (2015) showed that in the 1950, 85% of all the conventional low intensively managed *Arrhenatherion* grasslands reached QII harbouring on average 8.4 indicator species. Today only 30% of all the meadows registered as BPA reach QII (BLW 2018). In addition to the indication that the sole extensification of grassland management practices did not restore the former quality of these grasslands (Bosshard 2015), van Klink et al. (2017) showed that the plant species richness did not change over a period of five years of extensive management.

Positive effects of extensive management have been shown on vascular plants, butterflies, ground beetles and true bugs (Di Giulio, Edwards & Meister 2001; Knop *et al.* 2006; Aviron *et al.* 2009). Spiders, however, showed no difference between extensive and conventional management (Di Giulio, Edwards & Meister 2001; Knop *et al.* 2006; Aviron *et al.* 2009). Recently, Hallmann et al. (2017) shows a decline of 75% of flying insect biomass over the past 27 years across German nature protection areas regardless of the habitat type. They state that the changes in land use, habitat characteristics and weather cannot fully explain this decline. As mentioned above several studies have shown that extensive management favours many taxa of invertebrates, their number yet still do not reach the former estimations of abundances in the 1950s. Bosshard (2015) estimated that due to land use intensification and urbanisation less than 1% of the populations from 1950 remain or have gone extinct completely. Many invertebrate taxa have shown to react positively in species richness and abundance to plant related variables such as species richness, vegetation structure and plant species composition (Schaffers *et al.* 2008; Scherber *et al.* 2010; Manning *et al.* 2015), but see Koricheva et al. 2015 which has found negative correlations. Schaffers et al. (2008) have found that plant species composition performs better as predictor for invertebrate communities than the mere plants species richness and that local- and landscape factors act as relatively poor predictors. For predators it has been shown that they need heterogeneous habitat structures rather than sheer species richness of plants (Bell, Wheater & Cullen

2001; Woodcock *et al.* 2009). Habitat diversity on a landscape scale has also been shown to have a positive effect on invertebrates (Hortal *et al.* 2009; Birkhofer *et al.* 2015; Perovic *et al.* 2015; Maskell *et al.* 2019). As stated above the relationship between plants and invertebrates has been studied a lot but there are little studies that assessed the reaction of invertebrates to other factors in the environment than plant related. Invertebrates have a crucial role in maintaining the ecosystem processes of grasslands and act as a food source for higher tropic levels (Wilson *et al.* 1999; Yang & Gratton 2014). The reports about the drastic decline of invertebrates and the knowledge about their crucial role in the ecosystem maintenance makes it important to identify the variables that are driving their communities and ideally being able to enhance such variables to improve the conditions for invertebrate communities.

The extensive management is benefiting plants and invertebrates compared to the conventional management. Nevertheless, Weinrich et al. (2018) have shown that big variances between investigated meadows still exist even after the application of the same extensive management for many years. The underlying reason for this variance of sometimes a factor of seven is yet still unclear. Therefore, the aim of this study was to identify the key variables that drive invertebrate communities within grasslands that are extensively managed and registered as BPA meadows since at least 5 years. Based on the literature cited above we hypothesized that: (i) the ecological quality of a meadow (i.e. QI vs QII meadows) will positively affect the herbivorous communities (Weinrich *et al.* 2018); (ii) bigger meadows harbour a more abundant and richer invertebrate communities as they can sustain higher species numbers at the equilibrium of immigration and extinction rates (Brown & Kodricbrown 1977) as well as because of the potential to harbour a higher plant diversity and therefore provide a more heterogeneous habitat favouring many different invertebrate taxa at the same time; (iii) habitat diversity on a landscape scale will favour the invertebrate communities in the meadows (Duelli & Obrist 2003; Madeira *et al.* 2016). To answer the question, 72 BPA extensively managed meadows located in the Swiss lowland were sampled in 2018. Invertebrates were then analysed in response to the local management, soil- and plant communities, as well to the direct surrounding of the meadows.

2. Material and Methods

2.1. Study sites and design

72 meadows spread across the Swiss lowland (see Fig. 1) were selected in 2018. All selected meadows were registered as BPA since at least 2013 and were located within an altitudinal range of 420 and 760 m. The size of the meadow varied between 0.14-2.5 ha. The meadows were equally distributed into 12 regions with at least 10 km between two regions and the minimal distance between two meadows was 337 m. Each region contained five meadows with QI and one meadow with QII (see Introduction for a definition of QI and QII).

The sampling of plant- and invertebrate was split into two sessions. A first session was conducted before the first mowing event of 15 June, it included the plants and the invertebrates. The second session was conducted after the first mowing event and it included only the invertebrates. Originally, the 72 meadows were selected for the new Grassland Restoration project of the division of Conservation Biology of the University of Bern. This MSc study made use of the baseline data of this project gathered in 2018. As for the question that is aimed to be answered the selection of the meadows was not optimal as there were 60 QI meadows and 12 very high QII meadows selected. This led to a gap in the data for the intermediate range of the quality aspect.

2.2. Plant, invertebrate and meadow sampling

2.2.1 Plant and aboveground biomass production

Plant surveys were conducted in 2018 before 15 June after van Klink et al. (2017). Two vegetation subplots measuring 2 x 4 m were randomly placed in the meadow 8 m apart from each other. In each of the two subplots the plant diversity as well as the relative cover of each species has been assessed. In addition, in each meadow a QII assessment has been applied. Specifically, in each meadow a random assessment plot with a radius of 3 m has been placed between the vegetation plots. In addition, if the vegetation of the meadow seemed homogeneous one more plot with radius 3 m was placed where the ecological quality seemed the highest. If the meadows vegetation was very heterogeneous in each of the different areas a plot was placed at the location with subjectively the highest quality. The assessment has been conducted according to the assessment key (BLW 2014; see Weinrich *et al.* (2018) for more details). The above biomass production was sampled by cutting four 0.25 m^2 squares around the two random vegetation subplots (see Fig. 2). The cut biomass was put into a perforated plastic bag and then dried at least 48 hours at 80°C. When the collected sample did not change in weight for at least another 24 hours the final weight was recorded as aboveground biomass (dry matter) production in gram per m^2.

2.2.2 Pitfall traps

Spiders, ground beetles and rove beetles were sampled using pitfall traps (Buri *et al.* 2016). The traps were installed four times, for one week each time, two times before (28 May to 21 June) and two times after mowing (2 July to 13 August). Each session four traps were placed in a square of 10 x 10 m at each corner of the square, six meters away of the random vegetation plots in a random direction (see Fig. 3). Plastic cups (9 cm diameter and 15 cm deep) were used as traps, covered directly by a metallic grid to prevent mice from falling into the traps and a transparent plexiglass (20 x 20 cm) 5 cm above the cup to prevent overfilling by rain, nailed to the ground to ensure stability. Each cup was filled with a mixture of propylene glycol and water (0.166 l propylene glycol and 0.083 l water). Sodium dodecyl was added to the mixture to reduce the surface tension. The invertebrates were shortly stored in the cups in the cellar of the conservation biology building until being sorted into their order (spiders) or family (ground beetles and rove beetles) and counted. The sorted samples were then stored in 70% alcohol. For this study only ¼ of the collected cups were analysed.

2.2.3 Suction sampling

Vegetation dwelling spiders, snails, plant and leaf hoppers, beetles, weevils and true bugs were captured with the suction sampling method (Buri *et al.* 2016). Tow sampling sessions took place in 2018: the first before any mowing activity took place (24 May to 9 June) and the second after all the meadows have been mown (7 to 30 July). Five suction points were placed in the meadows between the random vegetation plots in a cross shape (see Fig. 4). At each suction point a metallic cylinder measuring 0.51 m in diameter and of a surface area of 0.2 m^2 was placed to prevent the invertebrates from escaping. The invertebrates were then sucked up with a reversed leaf blower. The caught individuals were transferred into a plastic bag and stored in the freezer at -20°C. Later the bags were sorted into the orders or families mentioned above and counted. For this study only 2/5 of the collected samples were analysed. To gain a representative and comparable picture on all the different meadows the bags were chosen systematically so that out of the 5 bags for every meadow the bags with intermediate content were chosen to be sorted. With that strategy it was tried to have the average abundance for every meadow excluding the possibility to sort bags which results in very high abundances for one meadow and bags resulting in very low abundances for the other meadow so that the abundances per meadow were not over or underestimated.

2.2.4. Biocenometer

The orthopterans were sampled using a biocenometer as described in Buri et al. (2013). The biocenometer is an open cylinder made of a rigid net covering an area of 1 m^2. Two sampling sessions took place in 2018: the first in July and the second in August. The sampling was only performed on sunny days between 9 am to 6 pm. On each meadow the biocenometer was thrown 16 times along 2 to 4 parallel transects with a minimum distance of 10 m between transects, excluding a 10 m buffer zone around the meadow edge to avoid edge effects (Knop *et al.* 2006). All the individuals caught in the biocenometer were identified, counted and immediately released. Adult individuals were identified to species level and juveniles classified into their respective suborder (Ensifera or Califera). To capture the full diversity of species, an additional qualitative visual and acoustic survey was performed for at least 30 minutes or 2 x 15 minutes by two people. Species richness per meadow included the biocenometer data as well as the additional species found during the qualitative survey.

2.2.5. Soil

In total 8 soil samples were taken per meadow located at the edges of the random vegetation plots (see Fig. 1). Samples were taken using a soil core measuring 3.6 cm in diameter and 10 cm in depth. The samples were analysed in the lab for pH, nitrate content and the grain size from < 0.002 (Clay) up to 2 mm (Sand).

2.2.6. Meadow history

To gather the information about the age, former use, grazing activities and sowing of the meadow. A questionnaire was created and presented to the farmer at the beginning of the project. The age is defined by number of years since the transformation from the formerly applied management to the current extensive management. The former use contains four categories of management types namely: extensive management with the regulations to get subsidies for QI, intensive management, cropland and other. Sown explains whether the meadow has been sown in recent years, which would affect plant occurrence on the meadow which then might not be 100% natural. The grazing activities refer to whether the meadow is grazed in autumn (September to November) by any type of farmland animal.

2.2.7. Surrounding area of the meadow

The explanatory variables that were recorded in the surrounding of the meadows (e.g. urban structures, waterbodies, hedges, management of adjacent fields etc.) were gathered within a radius of 50 meters through remote sensing and direct observations in the field. The variable landscape heterogeneity was assessed as the Shannon Index of the structures: extensive, intensive, wood, water, impervious, unsealed, hedges and permanent culture in the surrounding (see Table 2. for more information).

2.3. Statistical analysis

It has been shown by several studies that the mowing event has a direct negative effect on the invertebrates living in the meadow (Humbert *et al.* 2012; Buri, Arlettaz & Humbert 2013; Buri *et al.* 2016). Therefore, samples collected before and after mowing were analysed separately. To explain the abundance data before the first mowing event all the gathered explanatory variables were considered. For the analysis of the abundances after the first mowing event vegetation cover related variables have not been considered anymore as they cannot explain the populations after the mowing event. Categorical variables that have more than two categories such as northing were not included in any of the final models as the statistical power of the model decreases with more categories included. Age, former management, grazing and sowing are variables influencing a meadow over time and therefore are investigated separately as historic variables. The abundance data of the pitfall traps were pooled by taking the mean of the first two sessions and the last two sessions as they occurred before or after the mowing event respectively. Orthopteran abundance was analysed after mowing as both sampling periods took place after the first mowing event. The species richness for orthopterans was pooled over both sessions to gain the full picture of all different species living in the meadows independent of the sampling time.

Invertebrate abundances were grouped into the feeding guilds herbivores (snails, plant and leaf hoppers, weevils true bugs and orthopterans) and predators (spiders, ground beetles and rove beetles) using the concept of the multi-diversity index of (Allan *et al.* 2014). It creates a value between 0 and 1 where each taxonomic group is scaled to the highest count across all meadows. This index ensures that all the groups are weighted equally independent of the total abundance of individuals per group.

Some of the recorded variables in the surrounding were aggregated into the following groups: Extensive, intensive, impervious, unsealed, water, wood, hedges and permanent cultures (see Table 2 for details). To check for correlation between explanatory variables a correlation matrix has been created using the package corrplot (Wei & Simko 2017). If two values had a correlation > 0.7, one of the two was dropped. Variables that showed correlation were wood and forest edge (0.75), number of single trees and number of fruit trees (0.9) and impervious and unsealed (0.78). Forest edge has been dropped from the analysis as the woody area around the meadow also involves the forest edge and therefore explains more than the forest edge alone. Number of fruit trees has been dropped because the identity of the trees is not known and therefore the interesting part of this variable is the effect of the presence of trees in the meadow. Impervious and unsealed were both kept for further analysis because both can explain different changes in the environment and might be important to understand the needs of invertebrate communities. In case both variables showed a significant effect only the one with the lower p-value was kept for the multivariate analysis.

Relationships were explored using generalized linear mixed models GLMM with lmer() and glmer() of the lme4 package (Bates *et al.* 2015). "Region" was included as random effect. The response variables were always the abundance of single invertebrate groups or the multi-abundance index for the herbivorous or predatory invertebrates. The orthopterans have been included in the herbivorous invertebrates but were also as the only group analysed for species richness. In the first step of the analysis all the response variables were tested against the gathered explanatory variables. Variables that showed a correlation with p-value < 0.1 were kept. Linear and quadratic functions were tested simultaneously, and the quadratic model was only kept if it showed a better performance as the linear model by a Δ AIC of 2. All the kept variables from the first step were combined in a global model and analysed in the second step using the dredge function of the MuMIn Package (Bartoń 2018). The dredge function then checks all the possible combination of variables and returns a model selection table with the best performing models on top. If more than one model within a Δ AIC of 2 was returned model averaging was performed with all the models within the competitive AIC range (AIC of the top model + 2). The final model was built with all the variables that showed a significant effect either after the dredge directly or if needed after the averaging of the models. As a last step the confidence intervals of the variables returned for the final model were checked using the function confint() of the MASS package (Venables & Ripley 2002). If the calculated confidence interval crossed 0 (e.g. – 0.2 to + 0.6) the significance could not be trusted, and the variable was not further investigated. P-values were obtained with the lmerTest() package (Kuznetsova, Brockhoff & Christensen 2017). To show the goodness of fit of the model marginal and conditional R^2 were calculated using r.squaredGLMM() of the MuMIn package. The marginal R^2 shows how much variance is explained by the fixed, whereas the conditional R^2 shows how much variance is explained by the fixed and the random effect (Nakagawa & Schielzeth 2013). Gaussian error distribution could be applied to all the models, only exception were the spiders of the suction sampling method which showed a Poisson error distribution. If needed, the response variables were transformed using log or square root transformation to optimize the fitting of the model, showed by the residuals. All analyses were performed using the statistical computing environment R (R Core Team 2018).

3. Results

In the following section only the results of the multi-abundance analysis herbivores and predators will be shown since this study tries to explain the reaction of the communities of invertebrates. The model outputs for all the individual groups can be found in the Appendix A1 and are considered only if one single group is explaining most of the significance of one variable for either the herbivores or predators. The section is split into four subsections which addresses the results for both feeding guilds before and after the first mowing event. Detailed model outputs for the univariate and final models after dredging are presented in Table 3.

3.1. Herbivores

In total, 11’367 herbivorous invertebrate individuals were sampled with a mean of 158 ± 94 per meadow.

3.1.1. Herbivores before the first mowing event

Herbivores before the first mowing event positively correlated with the cover of Fabaceae (P = 0.069, see table 3 for more details on model output) and show a quadratic relationship with the pH of the soil (P = 0.005). However, after performing the dredge no model with a combination of these two variables competed within a Δ AIC of 2 as a better predictor than the null-model itself.

3.1.2. Herbivores after the first mowing event

After the first mowing event, herbivores showed a positive relationship with unsealed surrounding structure in the 50 m radius of the meadow (P = 0.092, Fig. 6).

3.2. Predators

9’600 predatory invertebrate individuals were sampled with a mean of 133 ± 47 per meadow.

3.2.1. Predators before the first mowing event

Predators before the first mowing event correlated positively with grass cover of the meadow (P = 0.036). Negative correlations were detected with the categorical assessment of the ecological quality of the meadow (QI meadows mean ± standard deviation = 0.41 ± 0.16, QII meadows 0.27 ± 0.15, P = 0.002), the slope of the meadow (P = 0.015), woody structures in the 50 m radius around the meadow (P = 0.012) and the pH of the soil (P = 0.013). A quadratic relationship was found with the hay biomass yield with an optimum between 200 and 400 g / m^2 (P = 0.003). After using the dredge function the only model within a Δ AIC of 2 of all the competing models was the one including only the quality variable (QI = 0.41 ± 0.16; QII = 0.27 ± 0.15, P = 0.002, Fig. 7a). The former management was the only significant historic variable showing that meadows which have always been managed extensively (0.32 ± 0.17) are poorer in multi-abundance of predators than meadows which have been managed intensively or as cropland before (intensive = 0.44 ± 0.16, P = 0.008; cropland = 0.39 ± 0.15, P = 0.071, Fig. 7b).

3.2.2. Predators after the first mowing event

After the first mowing event the multi-abundance of predators showed a positive correlation with hay biomass yield per m^2 (P = 0.026), the total plant coverage measured in the random plots of the meadow (P = 0.03), grass coverage of the meadow (P = < 0.001) and unsealed structure in the 50 m radius around the meadow (P = 0.038). Negative correlations were found with the ecological quality of the meadow (QI = 0.36 ± 0.14, QII = 0.21 ± 0.10, P = < 0.001), the slope of the meadow (P = 0.01), with woody structure in the 50 m radius around the meadow (P = 0.017), with the proportion of permanent culture within the 50 m radius around the meadow (P = 0.034) and with soil pH (P = 0.05). The only variable remaining after dredging was the quality variable (QI = 0.36 ± 0.14, QII = 0.21 ± 0.10, P = < 0.001, Fig. 8).

3.3. Orthopteran species richness

In total 19 different orthopteran species were found with a mean of 5.63 ± 1.8 per meadow. Orthopteran species richness correlated positively with the size of the meadow (P = 0.091), the ecological quality of the meadow (QI = 5.42 ± 1.75; QII = 6.67 ± 1.78), the slope of the meadow (P = 0.098), the number of plant species per vegetation plot (P = 0.051), the coverage of forbs in the vegetation plots (P = 0.095), the proportion of woody structure in the 50 m radius around the meadow (P = < 0.001), with the soil pH (P = 0.0793), and with the Nitrogen content of the soil (P = 0.036). Negative correlations were only found with impervious structures in the 50 m radius around the meadow (P = < 0.001). After dredging with all these significant variables pH, impervious and Nitrogen content of the soil stayed significant, but only impervious showed a trustworthy confident interval (Fig. 9a). The analysis with the former management revealed that the formerly intensively managed meadows harbour less species than the formerly extensively managed meadows (extensive = 6.17 ± 1.92; intensive = 5.15 ± 1.69, $P = 0.021$, Fig. 9b).

4. Discussion

Extensification of the grassland management practices is beneficial to invertebrates and plants (Knop *et al.* 2006; Aviron *et al.* 2009) but there is still a big variance in population sizes within extensively managed grasslands which could not be explained by now. The goal of this study was to find key variables that drive insect communities and might explain the observed big variance among meadows that are all similarly, extensively, managed since at least 5 years. It was hypothesised that the ecological quality of such extensively managed meadows (based on plant indicator species), and the size of the meadow would positively influence invertebrate abundances (Brown & Kodricbrown 1977). Predatory invertebrates correlated negatively with the ecological quality of the meadow. Meaning that meadows with a lower ecological quality harbour more individuals than meadows with a high ecological quality. No evidence for a beneficial effect of the size of the meadows was found. On the other hand, it was found that unsealed structures in the direct surrounding of the meadows have a beneficial effect on multi-abundance of herbivores and the species richness of orthopterans. Detailed results on herbivores, predators and orthopteran species richness are presented and discussed separately in the next subsections.

4.1. Herbivores

The null-model showed the best performance in predicting the herbivore populations before the first mowing event. This goes partially in line with the results of (Schaffers *et al.* 2008) which showed that environmental and local abiotic variables are relatively poor predictors for invertebrate assemblages. However, against expectations (Schaffers *et al.* 2008; Haddad *et al.* 2009; Koch *et al.* 2013), no effect of vegetation related variables, such as vegetation structure and plant diversity, were found. Also, the ecological quality of the meadow, which was found to be important for herbivorous invertebrates by Weinrich *et al.* 2018 did not have a significant influence on herbivorous communities analysed in this study. The null-model as the best performing predictor model is quite surprising but also underlines how hard it is to find the driving variables for whole invertebrate communities. The decision which variables to keep was made based on univariate models. In this step interactions between the variables were neglected. It might be that a variable that would show a significant effect if analysed in combination with others does not show a significance on its own and was dropped for further analysis. Also, all our study meadows are managed extensively since at least 4 years, which makes the signal we are trying to detect very small and might be missed with the used approach in this study.

Unsealed and more natural structures in the surrounding of the meadow increased the abundance of predatory invertebrates in the meadow. Gardens and unpaved areas made up most of this variable. An increase from 0 to 15% of unsealed structures around the meadow results in an increase of the multi-abundance index of 20%. The size of source populations in the surrounding and the distance from the meadows to such source populations is very important to ensure a stable community in the meadow (Brown & Kodricbrown 1977; Madeira *et al.* 2016) The variable unsealed used in this study adds towards naturalness and heterogeneity around the meadow and therefore favouring such source populations in the surrounding. The positive effect of leaving uncut grass refuges in the meadows has been shown by several studies (Humbert *et al.* 2012; Buri, Arlettaz & Humbert 2013). The same effect can be expected by our variable unsealed. Similarly like refuges in the meadows and source populations around the meadows gardens and green roofs in urban areas can help the invertebrate populations to survive (Jones & Leather 2012).

4.2. Predators

Predator multi-abundance was higher in QI meadows, i.e. meadows with less than 6 indicator species than in QII meadows, i.e. meadows with more than 6 indicator species. The strength of the trend was surprising as Weinrich *et al.* 2018 have shown the same trend but not significant. A possible explanation for the severity of this trend might be that in this study the range of the indicator species was less than 6 for QI meadows and more than 10 for QII meadows. This left a gap in the range from 6 to 9 indicator species. Bosshard 2015 has shown that today, meadows with ecological quality harbour on average 8.4 indicator species, exactly in the gap of the data of this study. The biomass yield per meter square for QI meadows averages 312 g ± 132 g whereas QII meadows average 246 ± 153 g. The difference is not significant, but the trend is also supporting the conclusion that the structural heterogeneity which is higher in meadows with more biomass is important for predatory invertebrates (Woodcock *et al.* 2009; Birkhofer *et al.* 2015). This point is further supported by the analysis of the former management which shows that meadows that have previously experienced a more intensive form of management harbour as well more predatory invertebrates than meadows that were always managed in an extensive way.

4.3. Orthopteran species richness

Orthopteran species richness was lower in meadows with more impervious structures in their 50 m surrounding. An increase from 0 to 30% impervious structures in the surrounding led to a loss of on average 2 orthopteran species which correspond to ca. 30% decrease. The same relationship with urban elements has been found by Marini *et al.* 2008 for alpine meadows in a 500 m radius around the meadows. Orthopterans are a taxonomic group which cover a wide range of microclimatic conditions and therefore benefit from heterogeneity around but also in the meadow as more species can co-occur the higher the structural heterogeneity (Schindler *et al.* 2013). Many orthopteran species lay their eggs into the soil (Hochkirch *et al.* 2016; Orthoptera.ch). Therefore, impervious structures take away breeding ground as well as lower the resources available for orthopterans. In addition, about one third of all the orthopteran species inhabiting Europe are flightless (Hochkirch *et al.* 2016) this can lead to a heavily decreased dispersal ability of most species due to barriers, such as buildings and large streets, which they are not able to overcome. Unsealed which consisted of gardens, the parameter which autocorrelated with buildings, did not show any significance on the species richness of orthopterans. Therefore, even though gardens which can have a reportedly beneficial effect on herbivorous communities (Jones & Leather 2012) are not able to compensate the orthopteran species that are lost due to the impervious urban elements. This study worked exclusively with extensively managed meadows. Therefore, the beneficial effect of this management cannot be found. However, the former management showed that meadows that have been always (> 20 years) managed extensively harbour significantly more orthopteran species than former intensively managed meadows. Marini *et al.* 2008 and Knop *et al.* 2006 have found that the extensive management indeed favours orthopteran species richness as well as their abundance in general.

4.4. Conclusion

Overall this study reveals that out of all the sampled influence variables none exist that is favourable for all the groups analysed. Furthermore, only very few variables emerged as statistically significant on a community level of the analysis. The complexity of the issue is underlined by the calculated marginal and conditional R^2 values. In this study the highest conditional R^2 across all models was 0.411. Meaning the best model explained only 41% of all the variance occurring in the system. Most of the values lay between 0.1 and 0.3. This shows that even with including more than one explanatory variable only about 10 to 30% of the whole variance can be explained. Similar R^2 values are reported in Weinrich *et al.* 2018 which was looking at the same response variables as this study in different but similarly managed meadows. However, for herbivorous invertebrates and the species richness of orthopterans, more natural area around the meadow was found to be beneficial. For predatory invertebrates the ecological quality of the meadow was found to be negative. Likely because the productivity and structural heterogeneity is lower in such meadows. These results combined suggest that landscape heterogeneity has a positive influence on predatory as well as herbivorous invertebrates and species richness of orthopterans, but that the total population size of predators is limited by the local productivity. Landscape heterogeneity is also favourable towards source populations around the meadows that ensure a stable population in the meadow (Duelli *et al.* 2003; Marini *et al.* 2008) Further analyses require the identification of the specimens of all the individuals found. This will reveal the traits of individuals and groups which also define the needs towards their habitat and the surrounding of the habitat. In addition, the interaction with plants can be investigated more closely e.g. host interactions or the difference across regions towards different plant ecotypes and communities. The identity of species could also be used to give recommendations towards the conservation of rare species. Even further, the genetic diversity and the ability to adapt to climate change and the changing habitat could be evaluated.

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Table 1. List of all the local explanatory variables used in the analyses. In the first column the name of the variable is indicated and in the second column a short definition of the variable is given. The unit is indicated in the square brackets.

Explanatory Variable	Definition and the respective unit
(a) Topographic Variables	
Slope	Slope of the meadow [%]
Elevation	Elevation of the meadow [m]
Exposition	Exposition of the meadow [°]
(b) Soil Variables	
pH	Soil pH [1-14]
N	N content of the soil [%]
Clay	Clay content of the soil [%]
Silt	Silt content of the soil [%]
Sand	Sand content of the soil [%]
(c) Vegetation Variables	
Quality	Ecological quality of the meadow [QI/QII]
Biomass	Aboveground biomass production [g/m^2]
Moss cover	Moss cover in the vegetation plots [%]
Bare ground	Bare ground cover in the vegetation plots [%]
Litter leave cover	Area covered by tree leave litter in the vegetation plots [%]
Litter grass cover	Area covered by herbaceous litter in the vegetation plots [%]
Plant cover	Total area covered by plants in the vegetation plots [%]
Grass cover	Grass coverage in the vegetation plots [%]
Legume cover	Legume coverage in the vegetation plots [%]
Forb cover	Forb coverage in the vegetation plots [%]
Number of species	Number of different species recorded in the vegetation plots [absolute]
Number of single Trees	Number of single trees which stand on the meadow [absolute]
(d) Meadow information	
Age	Time since extensive management [Years]
Area	Total area of the meadow [m^2]
Sown	Was the meadow sown in the past? [Yes/No]
Grazing	Grazing activity on the meadow in autumn [Yes/No]
Former management	Management conducted before extensive management
Extensive	Extensive management
Intensive	Intensive management
Cropland	Managed as cropland
Others	Managed in any other type

Table 2. List of all the surrounding explanatory variables recorded and used in the analyses. In the first column the name of the variable is indicated and in the second column a short definition of the variable is given. The unit is indicated in the square brackets.

Explanatory Variable	Definition and the respective Unit
Cropland	Amount of cropland in the 50 m radius around the meadow [%]
Roads	Total area of roads in the 50 m radius around the meadow [%]
Rivers	Total area of rivers in the 50 m radius around the meadow [%]
Grouped Variables	
Extensive management	Extensively managed area in the 50 m radius around the meadow [%]
Extensive meadows	
Extensive pastures	
Riparian vegetation	
Wildflower strip	
Intensive management	Intensively managed area in the 50 m radius around the meadow [%]
Artificial meadows	
Intensive meadows	
Intensive pastures	
Chicken pasture	
Horse pasture	
Impervious	Amount of impervious area in the 50 m radius around the meadow [%]
Buildings	
Paved area	
Unsealed	Amount of natural area in the 50 m radius around the meadow [%]
Gardens	
Road verges	
Ruderal area	
Unpaved area	
Water	Amount of wet area in the 50 m radius around the meadow [%]
Rivers	
Waterbodies	
Wood	Amount of woody area in the 50 m radius around the meadow [%]
Deciduous forests	
Mixed forests	
Riparian forests	
Forest edge	
Woody area	
Hedges	Amount of hedge or hedge like area in the 50 m radius of the meadow [%]
Hedges QI	
Hedges QII	
Shrubby area	
Single trees	
Tree rows	
Permanent cultures	Amount of permanent cultures in the 50 m radius of the meadow [%]
Orchards	

Table 3. Model outputs of the significant univariate linear mixed effect models (step 1) and of the final model after the model selection step (dredging) for multi-abundance of herbivores and predators before and after mowing. Distribution shows the used error distribution for the respective response variable, here always (G) for Gaussian, transformations are indicated in brackets with "sqrt" for square root transformation. Quadratic relationships are indicated with (q). SE indicates the standard error. The p-value indicates the level of significance and values < 0.05 are in bold. Conditional (Cond) and marginal (Mar) R^2 shows the goodness of fit of the model (the closer to 1 the better).

Model	Distribution	Slope	SE	p-value	Cond R^2	Mar R^2
Herbivores before mowing	G(sqrt)					
Univariate						
Legumes		0.002	0.001	0.069	0.365	0.037
pH (q)		0.044	0.015	**0.005**	0.396	0.084
Multivariate						
Null Model						
Herbivores after mowing	G(sqrt)					
Univariate						
Unsealed		0.021	0.012	0.092	0.152	0.041
Predators before mowing						
Univariate	G(sqrt)					
Biomass (q)		-0.035	0.011	**0.003**	0.323	0.123
Quality		-0.127	0.038	**0.002**		
Slope		-0.040	0.016	**0.015**	0.292	0.075
Grasses		0.034	0.016	**0.036**	0.244	0.054
Wood		-0.040	0.016	**0.012**	0.206	0.080
pH		-0.045	0.018	**0.013**	0.223	0.084
Former management						
Intensive vs Extensive		0.108	0.039	**0.008**		
Cropland vs Extensive		0.073	0.040	0.071		
Multivariate						
Quality		-0.127	0.038	**0.003**		
Predators after mowing	G(sqrt)					
Univariate						
Biomass		0.035	0.015	**0.026**	0.135	0.067
Quality		-0.138	0.037	< **0.001**		
Slope		-0.041	0.015	**0.010**	0.158	0.091
Plant cover		0.035	0.016	**0.030**	0.132	0.067
Grasses		0.052	0.015	< **0.001**	0.201	0.152

Unsealed		0.033	0.016	**0.038**	0.130	0.061
Wood		-0.037	0.015	**0.017**	0.117	0.077
Permanent cultures		-0.033	0.015	**0.034**	0.100	0.061
pH		-0.034	0.017	**0.050**	0.110	0.054
Multivariate						
Quality		-0.138	0.037	< **0.001**		
Orthopteran richness	G					
Univariate						
Area		0.384	0.224	0.091	0.224	0.036
Quality		1.250	0.502	**0.016**		
Slope		0.060	0.036	0.098	0.218	0.037
Nr of species		0.066	0.033	0.051	0.239	0.046
Forbs		0.026	0.016	0.095	0.219	0.034
Impervious		-8.333	1.913	< **0.001**	0.411	0.205
Wood		3.570	1.031	< **0.001**	0.216	0.141
pH		0.408	0.229	0.079	0.191	0.042
N		2.331	1.088	**0.036**	0.271	0.055
Former management						
Extensive vs Intensive		-1.192	0.488	**0.021**		
Multivariate						
Impervious		-8.333	1.913	< **0.001**	0.411	0.205

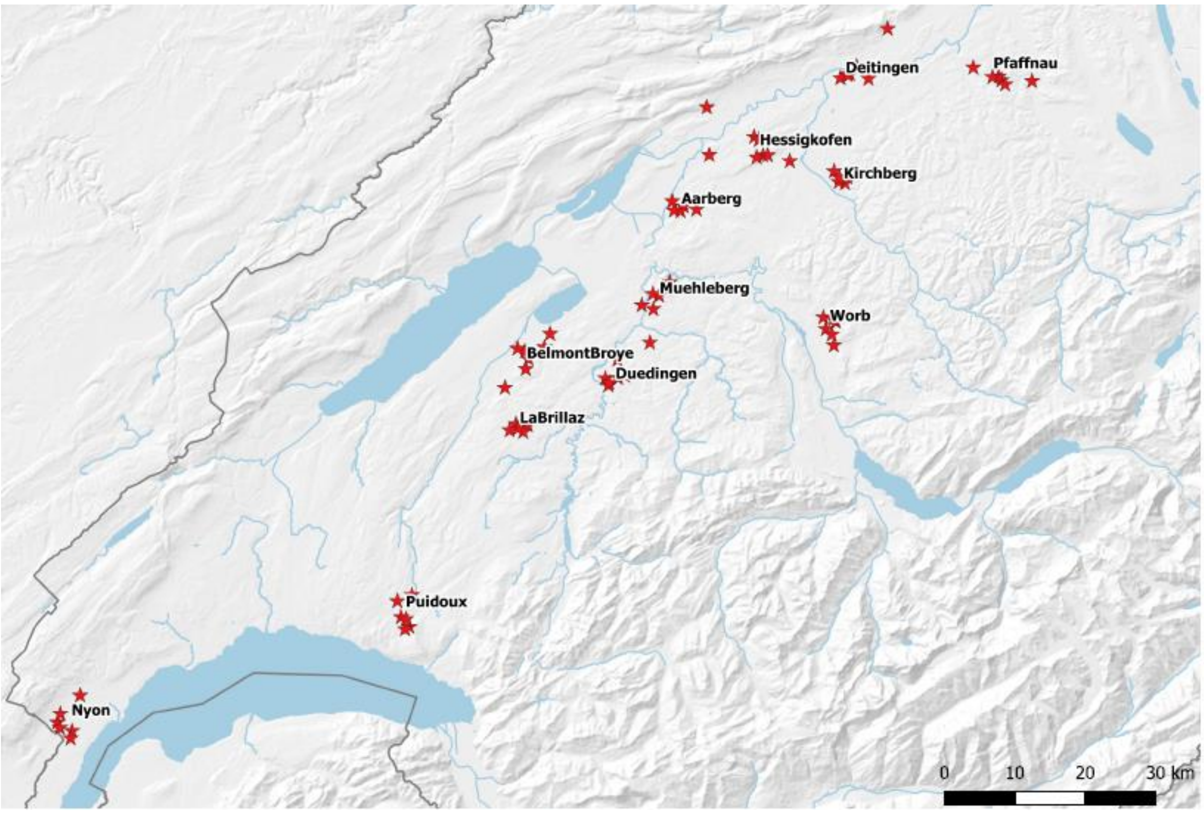


Figure 1. The 12 study regions each containing 6 meadows (indicated by the red stars); 1 QII meadow and 5 QI meadows. The distance between each region is at least 10 km and between meadows within a region 337 m.

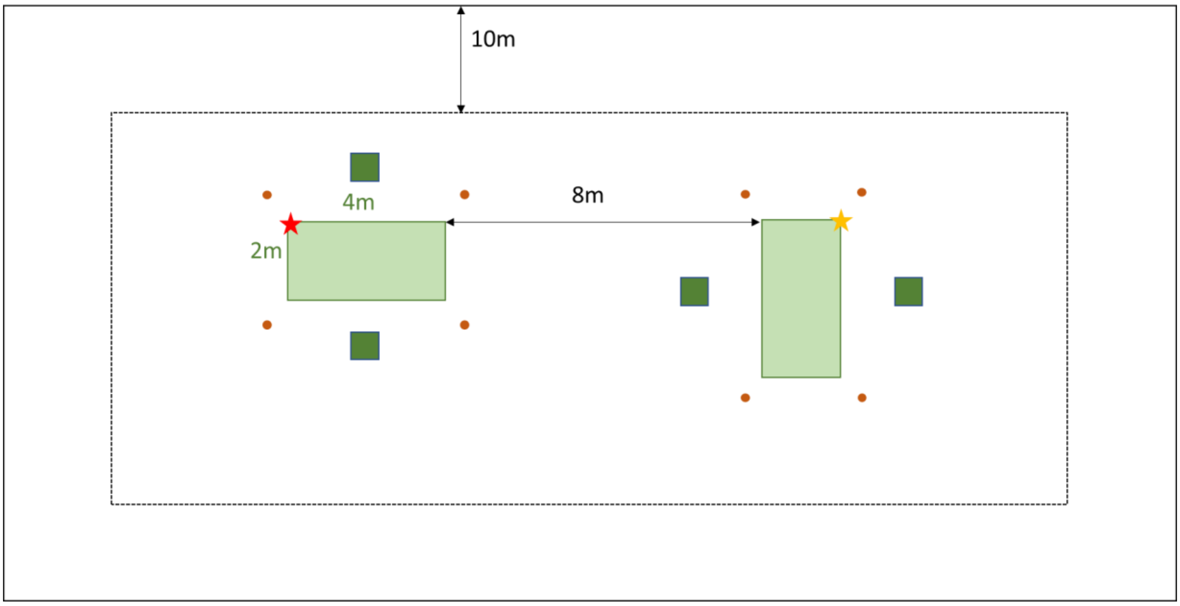
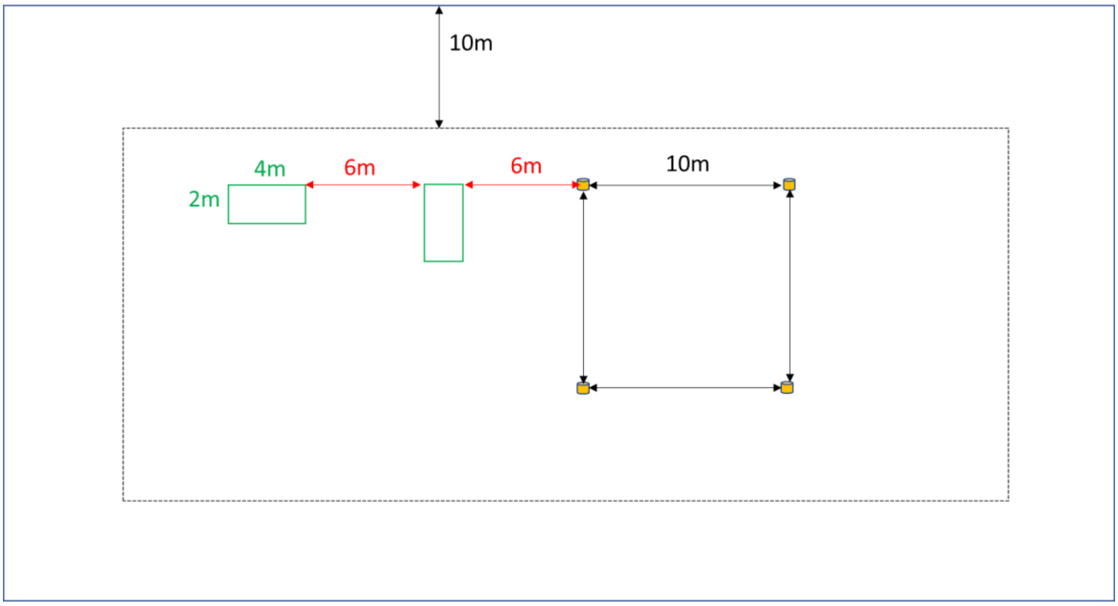


Figure 2. Vegetation relévés were carried out in two 2 x 4 m plots (indicated by the light green rectangles). Around the two vegetation plots the aboveground biomass was cut in 4 squares of 0.5 m^2 (dark green squares). The soil samples were taken at the edges of the vegetation plots using a soil core of 3.6 cm diameter and 10 cm depth (brown circles). A 10 m buffer zone was excluded from the sampling area to avoid edge effects.

(a)



(b)

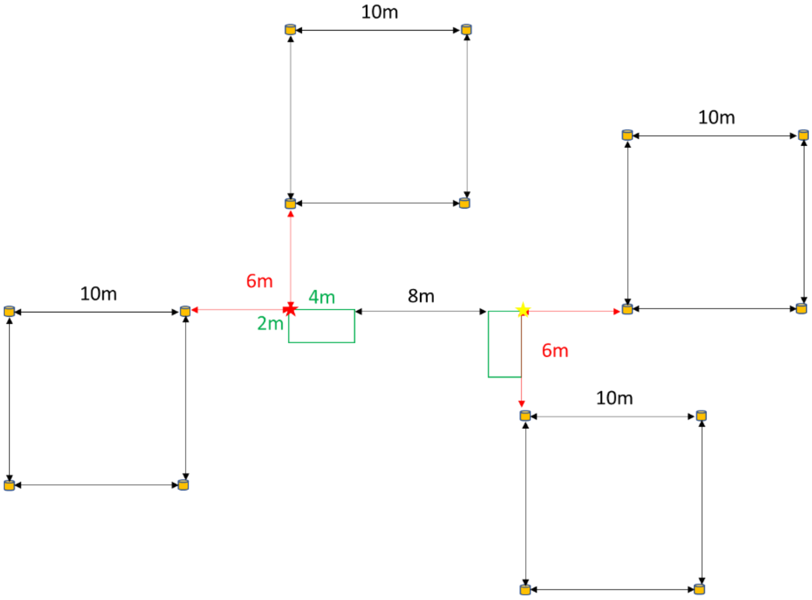
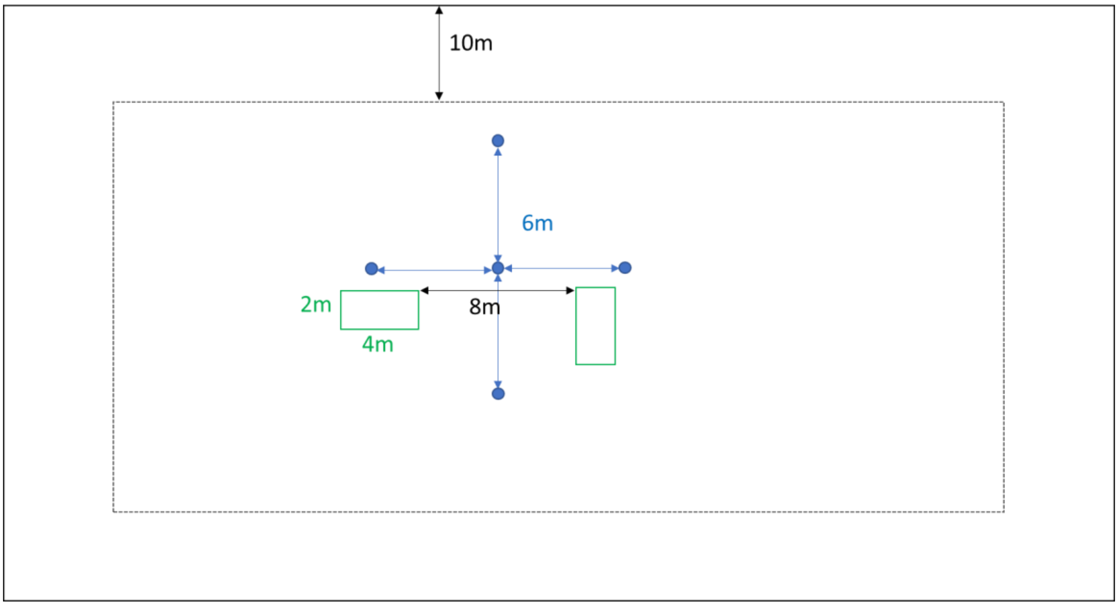


Figure 3. **(a)** The pitfalls were placed 6 m apart from the second vegetation plot in a 10 x 10 m square. If one of the pitfall traps ended up in the 10 m buffer zone of the meadow the pitfalls were rotated clockwise as shown in **(b)**.

(a)



(b)

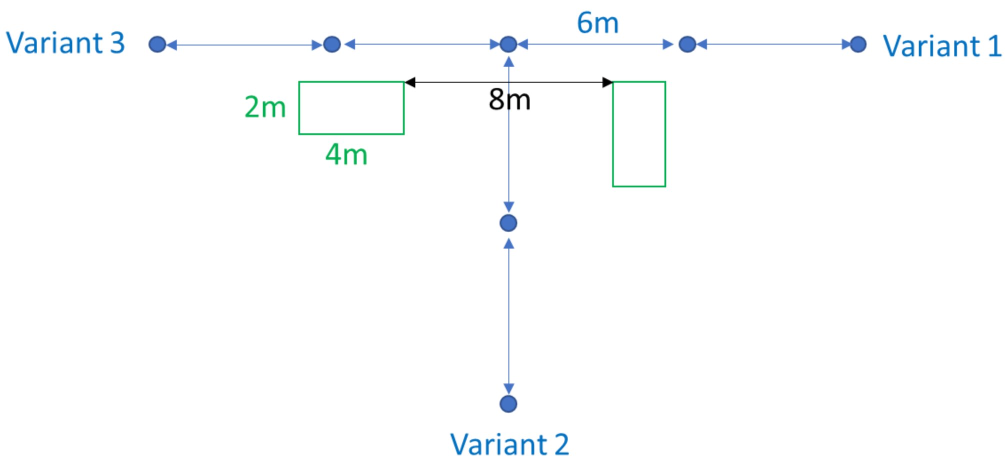


Figure 4. (a) For the suction sample an imaginary plus was placed in the middle of the two vegetation plots. At each end of a branch and the centre a circular area of 0.2 m^2 was sampled (indicated by the blue circles). If the top suction subsample ended up in the 10 m buffer zone of the meadow this sample location was rotated as shown in **(b)**.

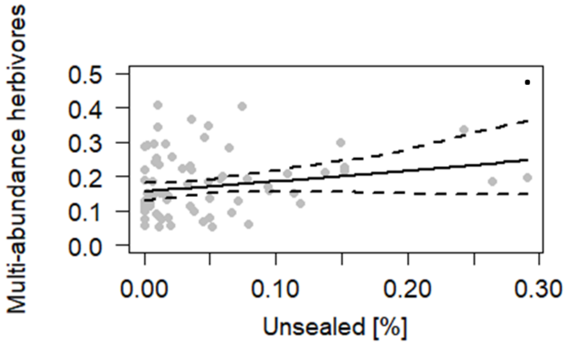


Figure 6. Multi–abundance of herbivores after the first mowing event in relation to the proportion of unsealed structures in the 50 m radius around the meadow. The predicted trend line from the GLMM is shown as the black line with its 95% confidence interval indicated by the black dashed line. See Table 3 for detailed test statistics. . 0.1 > *P* > 0.05.

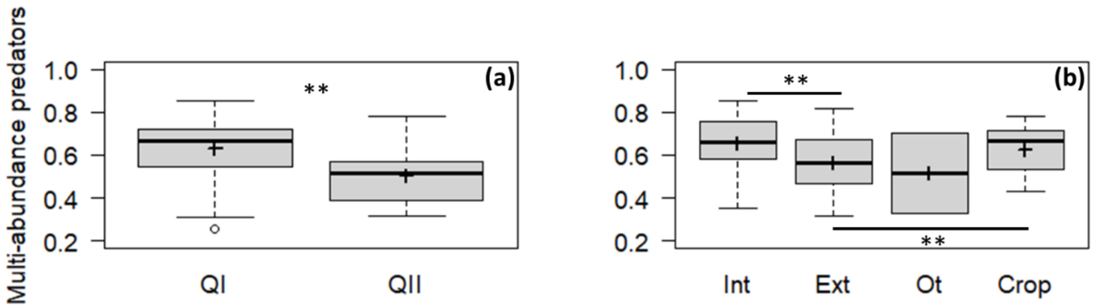


Figure 7. Multi–abundance of predators before the first mowing event in relation to the ecological quality of the meadow (a) or former management of the meadow (b). QI = meadows with less than 6 indicator species, QII = meadows with more than 6 indicator species, Int = Intensive management, Ext = Extensive management, Ot = Other, Crop = Cropland. The boxes represent the 75% and 25% quartile from the median indicated by the thick black line. Whiskers represent the minimum and maximum values. Outliers are indicated by the empty dots. The cross represents the mean. See table 3 for detailed test statistics. ** $P < 0.01$.

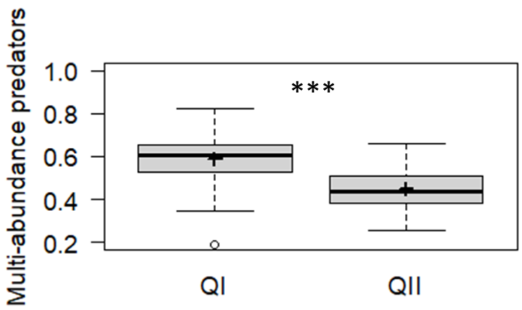


Figure 8. Multi–abundance of predators after the first mowing event in relations to the ecological quality of the meadow. Properties of the plots as in Figure 7. See table 3 for detailed test statistics. *** $P < 0.001$.

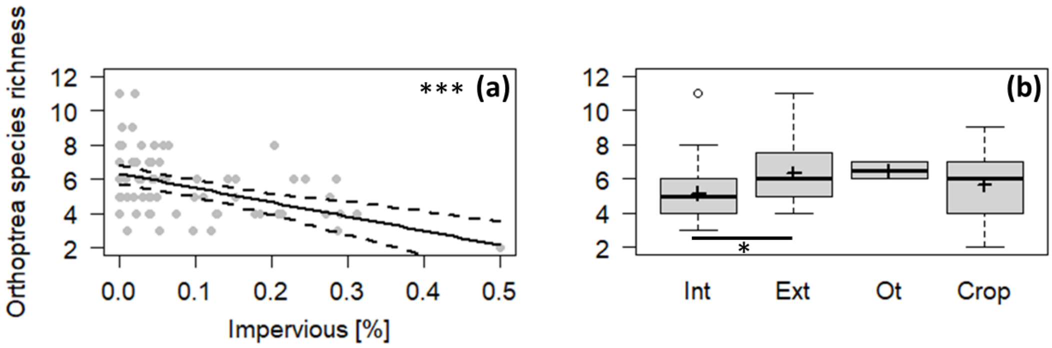
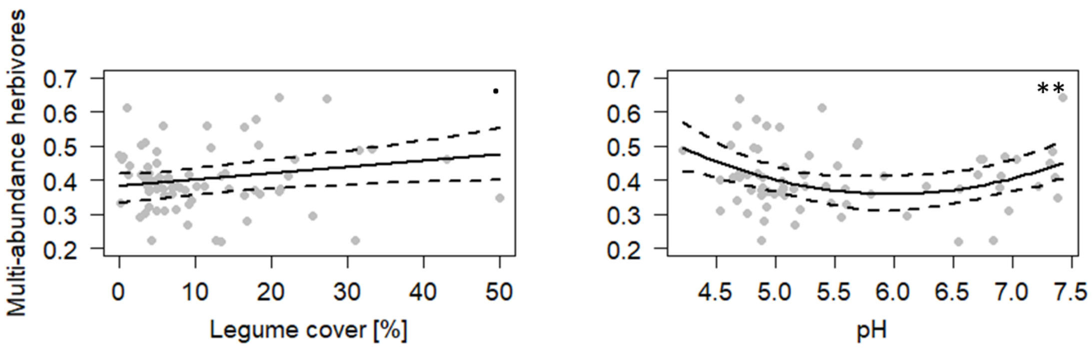


Figure 9. Species richness of orthopterans in relation to impervious structure in the surrounding (a) and the former management of the meadow (b). Properties of the plots as in Figure 7. See table 3 for detailed test statistics. * $P < 0.05$, *** $P < 0.001$.

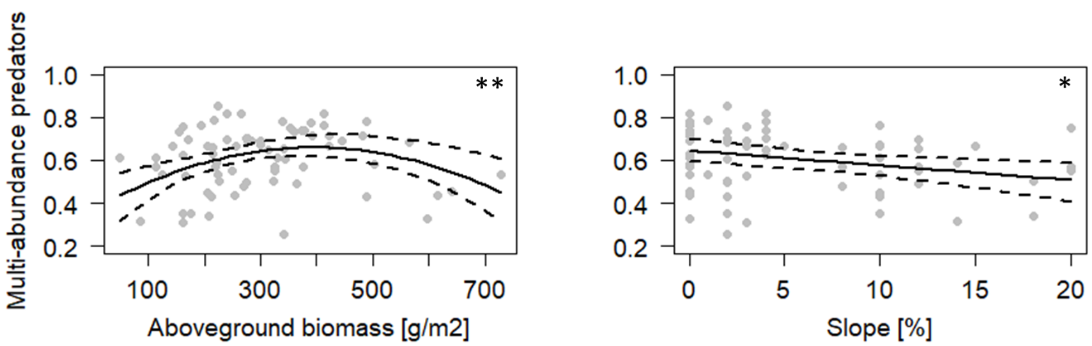
Appendix

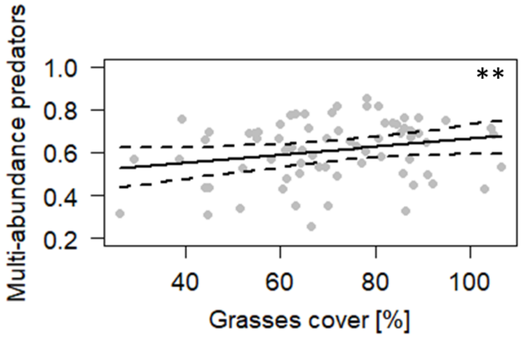
Appendix A1. Visual outputs of all the variables that were kept for the multivariate analysis (p > 0.1) for herbivores, predators and species richness of orthopterans. Boxplots boxes represent the 75% and 25% quartile from the median indicated by the thick black line. Whiskers represent the minimum and maximum values. Outliers are indicated by the empty dots. The cross represents the mean. In trend line graphs the predicted trend line from the GLMM is shown as the black line with its 95% confidence interval indicated by the black dashed line. For detailed test statistics see Table 3. . 0.1 > *P* > 0.05, * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

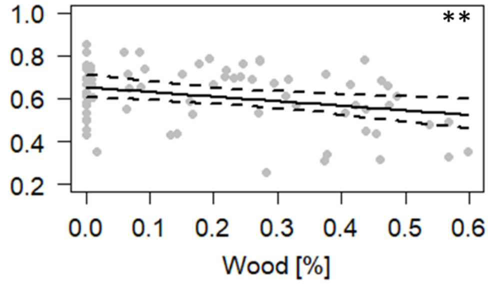
Herbivores before mowing

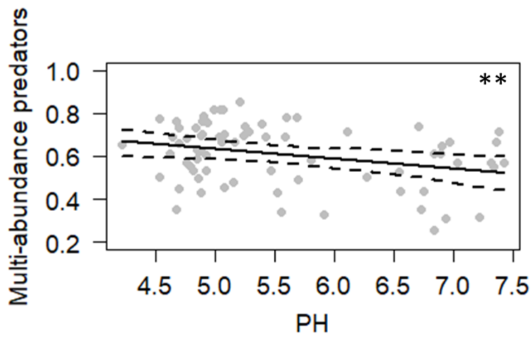


Predators before mowing

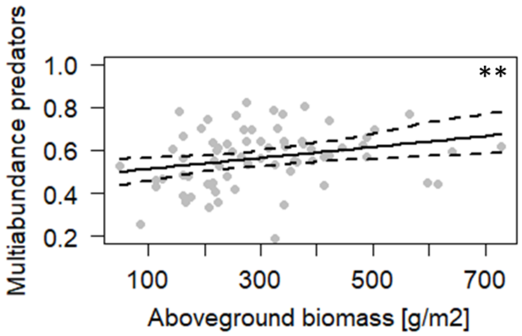


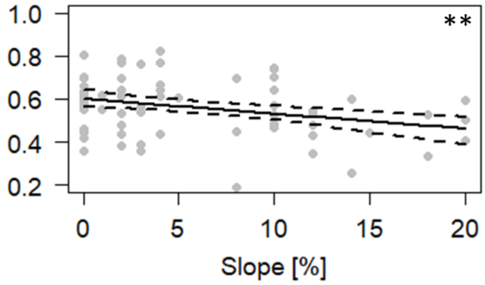


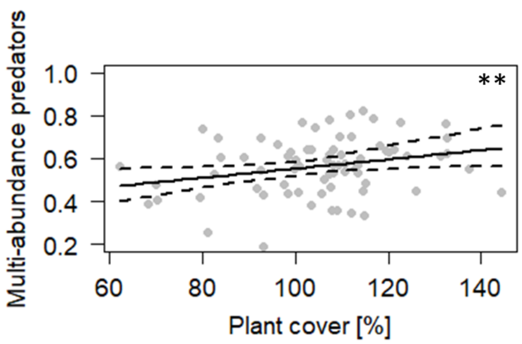


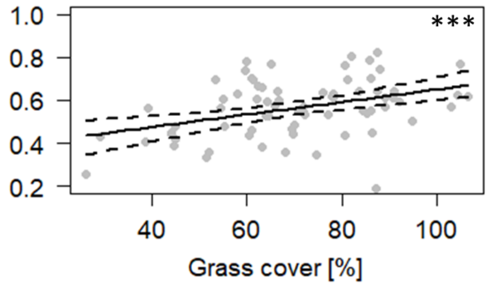


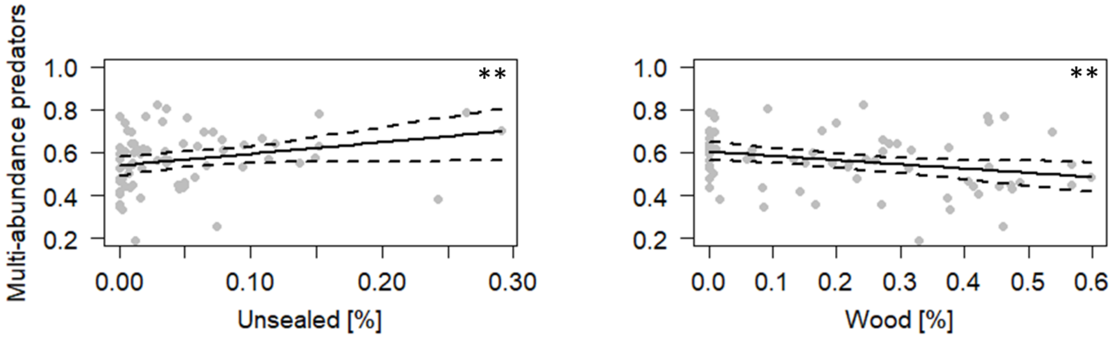
Predators after mowing

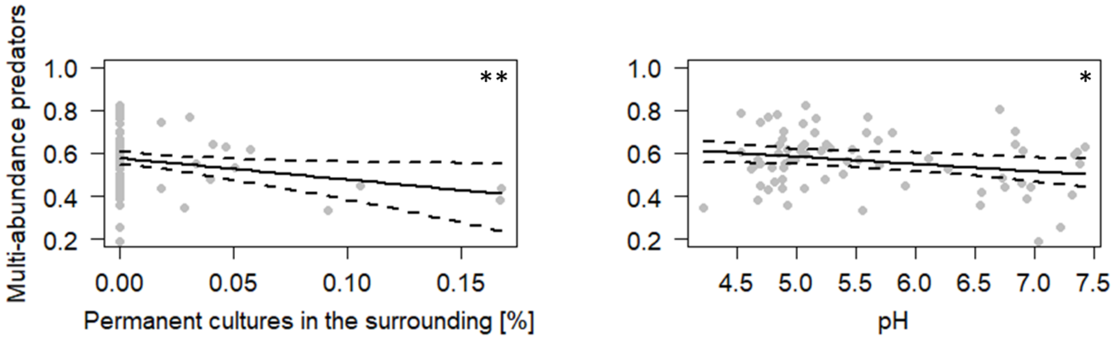




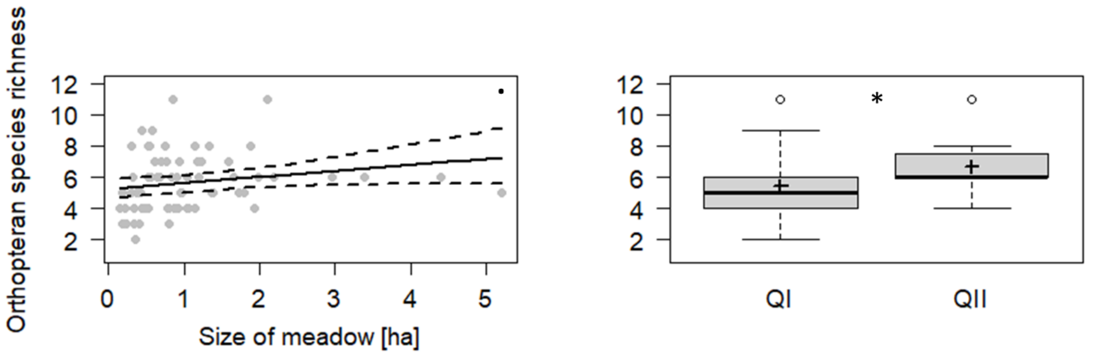


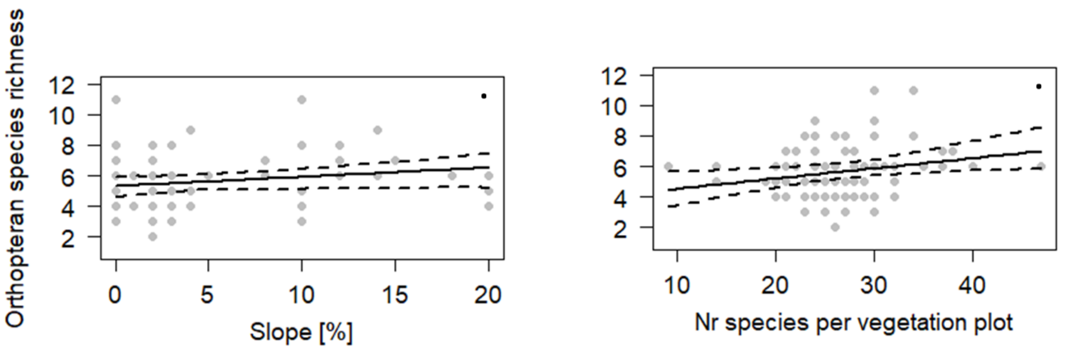


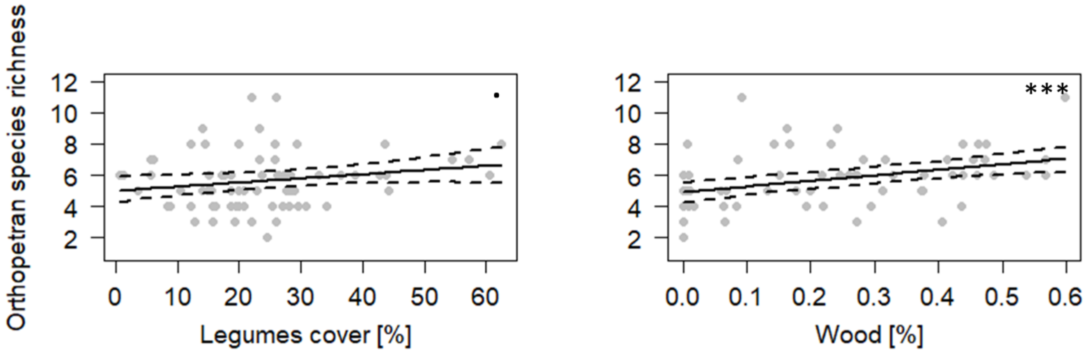


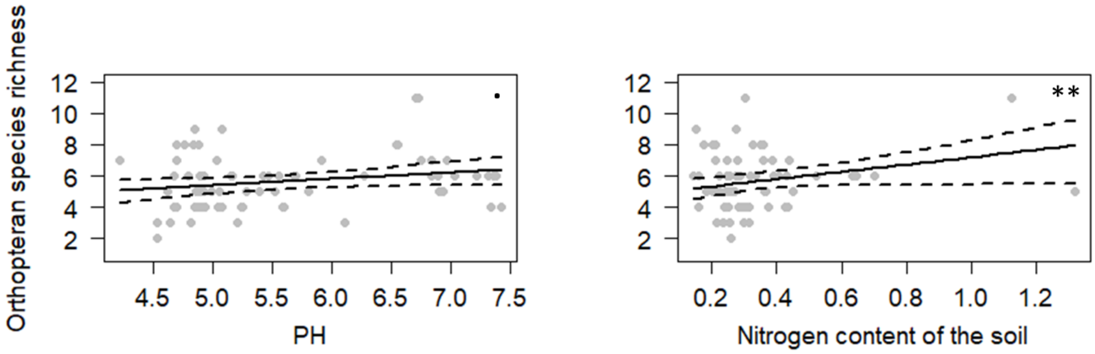


Orthopteran species richness






Orthopetran species richness
Legumes cover [%]
Wood [%]
***


Orthopteran species richness
PH
Nitrogen content of the soil
**