# Leaving uncut refuges within lowland extensively managed meadows secures wild bee species richness and diversity

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# Leaving uncut refuges within lowland extensively managed meadows secures wild bee species richness and diversity

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# Abstract

Wild bees and bumblebees play a key role in our ecosystems by ensuring the reproduction of many wild plants and agricultural crops. Pollination has become a threatened ecosystem service, however, mostly due to agricultural intensification. Agri-environment schemes (AES) were introduced in Europe in the late 1980s to counteract the loss of farmland biodiversity, and to secure the ecosystem services the latter provides for free. Yet, the effectiveness of these AES for promoting biodiversity in farmland has been at the best moderate. There is for instance no evidence that invertebrates could increase in abundance over the years after the implementation of AES, although it has been established that some AES can prompt their temporal concentration.

A previous study carried out in 2011 (Buri, Humbert & Arlettaz 2014 *PLoS ONE*) has shown that wild bees are promoted by spatio-temporal modification of mowing regimes within extensively managed AES meadows. Wild bee abundance and species richness significantly increased from one year to the next (cumulative effect) in meadows where uncut refuges (R-meadows) were implemented (i.e. at each cut 10-20% of a meadow area was left uncut while first mowing was performed not earlier than 15 June), in comparison to control meadows (C-meadows) which harboured no refuge but where first mowing was also not before 15 June. An immediate, i.e. within-season positive effect of delayed mowing (D-meadows, with first cut not before 15 July) was also observed, with 1.2 times more abundance in them than in C-meadows.

In 2014, the same meadows were resampled for wild bees to see whether the applied alternative mowing regimes might have even stronger cumulative effects after four years of experimental treatment. For that purpose, we compared the magnitude of the effects observed in 2011 and 2014. We also rebuilt a new single model combining the samples from 2011 and 2014 to test for effects based on a larger sample size.

A total of 981 wild bees were collected in 2014 (50% fewer than in 2011), which belonged to 64 species (62 in 2011). We found 28–30% fewer (abundance) wild bees in D-meadows than in C- and R-meadows, while abundance did not differ between C- and R-meadows. The difference between D- and C-meadows was mostly driven by lower abundances found in D-meadows in July, after C- but not D-meadows had been mown (thus a combination of cumulative and immediate negative effects). No effect on species richness was detected. When comparing the relative differences in means (effect size) between mowing regimes and sampling years, we found distinct responses of wild bee abundance to our experimental mowing regimes, which points to some year effect. Moreover, when combining the samples of the two years (2011 and 2014) in a single model, a significant positive effect of leaving an uncut refuge could be detected for wild bee species richness (14.1% more species) and diversity (plus 14.4%), which was not the case in Buri, Humbert & Arlettaz (2014).

As we could not evidence stronger effects of the experimental mowing regimes in 2014 compared to 2011, we conclude that no cumulative, carried-over effects exist beyond one year of modified mowing regimes. However, a slight effect on species richness and diversity was evidenced for the uncut refuge treatment when the samples of 2011 and 2014 were combined, showing that this measure is beneficial. These findings also highlight the importance of sampling bio-indicators over several years before concluding about the efficacy of management measures.

**Keywords**: Apoidea, agri-environment schemes, biodiversity, bowl traps, bumblebees, conservation, Hymenoptera, pan traps, pollinators, solitary bees

# 1. Introduction

Wild pollinators such as solitary bees and bumblebees play a key role in our ecosystems, where in addition to ensure most of wild plants reproduction (see Ollerton, Winfree & Tarrant 2011) they contribute significantly to the pollination of agricultural crops. Without them, many important crops would suffer from a considerable decrease in reproduction and fruit set (Kearns, Inouye & Waser 1998; Potts *et al.* 2010). Klein *et al.* (2007) found that 87 of the leading global food crops are dependent upon animal pollination, resulting in about 35% of the global food production. Unfortunately, this vital ecosystem service is nowadays threatened by the declines of honeybees, solitary- and bumblebee populations (Winfree *et al.* 2009; Potts *et al.* 2010). These declines probably started with the sharp intensification of agricultural practices in the 1960s (Carson 1962; Biesmeijer *et al.* 2006). Agricultural intensification within grassland consists mostly of increasing fertilizer inputs, higher grazing intensity or mowing frequency, and a general enlargement of field size, which altogether contributes to a radical landscape simplification and a subsequent loss of suitable habitat for wild bees (Tscharntke *et al.* 2005).

Agri-environment schemes (AES) were introduced in Europe in the late 1980s to reduce the loss of biodiversity along with natural habitats, and secure the ecosystem services provided by biodiversity (Albrecht *et al.* 2007; Scheper *et al.* 2013). Several studies have already established that AES are more efficient at preserving biodiversity when compared to conventional intensively managed meadows (Knop *et al.* 2006; Albrecht *et al.* 2007; Kohler *et al.* 2007; Scheper *et al.* 2013). However, the effectiveness of these AES has been debated, because the impacts on field invertebrates, including pollinators, are not as positive as expected (Kleijn *et al.* 2006; Scheper *et al.* 2013). More recently, studies have tried to determine the causes of this moderate success (see e.g. Concepcion *et al.* 2012; Littlewood, Stewart & Woodcock 2012). One cause might be the lack of landscape heterogeneity, since a great proportion of AES meadows are mown within a short time, depriving wild pollinators of nourishment in early summer. Benton, Vickery & Wilson (2003) and more recently Garibaldi *et al.* (2014) pointed out the importance of spatial and temporal variation within AES to enhance wild pollinators and the subsequent ecosystem services. In 2010, based on the knowledge from previous studies and with the aim to propose a concrete solution, our research group (the Division of Conservation Biology of the University of Bern) launched a research project across the Swiss lowland Plateau to investigate different potential solutions. In this project we experimentally modified the mowing regimes of extensively managed meadows that are currently under Swiss AES regulation, to increase spatial, temporal and hence ecological heterogeneity. The three different mowing regimes under investigation consisted of: 1) first cut not before 15 June as a standard regime for extensively managed meadows within Swiss AES; 2) first cut not before 15 July; 3) first cut not before 15 June with 10-20% of area left uncut serving as a refuge. In 2011, one year after the implementation of the alternative mowing regimes, results showed that wild bee abundance was significantly higher in meadows where uncut refuges were left the previous year than in meadows without refuges (Buri, Humbert & Arlettaz 2014). This indicates that spatio-temporal modification of mowing regimes within AES extensively managed hay meadows could therefore promote wild bee abundance (Buri, Humbert & Arlettaz 2014). However, Buri, Humbert & Arlettaz (2014) did not find a positive effect on the overall species richness. In 2014 we resampled the same meadows to determine if applied alternative mowing regimes have stronger effects on wild pollinator species richness and abundance after four years (in 2014) than after one year (in 2011) of implementation. A stronger effect would prove a long-term positive effect at the population level, meaning that the observed effect is more than merely a concentration effect (Kleijn *et al.* 2011; Wratten *et al.* 2012; Le Feon *et al.* 2013). A population-level response would reflect an effective local increase in bee population size due to the applied mowing regime and bring strong support to the respective management measure for the conservation of wild bees (Kleijn *et al.* 2011). We predicted that long-term effects of alternative mowing regimes would have a positive population-level effect on wild bees and bee diversity. To better understand responses within the bee community, we looked at different ecological traits of wild bee species.

Particular wild bee traits such as size, foraging and nesting behaviour can be differently affected by drivers of local bee extinctions (Cresswell, Osborne & Goulson 2000; Larsen, Williams & Kremen 2005; Murray, Kuhlmann & Potts 2009); it is therefore important to take into account the basic ecological traits of bees to predict their responses to the local management. Small sized species usually have small foraging ranges and are expected to require a more diverse local resources than species with greater body size and foraging range but similar needs (Cresswell, Osborne & Goulson 2000; Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007). Land management such as mowing also continuously alters potential nesting resources and sites for wild bees and thus may affect the local bee community composition (Potts *et al.* 2005; Winfree *et al.* 2009). Even if in the literature we find relatively little information on nesting requirements for many species (Murray, Kuhlmann & Potts 2009), it is expected that the alternative mowing regimes will offer better nesting conditions for ground-nesting species, i.e. less disturbance and nearer foraging resources, and thereby will support more wild bees and more species.

# 2. Material and Methods

## 2.1 Study areas

In 2010, 36 extensively managed hay meadows declared as biodiversity promoting areas (BPA) by the Swiss AES, were selected in 12 study areas (with three meadows per area) across the Swiss Plateau. The meadows were registered as BPA since latest 2004 (range: 1993-2004) and had a minimal area of at least 0.3 ha (range: 0.3-1.7 ha). The meadows were situated between 390 and 826 m in altitude. Areas were separated by ≥ 5 km and meadows were more than 440 m apart, but within a radius of 3.5 km.

## 2.2 Study design

The following mowing regimes were randomly assigned to the three meadows within each area: 1) control (abbreviated hereafter C-meadows) was managed according to the Swiss regulations for AES extensive hay meadows, i.e. the first cut is not before 15 June; 2) delayed (D-meadows) was the same as C-meadow, but the first possible cut was delayed by one month, i.e. not before 15 July; and 3) refuge (R-meadows) followed the same regulations as C-meadows, but at each cut 10-20% of the meadow area was left uncut.

Other management constraints included no fertilizer or pesticide application as well as grazing allowed only between 1 September and 30 November as specified in the present Swiss AES regulations (http://www.admin.ch/opc/fr/classified-compilation/20130216). Every year, each farmer was interviewed about mowing dates and other management practices using a questionnaire. In 2012 we lost a D-meadow.

## 2.3 Wild bees sampling

Wild bees were sampled using three plastic bowl traps (blue, white, yellow; 13 cm in diameter and 12.5 cm deep), fixed on a wooden pole just above the grass vegetation layer (Westphal *et al.* 2008; Vrdoljak & Samways 2012) and filled with a mix of water and liquid soap. Three such poles with traps were randomly placed in the field, forming an isosceles triangle (base: 14 m, side: 10 m) at least 10 m distant from meadow edges to reduce margin effects (Knop *et al.* 2006). We followed the same protocol as Buri, Humbert & Arlettaz (2014), i.e. using bowl traps and leaving them for one day during daylight (08:00–19:00) in the field, in order to compare our data with the previous study. Each meadow was sampled three times: the first time between 4–19 May (hereafter referred as “May” samples); the second time between 29 May and 9 June ("June" samples); and the third time between 26 June and 14 July ("July" samples). In this manner, first and second sampling sessions took place before any meadows were mown and the third sampling after C- and R-meadows were mown but still before D-meadows were first cut. Samplings were carried out on sunny, non-windy days with ambient temperature ≥ 15 °C. All three meadows within an area were sampled the same day. Samples of each trap were removed from the sampling fluid, stored in a plastic bag and frozen at -20 °C. Before being identified, defrosted samples were washed, pinned and dried (Droege *et al.* 2010). The specimens were identified according to identification keys for Central Europe (Amiet 1996a; Amiet, Müller & Neumeyer 1999b; Amiet *et al.* 2001b; Amiet *et al.* 2004b; Amiet *et al.* 2007b). All specimens were then given to an external specialist for confirmation of the identifications.

## 2.4 Data analysis

Data were analysed using generalized linear mixed models (GLMMs) with the *glmer* function of the *lme4* (Bates *et al.* 2014) package in the statistical software R v 3.03 (R Development Core Team 2012). The number of wild bee individuals and species for each meadow were derived from the sum of all three wooden poles, i.e. nine bowl traps. Wild bees consisted of solitary bees and bumblebees. In the GLMMs, mowing regimes were set as fixed effects and areas (our geographical replicates) as random effect. Response variables were wild bee abundance, species richness and species diversity (Shannon-Wiener index *H'*) per meadow. Wild bee abundance and species richness were analysed with a Poisson distribution, whereas species diversity fitted a normal distribution. To understand underlying patterns and be able to compare our 2014 samples with the results published in Buri, Humbert & Arlettaz (2014), May, June and July samples were first analysed pooled, then June and July samples only, then May, June and July separately.

The relative differences in wild bee abundance and species richness between the control and the alternative mowing regimes (D and R) were calculated to assess the effect size of the different mowing regimes. These effect sizes were then compared with the ones of Buri, Humbert & Arlettaz (2014).

Furthermore, to fully take advantage of resampling, data of the two sampling years (2011 and 2014) were included in the same model with year as a fixed factor. This way statistical power increases and effects that stay undetected when analysing a single year, may become apparent. Data were log-transformed to fit a normal distribution and response variables were wild bee abundance, species richness and diversity.

To better understand and predict wild bee responses to local management, we took into account the basic ecology of the bee species. Life-history traits of wild bees were extracted from Amiet *et al.* (1996-2007) and Westrich (1989) and each guild analysed separately. Wild bees were divided according to their foraging strategy (polylectic, oligolectic, cuckoo), nesting sites (ground, wood, rocks, generalist, cuckoo), and size (< 10 mm as "small" and ≥ 10 mm as "large"). Bumblebees (*Bombus* sp. and *Psithyrus* sp.) were also analysed separately. Furthermore, wild bees were classified according to the Swiss Red List (Duelli 1994; and see Appendix 2), with all threatened species grouped as "Red List species". For the analyses, sampling sessions within year were pooled and both years were included in the model. Guilds were analysed separately, with mowing regimes and year as fixed factors and sites as a random effect in the models. Response variables were wild bee abundance and species richness for the given guild.

## 3. Results

We collected a total of 981 wild bees (839 solitary bees and 142 bumblebees) and 369 honeybees (see Appendix 1). Cryptic, sibling species of wild bees were grouped within their respective taxonomic group: *Bombus terrestris* aggr. (*B. terrestris*, *Bombus lucorum*, *Bombus magnus*, *Bombus cryptarum*); *Halictus simplex* group (*H. simplex*, *Halictus eurygnathus*, *Halictus langobardicus*) and *Andrena ovatula* group (*A. ovatula*, *Andrena albofasciata*). Overall 64 wild bee species were identified (12 bumblebee and 52 solitary bee species, see full species list in Appendix 2). The most common species were *Halictus simplex* group (112 individuals), *Lasioglossum zonulum* (96), *Lasioglossum pauxillum* (87), *Lasioglossum calceatum* (87), *Lasioglossum morio* (72) and *Lasioglossum malachurum* (65). During the first sampling session (May) seven early-active species not occurring in 2011 nor later on in 2014 were found: *Andrena haemorrhoa*, *Andrena nitida*, a different unidentified *Andrena* species, *Chelostoma florisomne*, *Lasioglossum pallens*, *Nomada lathburiana* and *Sphecodes gibbus* (see Appendix 2). The cleptoparasite *Nomada lathburiana* parasitises nests of *Andrena cineraria*, the only host species present in our study, whereas *Sphecodes* species parasitises nests of *Halictus* and *Lasioglossum*.

## 3.1 2014 data; effects on wild bee abundance, species richness and diversity

In the analyses with all three sampling sessions pooled together, the mean abundance (± standard error, SE) of wild bees in D-meadows (21.82 ± 6.75) was significantly lower than in C-meadows (30.5 ± 7.67) and R-meadows (31.25 ± 6.49; see Fig. 1 and Table 1 for detailed model outputs). When including only June and July samples, the mean abundance ± SE of wild bees in D-meadows (18.27 ± 5.94) was significantly lower than in both R-meadows (24 ± 5.83) and C-meadows (23.83 ± 5.9). In May, wild bee abundance in D-meadows (3.55 ± 0.99) was significantly lower than in C-meadows (6.67 ± 2.14) and R-meadows (7.25 ± 1.16). In June, no difference in wild bee abundance among mowing regimes was detected. In July, the mean abundance of wild bees in D-meadows (10.36 ± 3.20) was significantly lower than in C-meadows (17.75 ± 4.53) and R-meadows (16.58 ± 5.49).

No difference in species richness among the different mowing regimes was found when data from all three sessions were pooled, and only June and July (see Fig. 2 and Table 1 for detailed model outputs). In May, species richness in R-meadows (4.92 ± 0.75) was significantly higher than in D-meadows (2.36 ± 0.51). In June and July no difference in species richness among the mowing regimes was detected. When all sessions were pooled, we found no differences in species diversity (Shannon-Wiener index) between the mowing regimes. In May, wild bee species in D-meadows were significantly less diverse than in R-meadows (Estimate = 0.741, t-value = 3.543, $P < 0.001$). As for species richness, in June and July no differences in diversity among the mowing regimes were found.

## 3.2 2011 and 2014 data; comparisons and effects on wild bee abundance, species richness, diversity and guilds

When including data of both sampling years in the models (i.e. five sampling sessions: two in 2011 and three in 2014) no significant effect of mowing regimes on wild bee abundance was found. In contrast, a positive effect of leaving a refuge on wild bee species richness and diversity was found (Fig. 3). More wild bee species were found in R-meadows (12.17 ± 0.76) than in both D-meadows (10.22 ± 1.03; Estimate = -0.276, SE = 0.10, $P = 0.009$) and C-meadows (10.67 ± 1.08; Estimate = -0.232, SE = 0.10, $P = 0.025$). Species diversity was higher in R-meadows ($H' = 2.08 \pm 0.07$) than in C-meadows ($H' = 1.82 \pm 0.10$; Estimate = -0.262, SE = 0.12, $P = 0.033$).

Comparing the effect sizes of the different mowing regimes (i.e. the relative effects of R vs. C, D vs. C and R vs. D) in 2014 with those from 2011 (see Buri, Humbert & Arlettaz 2014), revealed no statistically significant increases in effect sizes (Fig. 4 and 5). In June 2014 we collected 30.1% more wild bees in D- than in C-meadows, while in June 2011 (Buri, Humbert & Arlettaz 2014) we found 20.9% less wild bees in D- than C-meadows (Fig. 4). Furthermore, in June 2014 there were 22% more wild bees in R- than in C-meadows (in 2011: 100.1% more), and 6.2% less wild bees in R- than in D-meadows (in 2011: 153.4% more). When looking at the July samples, in 2014 we collected 41.6% less wild bees in D- than in C-meadows (in 2011: 21.4% more), 6.6% less in R- than in C-meadows (in 2011: 10.7% more), and 60% less in D- than in R-meadows (in 2011: 8.8% more; see Fig. 5).

Regarding the guild analyses, more threatened species were found in R-meadows (2.21 ± 0.32) than in C-meadows (1.45 ± 0.33; Estimate = 0.667, t-value = 2.23, *P* = 0.03, see Fig. 6). We did not find any other significant difference in abundance nor species richness of any other species guilds between control and alternative mowing regimes.

## 4. Discussion

In 2014 we resampled the same meadows as Buri, Humbert & Arlettaz (2014) sampled in 2011, to investigate whether there were stronger effects of alternative mowing regimes after four years of implementation than after one year. Results show no stronger effects in 2014 compared to 2011, i.e. no specific population-level responses were detected. In fact, a negative effect of D-meadows and no effect of R-meadows were found in 2014. However, when data from both years (2011 and 2014) was included in the analyses, we revealed a positive effect of leaving an uncut refuge for wild bee species richness and diversity. Compared to control meadows (C-meadows), wild bee species richness and diversity were both 14% higher in meadows where an uncut refuge was maintained during mowing operations (R-meadows).

### 4.1 2014; effects on wild bee abundance, species richness and diversity

Overall, in 2014 we found fewer bees in D-meadows than in C-meadows. A potential biological explanation could be that delaying mowing favours grass reproduction, which may on a long-term outcompete smaller forbs and legumes and have thus a negative impact on floral resources (Smith & Jones 1991; but see Woodcock *et al.* 2014). Floral resources are strongly correlated with wild bee diversity, and a loss of floral diversity can drive wild bee diversity loss, and vice versa (Biesmeijer *et al.* 2006; Potts *et al.* 2009; Garibaldi *et al.* 2014). However, we consider this potential biological explanation unlikely because we could neither detect a relationship between bee abundance and plant species richness nor between bee abundance and coverage of plant functional groups (i.e. grasses, forbs or legumes; results not shown). We predicted that there would be a higher abundance of wild bees in D-meadows during the July sampling session, i.e. after C-meadows were mown. Surprisingly, in the July session we sampled more bees in C-meadows. A reason for this result might be that bees searching for resources do not have to fly as far as when forbs are scarce (Baum & Wallen 2011). Thus, pan traps are not as attractive to bees when there is ample forage available (Morandin & Kremen 2013), while bees coming across C-meadows are more likely to encounter pan traps than the ones flying within R- and D-meadows, where floral resources would be more abundant (Baum & Wallen 2011). This can bias results toward lower sampling efficiency and detectability in D-meadows compared to C- and R-meadows.

The 2014 data was impoverished in terms of statistical power due to the lower bee abundance compared to 2011. The low sample size collected in 2014 (50% less than in 2011) was probably due to adverse weather conditions during the previous overwintering period (Frund, Zieger & Tscharntke 2013) and in spring/summer 2014 (http://www.meteoswiss.admin.ch/content/dam/meteoswiss/de/Ungebundene-Seiten/Publikationen/Klimabulletin/doc/klimabulletin_jahr_def_d.pdf). Moreover, it is widely known that bee populations can display considerable spatial-temporal variation in abundance and composition from one year to another (Tylianakis, Klein & Tscharntke 2005; Petanidou *et al.* 2008; Potts *et al.* 2009). Nevertheless we could collect and identify more than 60 wild bee species, i.e. as in 2011. This fact highlights a temporary low abundance, but a stable species richness, which makes an unbalanced sampling effort among the two years rather unlikely. However, the low sample size and the high variation within C- and D-meadows did not allow us to detect any significant difference among regimes in wild bee species richness nor diversity.

## 4.2 2011 and 2014; comparisons and effects on wild bee abundance, species richness, diversity and guilds

Wild bee populations showed distinct responses to our experimental mowing regimes between sampling years. This prevented us from detecting a significant difference in wild bee abundance between mowing regimes.

In 2011 and 2014, the mean number of wild bee species sampled in R-meadows was higher compared to C-meadows, though the difference between the means was not statistically significant when years were analysed independently. However, when both sampling years (2011 and 2014) were included in the model, a positive effect of leaving a refuge on wild bee species richness (14.1% more) and diversity (14.4% more) was detected. Leaving a refuge can influence wild bees in at least three different ways: first, it reduces the overall disturbance during the mowing time; second, it allows an extended window for some forbs to reproduce and thereby offers a broad spectrum of foraging resources (see Menz *et al.* 2011), and third, it provides continuity of foraging resources throughout the season, which is essential to support many bee species and may allows rare and sensitive species to better cope when nearby areas that are mown (Garibaldi *et al.* 2014; Woodcock *et al.* 2014). Indeed, we detected a positive effect of leaving a refuge on wild bee species (Fig. 3), and on rare wild bee species (Fig. 6).

# 5. Conclusions and management recommendations

Significant positive effects of both alternative mowing regimes on wild bee abundances were detected in 2011 (higher abundances in D- and R-meadows compared to C-meadows), though a negative effect of D-meadows and no effect of R-meadows were found in 2014. These distinct responses of wild bee populations to our experimental mowing regimes emphasize some year effects; i.e. probable mowing regimes effects interacting with yearly climatic conditions (Potts *et al.* 2009). Regarding species richness responses, no effects were detected in 2011 or 2014 when sampling years were analysed independently, however, when analysed together, a positive effect of leaving a refuge (R-meadows) on species richness was found. Similarly, a higher bee diversity (Shannon index) was found in R- compared to C-meadows when 2011 and 2014 data were analysed together. Overall, this study enhances the importance of sampling bio-indicator groups over several years.

Based on the results of the analyses including both sampling years (2011 and 2014), we can refine the management recommendations stated in Buri, Humbert & Arlettaz (2014) as follows: within extensively managed meadows we recommend leaving an uncut refuge of 10-20% of the area each time the meadows are mown. As shown in this study, wild pollinator species can be secured and even enhanced with this specific well-targeted agri-environment measure. Concerning delaying the first possible cut to 15 July (D-meadows), current evidence is not sufficient to recommend or not-recommend this measure, because our results show both positive and negative effects of this measure on bee abundance (depending on sampling year), and no effect on species richness. Finally we could not find long-term benefits at the population-level. Further studies are needed, especially those collecting additional information about foraging resources such as nectar, pollen and nesting resources (see Cresswell, Osborne & Goulson 2000; Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007; Murray, Kuhlmann & Potts 2009).

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**Table 1.** Summary outputs of the GLMMs testing the effects of the mowing regimes on wild bee abundance and species richness in 2014. Associated sampling session(s) are in brackets. Abbreviations are: (C) C-meadows: control meadows with first cut not before 15 June; (D) D-meadows: mowing delayed by a month, i.e. after 15 July; (R) R-meadows: as C-meadows, but uncut refuge left over 10-20% of meadow area.

| | **Wild bee abundance** | | | **Wild bee species richness** | | |
|---|---|---|---|---|---|---|
| | Estimate | SE | *P* (>\|z\|) | Estimate | SE | *P* (>\|z\|) |
| **Model 1 (all sessions)** | | | | | | |
| D vs. C | -0.331 | 0.08 | < **0.001** | -0.052 | 0.13 | 0.691 |
| R vs. C | 0.024 | 0.07 | 0.740 | 0.146 | 0.12 | 0.226 |
| D vs. R | -0.355 | 0.08 | < **0.001** | -0.198 | 0.13 | 0.117 |
| **Model 2 (June & July)** | | | | | | |
| D vs. C | -0.255 | 0.09 | **0.006** | 0.044 | 0.14 | 0.757 |
| R vs. C | 0.007 | 0.08 | 0.933 | 0.067 | 0.14 | 0.627 |
| D vs. R | -0.262 | 0.09 | **0.005** | -0.023 | 0.14 | 0.870 |
| **Model 3 (May)** | | | | | | |
| D vs. C | -0.647 | 0.19 | < **0.001** | -0.479 | 0.25 | 0.051 |
| R vs. C | 0.084 | 0.15 | 0.585 | 0.249 | 0.20 | 0.204 |
| D vs. R | -0.731 | 0.19 | < **0.001** | -0.728 | 0.24 | **0.002** |
| **Model 4 (June)** | | | | | | |
| D vs. C | 0.190 | 0.16 | 0.227 | 0.915 | 1.06 | 0.398 |
| R vs. C | 0.198 | 0.16 | 0.205 | 0.833 | 1.03 | 0.428 |
| D vs. R | -0.008 | 0.15 | 0.957 | 0.082 | 1.06 | 0.939 |
| **Model 5 (July)** | | | | | | |
| D vs. C | -0.488 | 0.12 | < **0.001** | 0.118 | 0.18 | 0.524 |
| R vs. C | -0.068 | 0.10 | 0.488 | 0.212 | 0.18 | 0.246 |
| D vs. R | -0.420 | 0.12 | < **0.001** | -0.093 | 0.18 | 0.614 |

# Figure legends

**Fig. 1**. Wild bee abundance in 2014. The different panels show total abundance (all sampling sessions pooled, i.e. May, June and July), in June and July only, in May only, in June only and in July only, according to mowing regimes. Mowing regime abbreviations are: (C) C-meadows: control meadows with first cut not before 15 June; (D) D-meadows: mowing delayed by a month, i.e. after 15 July; (R) R-meadows: as C-meadows, but with an uncut refuge left over 10-20% of the meadow area. Bold transversal bars represent medians; + indicates the mean; box boundaries are the first and last quartiles; whiskers the inter-quartile distance multiplied by 1.5; open dots the outliers. Different letters indicate significant differences among regimes at an alpha rejection level of 0.05; “NS” indicates no significant difference.

**Fig. 2**. Wild bee species richness in 2014. The different graphs show total species richness (all sampling sessions pooled, i.e. May, June and July), June and July only, May only, June only and July only, according to mowing regimes. For abbreviations, see legend of Fig. 1.

**Fig. 3**. Wild bee abundance, species richness and diversity (Shannon-Wiener Index) when both sampling years (2011 and 2014) were included in the model, plotted according to mowing regimes. For abbreviations, see legend of Fig. 1.

**Fig. 4**. Effect size and relative differences (%) between C-meadows and alternative mowing regimes with samples of June 2011 and 2014 analysed separately. Plotted is the mean ± standard error of individuals sampled in June according to mowing regimes. Mowing regimes are: Control, with first cut not before 15 June; Delayed, with the mowing delayed by one month, i.e. after 15 July; Refuge, as control meadows, but with an uncut refuge left over 10-20% of the meadow area.

**Fig. 5**. Effect size and relative differences between C-meadows and alternative mowing regimes with samples of July 2011 and 2014 analysed separately. Plotted is the mean ± standard error of individuals sampled in July according to mowing regimes. For abbreviations, see legend of Fig. 4.

**Fig. 6**. Abundance and species richness of threatened wild bees when both sampling years (2011 and 2014) were included in the model, plotted according to mowing regimes. Mowing regimes are: Control, with first cut not before 15 June; Delayed, with the mowing delayed by a month, i.e. after 15 July; Refuge, as control meadows, but with an uncut refuge left over 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; open dots the outliers. Different letters indicate significant differences among regimes at an alpha rejection level of 0.05.

**Fig. 1**

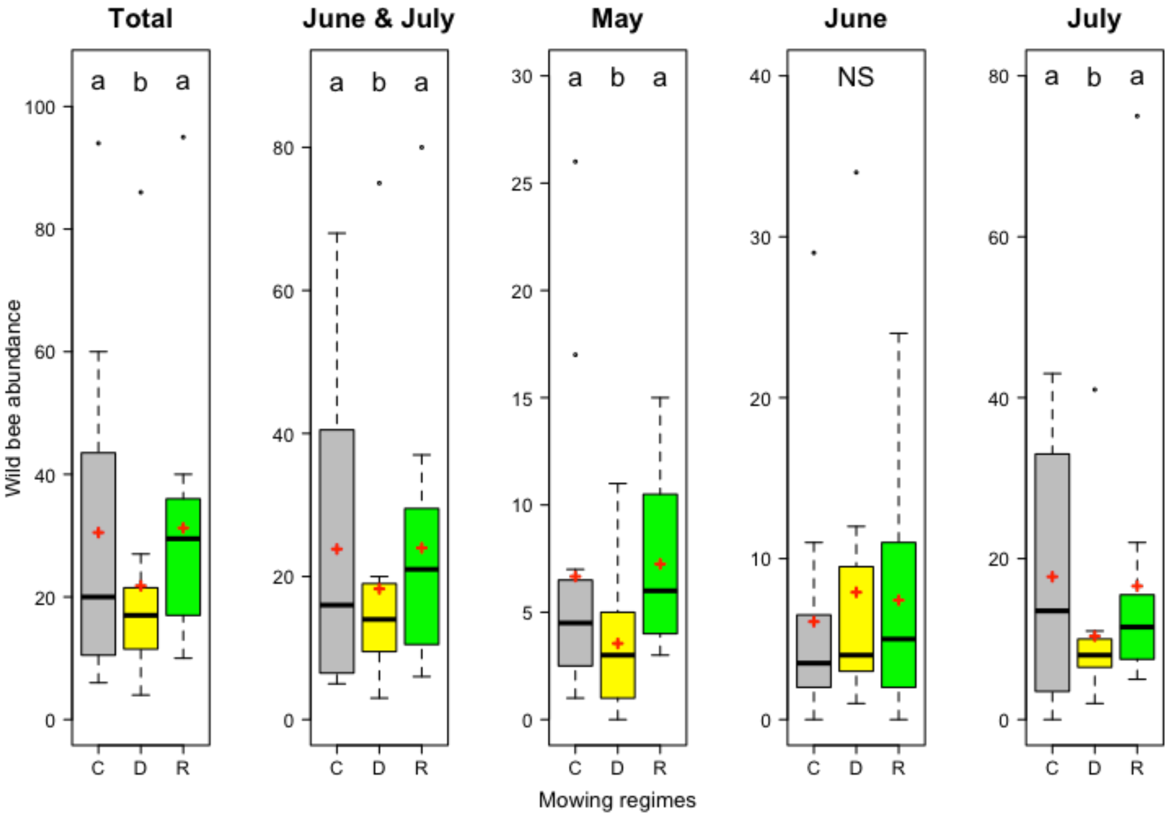

Total
June & July
May
June
July
Wild bee abundance
a b a
a b a
a b a
NS
a b a
0
20
40
60
80
100
0
20
40
60
80
0
5
10
15
20
25
30
0
10
20
30
40
0
20
40
60
80
C D R
C D R
C D R
C D R
C D R
Mowing regimes

**Fig. 2**

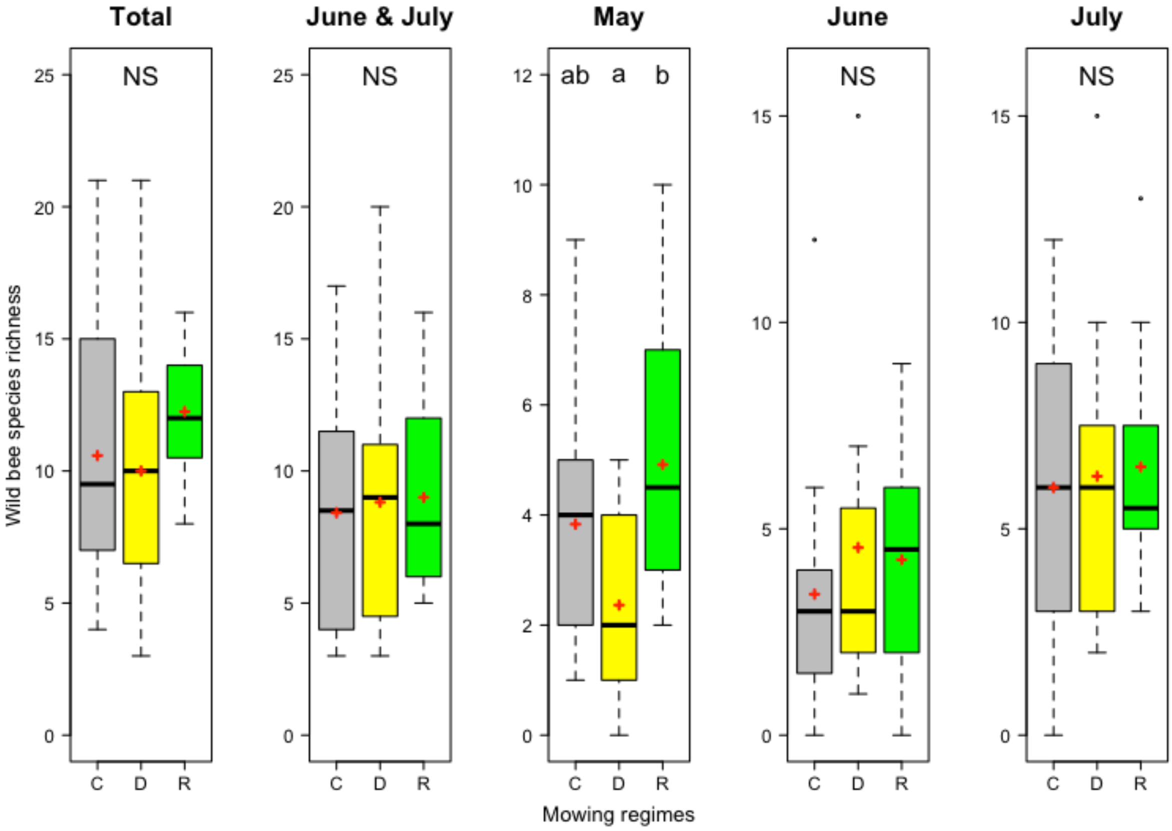

Total
June & July
May
June
July
NS
NS
ab
a
b
NS
NS
Wild bee species richness
0
5
10
15
20
25
0
2
4
6
8
10
12
C
D
R
Mowing regimes

**Fig. 3**

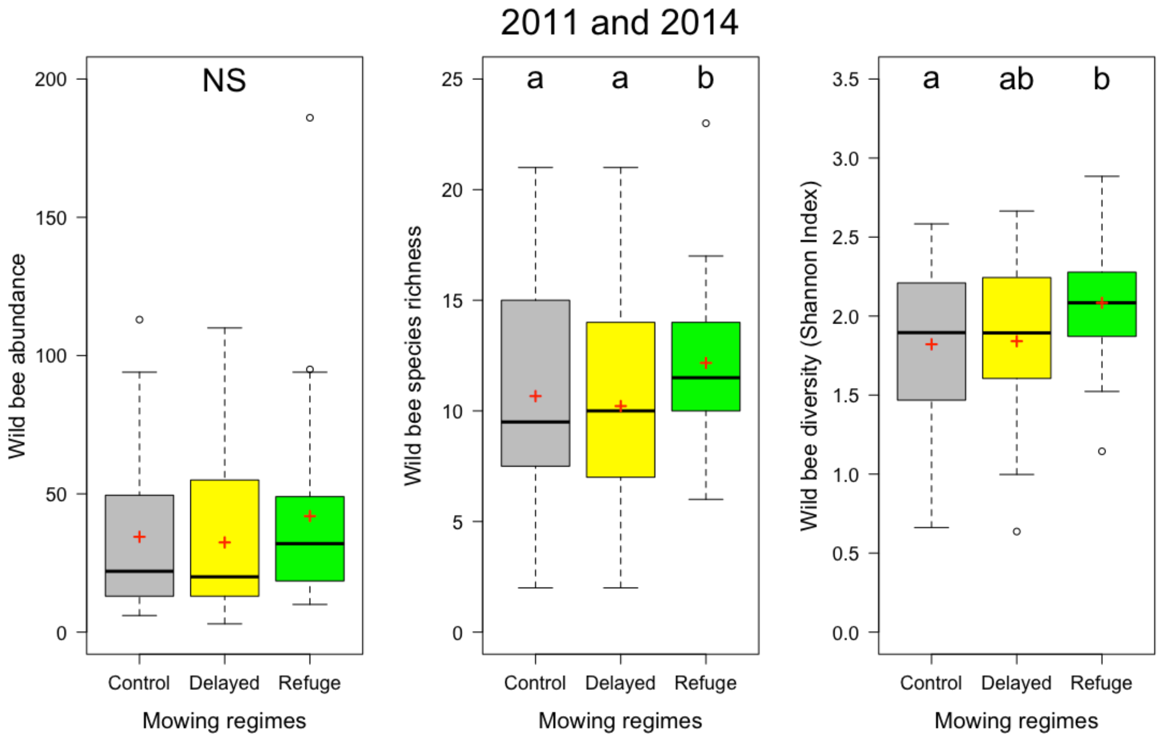

2011 and 2014
NS
a
a
b
a
ab
b
Wild bee abundance
0
50
100
150
200
Wild bee species richness
0
5
10
15
20
25
Wild bee diversity (Shannon Index)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Control
Delayed
Refuge
Control
Delayed
Refuge
Control
Delayed
Refuge
Mowing regimes
Mowing regimes
Mowing regimes

Fig. 4

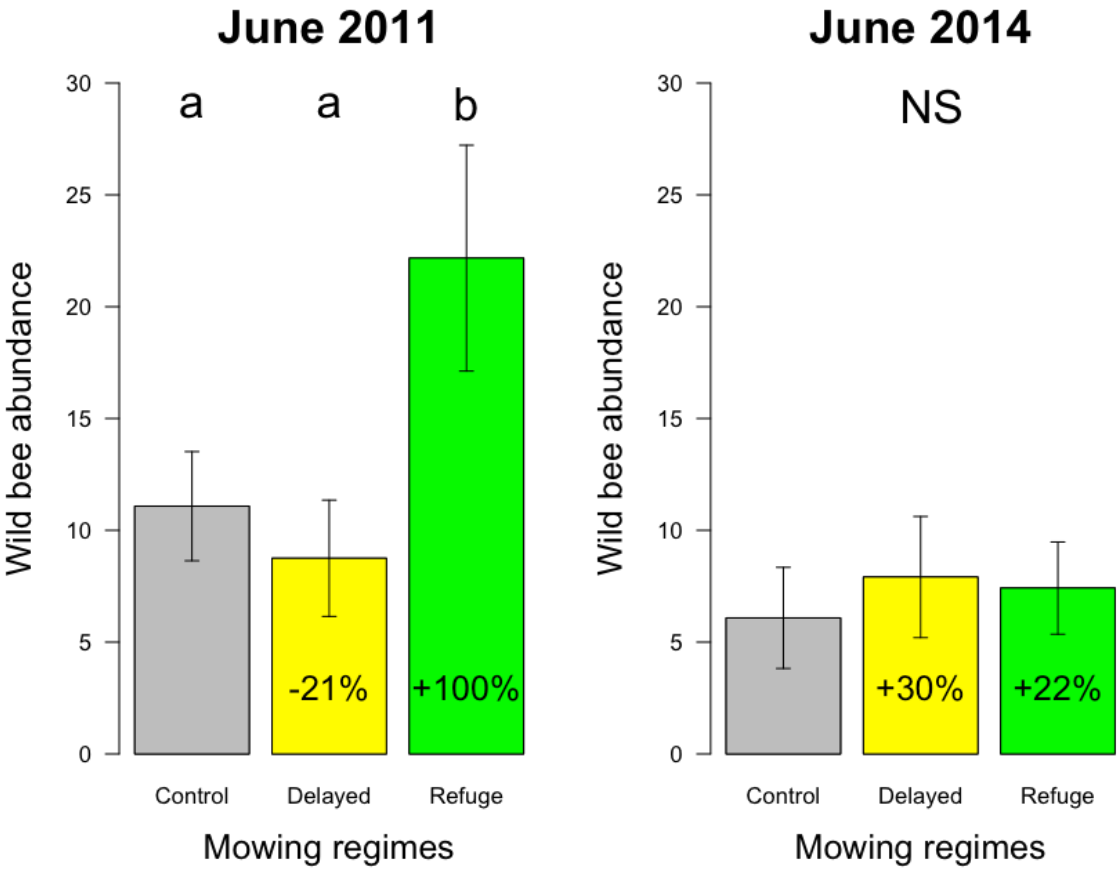

June 2011
June 2014
30
25
20
15
10
5
0
a
a
b
NS
Wild bee abundance
-21%
+100%
+30%
+22%
Control
Delayed
Refuge
Mowing regimes

Fig. 5

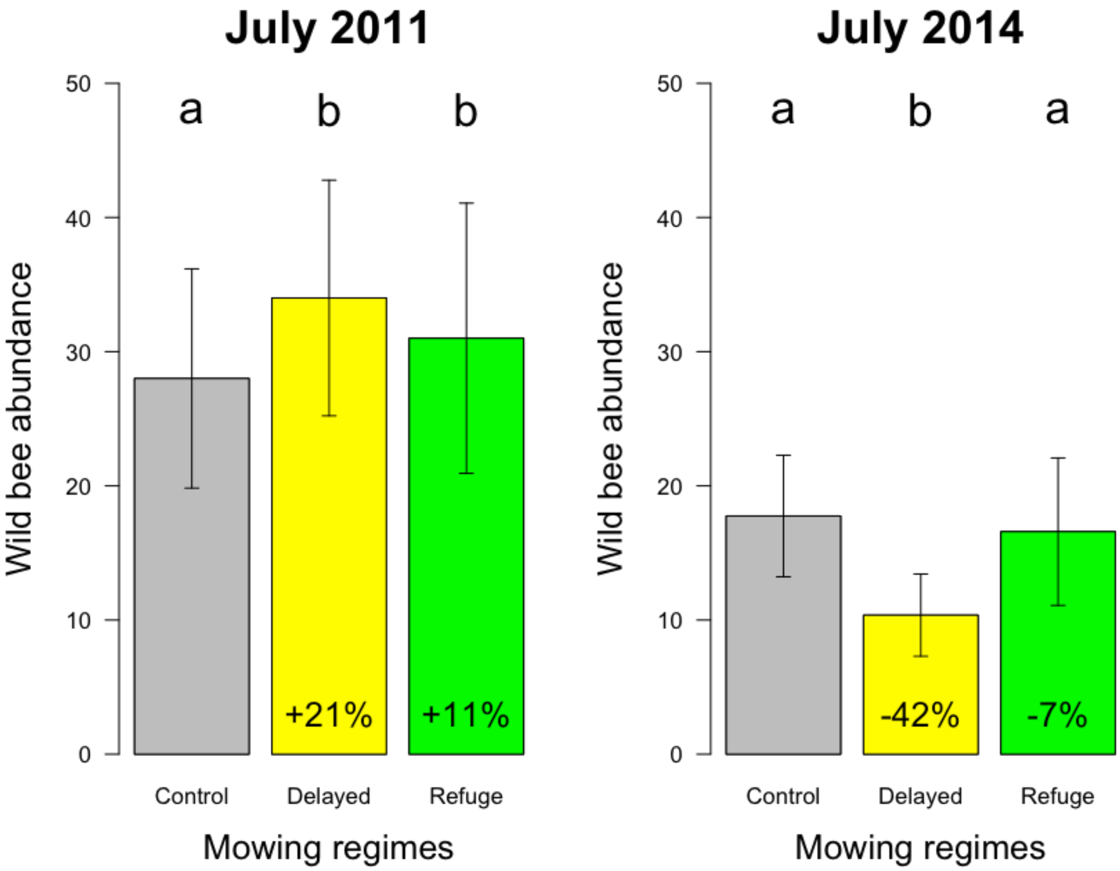
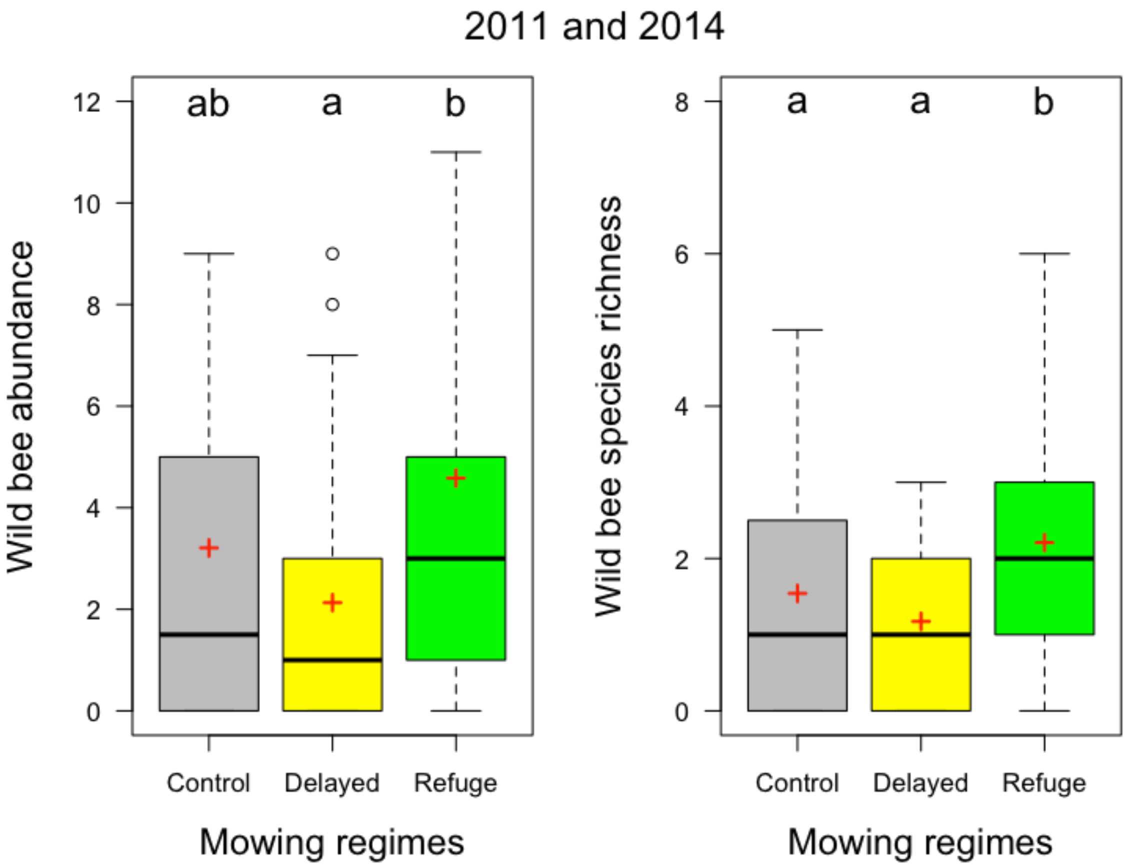

July 2011
July 2014
Wild bee abundance
0
10
20
30
40
50
a
b
b
a
b
a
+21%
+11%
-42%
-7%
Control
Delayed
Refuge
Mowing regimes

**Fig. 6**


2011 and 2014
Wild bee abundance
0
2
4
6
8
10
12
ab
a
b
Control
Delayed
Refuge
Mowing regimes
Wild bee species richness
0
2
4
6
8
a
a
b
Control
Delayed
Refuge
Mowing regimes

# Erklärung

gemäss Art. 28 Abs. 2 RSL 05

| | |
|---|---|
| Name/Vorname: | Unternährer Debora |
| Matrikelnummer: | 10-100-030 |
| Studiengang: | Biologie |
| | Bachelor ☐ Master ☒ Dissertation ☐ |
| Titel der Arbeit: | Leaving uncut refuges within lowland extensively managed meadows secures wild bee species richness and diversity |
| LeiterIn der Arbeit: | Dr Jean-Yves Humbert, 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 Gesetztes 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.

Bern, 12.08.2015
Ort/Datum

DUnternaehrer
Unterschrift