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Mowing meadows without conditioner and the availability of bee-friendly habitats synergistically benefit wild bees in agricultural landscapes

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ABSTRACT

Healthy populations of wild bees are essential for the pollination of wild plants and many crops. However, wild bees are under pressure, in particular due to the intensification of agriculture. To counteract negative effects, mitigation measures are being implemented via agri-environment schemes. While agricultural meadows offer valuable floral food resources for bees, the technique and timing of their harvesting are likely critical aspects determining their value for pollinators. Early mowing before or during peak flowering and the use of conditioners, devices commonly used to accelerate grass drying and increase feed quality, could negatively affect bees. Over a period of six years, we sampled wild bees in 74 landscapes in western Switzerland differing in conditioner use in ley- and permanent meadows as well as delayed mowing of ley meadows to investigate the individual and combined impacts of these measures on wild bees. We found that refraining from conditioner use in extensively managed permanent meadows in combination with increased proportions of bee-friendly habitats synergistically benefitted overall wild bee abundance and richness as well as bumblebee abundance. Moreover, to benefit bumblebees, the share of no conditioner use needed to be high in both, leys and intensively managed permanent meadows. There was, however, substantial variation of the effects of the measures between years, emphasizing the need for long-term monitoring of such measures to better understand their effectiveness.

1. Introduction

Wild bees play a vital role as pollinators of wild flowering plants and crops (Ollerton et al., 2011; Garibaldi et al., 2013; IPBES et al., 2016). However, they are jeopardized by multiple interacting pressures in intensively managed agroecosystems, including land-use intensification and the associated loss, degradation and fragmentation of habitats offering suitable floral food resources and nesting sites (Vanbergen and the Insect Pollinators Initiative, 2013; Goulson et al., 2015; Ekroos et al., 2020). As a consequence, a decline in the abundance and diversity of wild bees has been reported in several regions of the world in recent decades (e.g., Biesmeijer et al., 2006; Cameron et al., 2011; IPBES et al., 2016). Concerns over pollinator losses have triggered incentives to promote their presence in agroecosystems, for example through agri-environment schemes and other conservation measures (Albrecht et al., 2007; Batáry et al., 2015; Albrecht et al., 2020). Most of these measures focus on increasing the availability of floral food resources for pollinators e.g., through wildflower strips or flower-rich hedgerows (e.g., Blaauw and Isaacs, 2014; Kremen et al., 2019; Albrecht et al., 2020; Ganser et al., 2021). There are also efforts to study the effects of providing additional nesting resources, such as e.g., dead wood or raw soil and implement respective measures (Eckerter et al., 2021; Neumüller et al., 2022; Agrofutura., 2025; O'Leary et al., 2026).

Agricultural grasslands can offer floral resources throughout most of the growing season, as well as nesting opportunities for wild bees (Albrecht et al., 2007; Öckinger and Smith, 2007; Batáry et al., 2010; Albrecht et al., 2023), and are therefore considered key habitats for pollinators in mosaic-type agricultural landscapes with production of

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various crops and dairy farming (Sutter et al., 2017; Maurer et al., 2022). Nesting opportunities can be provided by extensively managed meadows or pastures with relatively sparse and heterogeneous vegetation and open soil patches (Gardein et al., 2022; Albrecht et al., 2023), as the majority of European bee species are ground-nesting, even though some nest above ground, occupying existing cavities or excavating their own, e.g., in pithy stems (Westrich, 2019). Beyond nesting, grasslands are especially important later in the growing season during summer, when floral resources offered by crops and woody semi-natural habitats are often scarce (Mallinger et al., 2016; Ammann et al., 2024). However, the potential of grasslands to sustain wild bee pollinators in agroecosystems can vary greatly (Mallinger et al., 2016; Buchholz et al., 2020) and may critically depend on the type of grassland (e.g., permanent hay meadows, pastures, ley meadows; Saarinen and Jantunen, 2005; Potts et al., 2009; Michelot-Antalik et al., 2021) and management intensity (Albrecht et al., 2007; Potts et al., 2009; Ekroos et al., 2020). The most common measures to promote biodiversity in permanent meadows in Europe are postponed first cut or reduction of fertilizer input (Humbert et al., 2012; Dahlström et al., 2013), both of which may contribute to sustaining insect pollinators by maintaining high flower richness (Albrecht et al., 2007; Buri et al., 2014; Ekroos et al., 2020). Such measures are implemented through agri-environment schemes in the Common Agricultural Policy of the EU (Batáry et al., 2015) or similar national programs (Knop et al., 2006; Albrecht et al., 2007). Postponed mowing of permanent meadows (usually defined as postponed first cut) has been shown to benefit wild bees (Buri et al., 2014; Meyer et al., 2017) and other invertebrates (Humbert et al., 2012; Buri et al., 2016).

The role of ley meadows as a foraging habitat for pollinators has received much less attention. Most ley meadows in Central and Northwestern Europe are sown as grass-legume mixtures, often with a high share of legumes of up to 50% (mostly red clover (*Trifolium pratense* L.) and white clover (*T. repens* L.) or a mix of the two species). Such leys provide high-quality fodder for livestock and improve soil structure and fertility through, amongst others, symbiotic N_2-nitrogen fixation (Hoeffner et al., 2021; Cooledge et al., 2022). Potentially, they can also offer abundant floral resources for pollinators foraging on clover, especially for bumblebees (Rundlöf et al., 2014; Riggi et al., 2021). Bumblebees (*Bombus* spp.) are a group of highly important crop pollinators (Khalifa et al., 2021) and therefore of specific interest in agricultural systems. Clovers are key foraging plants for bumblebees in European agroecosystems (Riggi et al., 2021), and clover-rich ley meadows could be especially beneficial for their promotion. However, ley meadows are typically intensively managed, with frequent mowing often occurring before or during clover flowering, which strongly limits their value as foraging habitat for pollinators. Delayed mowing of ley meadows allows for a prolonged period of clover flowering, and could therefore have a high potential to improve ley meadow value as forage habitat for bumblebees and other pollinators. Apart from their preference for clover, bumblebees depend on continuous and abundant floral resources due to their prolonged seasonal activity period (Scheper et al., 2015) and may therefore particularly benefit from extended clover flowering achieved through delayed mowing. However, research about the effects of delayed mowing has largely focused on permanent meadows, while such measures have rarely been studied and implemented in ley meadows (but see Cong et al., 2020).

While the timing of mowing might play an important role (Humbert et al., 2010; Buri et al., 2014; Berger et al., 2024), the mowing technique itself can also have profound consequences for pollinators and other arthropods (Humbert et al., 2009; van Klink et al., 2019; Künast et al., 2025). Mowing has undergone increases in mechanization over the past decades and now often includes conditioners to accelerate the drying of cut grass to improve its quality as cattle feed (Humbert et al., 2009). Conditioners are usually fixed to the mower and operate by crimping or rolling the cut herbage (Humbert et al., 2009), which increases the mortality of insects (Fluri and Frick, 2002; Humbert et al., 2009; Hecker et al., 2022). To minimize the negative impacts of conditioners, several low-threshold measures are recommended for farmers, such as mowing in the absence of bee flight, e.g., in the evening or when flowers have finished blooming (Schweizer Bauernverband, 2023). While the few studies on the use of conditioners have found increased local mortality of, e.g., plant lice, beetles, thrips and caterpillars (Humbert et al., 2010; Hecker et al., 2022; but see Berger et al., 2024), we lack knowledge about their impact on wild bees and particularly on their long-term consequences. Bumblebees could specifically profit from the no conditioner measures in both, leys and extensively managed meadows, as they have generally high foraging activities in agricultural meadows. Moreover, larger organisms may be more susceptible to direct mowing mortality than smaller ones (Humbert et al., 2010) and mowing practices that reduce mechanical damage may therefore disproportionately benefit larger-bodied bumblebees compared to smaller bees.

In the framework of agri-environment schemes, often multiple measures are applied together to promote pollinators and biodiversity in general. Therefore, it is crucial to investigate not only individual measures, but also whether they act additively or even synergistically on target species when applied in combination. Moreover, the surrounding landscape may affect the effectiveness of measures (Aguilera et al., 2020). For example, the availability of bee-friendly habitats, such as flower strips, hedgerows, ruderal areas or other elements that provide food resources or nesting sites/materials, may increase the effectiveness of measures. Studies investigating potential synergistic interactions between multiple (agri-environmental) measures and bee-friendly habitats over numerous years on wild bee pollinators are scarce (e.g., Scheper et al., 2015; Aguilera et al., 2020). Thus, the combined effects of no conditioner use in permanent- and ley meadows and delayed mowing of ley meadows, and how these effects are influenced by the presence of bee-friendly habitats, remains unexplored.

In this study, we assess how the proportion of different meadow types in the landscape affects wild bee abundance and species richness during spring and summer. A special focus is given to meadows mown without conditioner and ley meadows under a delayed mowing regime. We hypothesize that (1) mowing ley meadows and permanent meadows without conditioner, as well as delayed mowing of leys, is beneficial for wild bee abundance and species richness; (2) implementing these two measures in ley meadows with clovers increases bumblebee (*Bombus* spp.) abundance because bumblebees particularly benefit from enhanced clover flowering; (3) the effectiveness of no conditioner use and delayed mowing can be enhanced if they are applied together and/or if they are implemented in landscapes with a high share of bee-friendly habitats.

2. Material and methods

2.1. Study design

This study was conducted in western Switzerland in the cantons of Bern, Jura and Vaud as part of the project “AgriPol – Agriculture et pollinisateurs”. The study region is characterized by grasslands, arable crops and patches of forest (Lachat, 2010). Farmers in the study region were invited to participate by implementing bee-promotion measures on their meadows (mowing without a conditioner or delayed mowing, see Section 2.3. for details), receiving contributions for their efforts. Three different meadow types were differentiated in this study: (1) Ley meadows, which are intensively managed sown meadows part of the crop rotation and generally last up to three years. The majority of seed mixtures consists of grasses combined with white clover (*Trifolium repens* L.) and/or red clover (*T. pratense* L.). In the study region, grass-only mixtures or mixtures of grasses with lucerne (*Medicago sativa* L.) or sainfoin (*Onobrychis viciifolia* Scop.) are also present, but considerably less common. (2) Intensively managed permanent meadows, which are not part of the crop rotation, but cut several times a year and fertilized. These meadows, as well as ley meadows, receive up to around 170 kg N ha^{-1} $year^{-1}$ and are mown up to five or six times annually, with a first

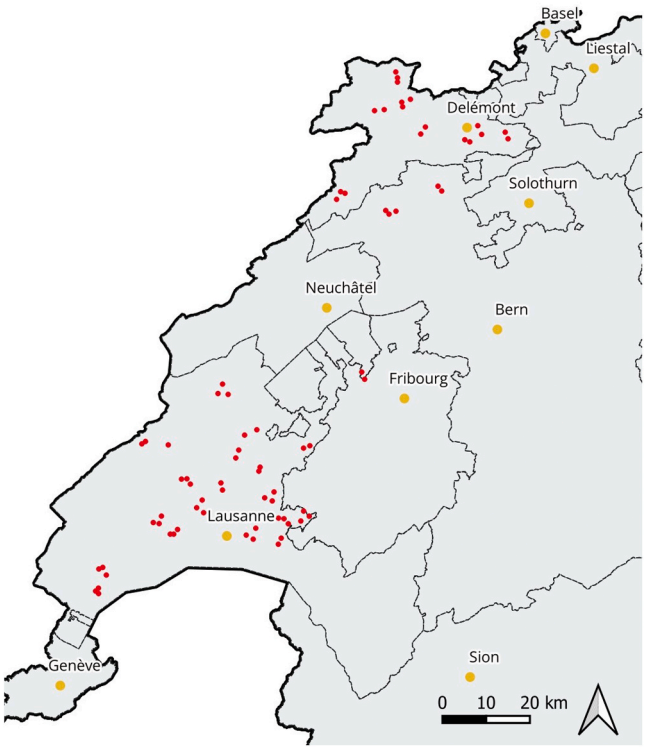


Fig. 1. Locations (red dots) of the 74 wild bee combi-traps in western Switzerland. Lines depict cantonal boundaries and yellow dots the capitals (Basemap: © Swisstopo. Source: Swiss Federal Office of Topography swisstopo, provided under the Open Government Data (OGD) Switzerland license).



Fig. 2. Picture of a 'combi-trap': It consists of a large yellow pan trap (upper diameter: 42.5 cm, volume: 12 L) combined with a passive window intersection trap constructed from two plexiglasses of 50 × 42 cm (Duelli et al. 1999). To activate the trap, it was filled with water and a drop of detergent to reduce the water surface tension, preventing captured insects from remaining on the surface and escaping, thereby increasing trapping success.

cut in April or May (Knop et al., 2006; Huguenin-Elie et al., 2017). (3) Extensively managed permanent meadows, i.e., managed according to the requirements of the Swiss agri-environment scheme for extensively managed meadows, which includes no mowing before 15 June (lowland and hill zone), 1 July (mountain zone I, II) and 15 July (mountain zone III, IV) and no fertilizer application (Bundesrat, 2013). Extensively managed meadows are mown less frequently than intensively (conventionally) managed ones, generally twice a year (Knop et al., 2006; Huguenin-Elie et al., 2017). In our study, the category extensively managed meadows also included low-intensity meadows, which are less common. Low-intensity meadows are also mown after 15 June but may receive low amounts of manure or compost. During six years (2018 – 2023), wild bees were sampled in landscapes with varying proportions of implemented measures (no conditioner use during mowing, delayed

Table 1
Proportions of different land-use types and measures in 500 m landscapes. Proportions are averaged over all sampling years (2018 – 2023). Measure covers are given (1) as percentage of a measure in a certain meadow type in the total 500 m landscape, and (2) as percentage of a measure within the corresponding land-use type. Values are mean percentages (minimum - maximum).

Land-use type / Measure	Area in 500 m landscape (%)	Measure area within land-use type (%)
Ley meadows	**14.1 (0.0–49.3)**[b]	
- no conditioner	2.8 (0.0–29.8)	19.9 (0–100)[b]
- delayed mowing	1.1 (0.0–12.1)	8.8 (0–100)[b]
Intensive permanent meadows	**9.6 (0.0–72.8)**[b]	
- no conditioner	2.0 (0.0–29.5)	16.2 (0–100)[b]
Extensive permanent meadows	**6.8 (0.4–19.6)**[b]	
- no conditioner	3.2 (0.0–12.7)	44.2 (0–100)[b]
Bee-friendly habitats[a]	**1.2 (0.0–7.6)**[b]	
Bee-attractive crops	**8.3 (0.0–34.3)**[b]	
Other crops	**31.1 (0.0–65.3)**[b]	
Intensive pastures	**3.7 (0.0–24.7)**[b]	
Extensive pastures	**3.6 (0.0–41.6)**[b]	

[a] flower strips, hedgerows, ruderal areas, fallows, etc.
[b] included in the statistical analysis

mowing of ley meadows) by using combi-traps (see below) to investigate how bee abundance and richness might benefit from these two promotion measures.

2.2. Site selection and sampling of wild bees

For the site selection, 30 subregions of a 2 km radius were chosen across the study region where the two measures could be implemented by farmers (described in Hernandez et al., 2023). Within these subregions, one to three sites were selected, at which combi-traps were set up directly at the start of the first sampling round, resulting in a total of 74 landscapes of 500 m radius around combi-traps (hereafter '500 m landscapes', Fig. 1, please refer to Table 1 for a characterization of land-use types around traps). To minimize the potential impact of small-scale variation on sampling, combi-traps were always placed in the same local focal habitat, namely extensively managed meadows. A radius of 500 m was selected as it spans typical foraging ranges for wild bees (Zurbuchen et al., 2010; Kendall et al., 2022). The combi-traps consisted of large yellow pan traps (upper diameter: 42.5 cm, volume: 12 L) combined with a passive intersection trap constructed from two plexiglass windows of 50 × 42 cm (see Fig. 2 for details; Duelli et al., 1999). To activate a trap, it was filled with water just below the brim and a drop of detergent to reduce the water surface tension and increase trapping success. To prevent the traps from overflowing during rain, small holes were added along the upper edge so the water could drain out without losing any samples. Trap locations were selected so that traps were (1) at least 750 m apart from each other (mostly > 1000 m), (2) at least 100 m from forest (to avoid shading and forest edge effects), and (3) at least 250 m from the nearest managed honeybee hive (to avoid strong competition by honey bees). Wild bee sampling was performed four times per year. During each sampling round (late April, late May, late June, late July), traps were activated (i.e., filled with water and detergent) for seven consecutive days (for dates see Supplementary Table 1). Weather forecasts were taken into account, and sampling was scheduled during periods of low rainfall whenever possible, while keeping the timing roughly consistent across years. After seven days, bees were collected and stored in 70% ethanol before subsequent washing, drying, pinning and identification to species level by expert taxonomists. Red List species were identified based on the recently published Swiss Red List of Bees (Müller and Praz, 2024). In 2018 and 2023, traps were activated in all 30 subregions, while in 2019, 2020, 2021, and 2022, traps were activated in half of the subregions alternately, i.e., one set of subregions was sampled in 2019 and 2021, the other in 2020 and 2022. This was done to prevent strong negative effects of sampling on the wild bee populations. One 500 m landscape was sampled in 2018 only, and another in 2018/19. In between sampling rounds, the traps were emptied and placed upside down to inactivate them.

2.3. Measures to promote wild bees

In the studied landscapes around the traps, two different measures to promote wild bees were implemented at various proportions: (1) refraining from using a conditioner during the mowing of meadows and (2) delayed mowing of ley meadows. Measure 1 (hereafter called 'no conditioner') was implemented either in ley meadows, intensive permanent meadows or extensive permanent meadows, whereas measure 2 ('delayed mowing') was only implemented in ley meadows. The no conditioner measure consisted of not using a conditioner during all mowing activities in a selected meadow. For the delayed mowing measure, farmers delayed one cut of a selected ley meadow between 1 June and 31 August until the first leguminous flowers wilted. Farmers were only allowed to implement this measure on ley meadows with at least 15% of red or white clover or lucerne in the seed mixture. This threshold was selected because the purpose of delayed mowing was to increase floral resources for bees. In meadows with negligible clover abundance—such as grass-only ley meadows, which are very rare in Switzerland—this would not be meaningful. In case of ley meadows, farmers were also allowed to implement both measures on the same meadow. Delayed mowing of permanent meadows is part of the management prescriptions of extensively managed permanent meadows and was not the focus of this study. Its effects on bee pollinators have been studied before (e.g., Albrecht et al., 2007).

2.4. Characterization of land use types around wild bee traps

In each 500 m landscape, the following land-use types were characterized: ley meadow, intensively and extensively managed permanent meadow, meadow harvested without conditioner (measure 1), ley meadow with delayed mowing (measure 2), bee-friendly habitats, bee-attractive crop, other crop, intensive pasture and extensive pasture, i.e., grazed grasslands. The classification as areas as bee-friendly habitats was based on previous research on the importance of various semi-natural land-use types for bee pollinators in the study region (e.g., Bartual et al., 2019; Maurer et al., 2022) and accordingly included e.g., flower strips, hedgerows, ruderal areas or fallows, but not forests. Moreover, the landscape characterization did not include water bodies and urban areas, as the focus of the study lay on agricultural landscapes. Georeferenced information about the agricultural types of land-use were obtained directly from Cantonal Services of Agriculture (Bern, Jura, Fribourg and Vaud). The calculations of proportions of different land-use types in each 500 m landscape were performed using ArcGIS pro 3.21 (ESRI Schweiz AG). The proportion of the implemented measures within the different meadow types was calculated based on farmers' information. The average proportions of different land-use types across years are given in Table 1.

2.5. Data analysis

Wild bee abundance, bumblebee abundance and species richness were analyzed with generalized linear mixed-effects models (GLMMs) with log link function and negative binomial distribution, as preliminary models indicated overdispersion. For the analyses of abundance data, we used the total number of wild bees (including bumblebees), as well as the total number of bumblebees as response variables (per trap and sampling round, without pooling). For wild bee species richness, we first applied rarefaction and extrapolation to estimate the expected asymptotic species richness per 500 m landscape and year. To this aim, data from the four sampling rounds per year were pooled. For rarefaction, individual-based abundance data were used. Importantly, because different species are expected to appear in different sampling rounds due to varying activity periods of bees, only landscapes that were sampled in all four sampling rounds for a given year were included in the rarefaction procedure.

Predictor variables of Table 1, i.e., the proportions of the two focal measures within the meadow area (2nd column) and the proportions of the land-use types in the landscapes (1st column, bold), were included in the models as fixed main effects. Further, year (6-level factor), sampling round (4-level factor), and climatic information on temperature and precipitation during the sampling period were also included as fixed effects (see Supplementary Information for details to climate variables). The inclusion of two-way interactions in the models was assessed by forward selection and followed always a set of *a priori* meaningful scenarios that tested the interactions of the base set of variables listed in Table 1 with year, sampling round, bee-friendly habitats, and interactions between the focal measures themselves (see Supplementary Information for details). We used the second-order Akaike Information Criterion (AICc; Burnham and Anderson, 2002) to determine whether to include the interaction terms in the model (i.e., if $\Delta AICc > 2$). Inference of main effects was calculated by single term deletion from main effect models (each effect in turn) and subsequent likelihood ratio tests. Inference of interactions were similarly tested, but from the full model

that contained all interactions defined by the forward selection procedure. To account for the clustering of the 500 m landscapes within subregions, as well as repeated sampling per landscape, subregion ID and landscape ID were each modeled as random factors (random intercepts). Further, it was tested by likelihood ratio tests whether these intercepts were allowed to vary between years, i.e., whether the random ID:year interactions should be included. The final models are provided in the Supplementary Information. Finally, potential collinearity of the land-use variables was assessed by the variance inflation factor (VIF; O'Brien, 2007). It turned out that 80% of the VIF values were below 1.6, with the highest value being 2.6, indicating that multi-collinearity among our predictor variables was not an issue.

All data analysis was performed with the statistical software *R*, version 4.6.1 (R Core Team, 2026) using packages *glmmTMB* (Brooks et al., 2017) for GLMMs and *iNext* (Chao et al., 2014) for rarefaction. Model assumptions were evaluated using a simulation-based approach that generated scaled residuals from the fitted model using the R package DHARMa (Hartig, 2022), and overdispersion as well as multicollinearity of variables were checked using the package *performance* (Lüdecke et al., 2021). For visualization, fixed model means and their 95% confidence interval were derived with *emmeans* (Lenth, 2021).

3. Results

3.1. Wild bee abundance

During the six study years 2018–2023, a total of 7086 wild bee individuals belonging to 166 species (thereof two aggregates: *Bombus terrestris* aggr. and *Halictus simplex* aggr.) were sampled in the 500 m landscapes. The most commonly sampled species were *Lasioglossum pauxillum* followed by *L. zonulum*, *Bombus terrestris* aggr., *Andrena haemorrhoa* and *A. flavipes* (705, 646, 592, 333 and 310 individuals, respectively). For *Bombus* spp., the most commonly sampled were *B. terrestris* aggr., *B. hortorum*, *B. sylvarum*, *B. pascuorum* and *B. lapidarius* (592, 150, 109, 105 and 97 individuals, respectively). Of the sampled bees, 68 individuals (14 species) are listed on the Swiss Red List of Bees (Müller and Praz, 2024; see Supplementary Table 2 for a list of all species). Although we did not find direct positive effects of the two implemented measures (no conditioner use, delayed mowing of ley meadows) on wild bee abundance, we observed a synergistic interactive effect between the proportions of no conditioner within the extensive permanent meadow area and bee-friendly habitats in the surrounding

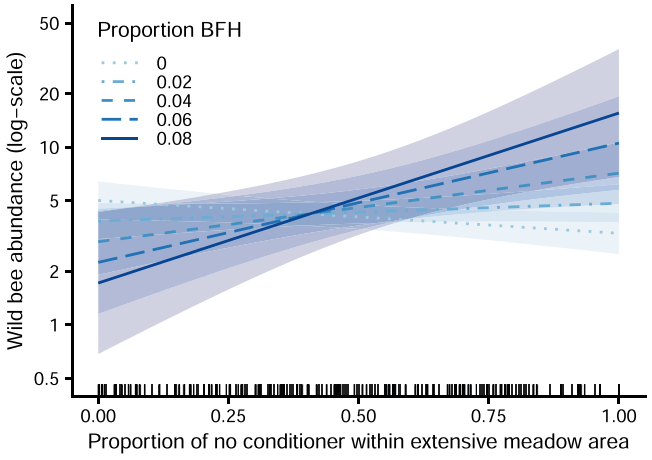


Fig. 3. Interactive effect of the proportions of no conditioner use within the total extensive permanent meadow area and bee-friendly habitats (BFH) on wild bee abundance. Predicted lines show the effect of the no conditioner measure at different covers of BFH in the 500 m landscapes. Predictions and 95% confidence intervals (shaded areas) are based on a generalized linear mixed-effects model (Table 2).

500 m landscape (Fig. 3, Table 2). For example, given a proportion of BFH of 0.04 in a landscape, increasing the proportion of no conditioner within the extensive meadow area from 0.25 to 0.5 (or, e.g., from 0.5 to 0.75) resulted in a 1.28 times higher bee abundance (95% CI: 1.08 – 1.52). However, when the proportion of BFH was 0.08, increasing the proportion of no conditioner by the same percentages resulted in a bee abundance being 1.78 times higher (CI: 1.24 – 2.58), demonstrating the interactive effect between the two factors (Fig. 3). The effect of delayed mowing of ley meadows varied with year (Table 2, Supplementary Fig. 1), but there was no overall positive main effect of this measure on wild bee abundance. Likewise, the proportion of bee-friendly habitats had no overall positive effect on wild bee abundance, but the effect varied considerably between sampling rounds (Table 2, Supplementary Fig. 2). Wild bee abundance further varied between years and sampling rounds, and was negatively affected by precipitation (Table 2).

3.2. Bumblebee abundance

Similar to overall wild bee abundance, bumblebee abundance was only increased if the no conditioner measure in extensive permanent meadows was implemented where the proportion of bee-friendly habitats in the 500 m landscapes was comparably high, as indicated by the respective interaction (Fig. 4a, Table 2). However, the effect of the no conditioner measure in extensively managed permanent meadows varied with year (Table 2), being clearly positive only in 2018 and 2020 (Supplementary Fig. 3). For example, in 2018, given a proportion of BFH of 0.06 in a landscape, increasing the proportion of no conditioner within the extensive meadow area from 0.25 to 0.5 resulted in an increase of bumblebee abundance by a factor of 1.91 (CI: 1.40 – 2.61). Yet, no such positive interaction was observed in the following year, 2019 (Supplementary Fig. 3). In addition, bumblebee abundance benefitted from increasing the share of no conditioner in both, leys *and* intensive permanent meadows (Fig. 4b, Table 2). Thus, when conditioners were absent from 0.75 of the area of intensive permanent meadows, increasing the absence of conditioners from 0.25 to 0.5 of the ley area resulted in bumblebee abundance being 1.27 times higher (CI: 1.05 – 1.55). However, no such effect was observed when conditioners were absent from only 0.25 of the intensive permanent meadow area (Fig. 4b). The effect of the proportion of bee-friendly habitats varied between sampling rounds, suggesting that they are more important in summer (June and July) compared to spring (April and May; Table 2, Supplementary Fig. 4). Bumblebee abundance was further weakly positively affected by the proportion of intensive pastures in the 500 m landscape (Supplementary Fig. 5, Table 2). Similar to overall wild bee abundance, bumblebee abundances varied between years and sampling rounds, and was negatively affected by precipitation (Table 2).

3.3. Wild bee species richness

As for wild bee abundance, wild bee species richness benefitted from the synergistic interactive effect between the no conditioner measure in extensively managed permanent meadows and the proportion of bee-friendly habitats in the 500 m landscapes (Fig. 5, Table 2). Overall, the measure no conditioner use in intensive permanent meadows had a rather negative than positive effect on wild bee richness (Supplementary Fig. 6). Moreover, delayed mowing within the ley meadow area negatively affected wild bee richness when the proportion of no conditioner use within the extensive permanent meadow area was high (Supplementary Fig. 7). Wild bee richness further varied with year and was positively affected by temperature (Table 2).

4. Discussion

Covering six consecutive years with data on wild bee abundance and richness, our study shows that bee-promotion measures harbor the potential to benefit wild bees in agricultural landscapes. Yet, there should

Table 2
Effects of land-use types and applied measures on wild bee abundance, bumblebee abundance, and wild bee species richness. Statistical inferences (LRT: likelihood-ratio chi-square tests) of generalized linear mixed-effects models with log link and negative binomial distribution on the effect of measures (no conditioner use, delayed mowing of ley meadows) and different land-use types on the abundance of wild bees and bumblebees and wild bee species richness in combi-traps in 2018–2023 (total N: 1064 observations for abundances, 210 for species richness). Statistically significant effects ($P \leq 0.05$) are highlighted in bold. Dashes (–) indicate no inclusion of the term, based on model selection. Delta temperature explains variation in bee abundance/richness in addition to the variation that is explained by the temperature differences in the six years and the four sampling rounds (see Supplementary Information for details).

		Wild bee abundance		Bumblebee abundance		Wild bee species richness	
Variable	**Df**	**LRT**	**P-Value**	**LRT**	**P-Value**	**LRT**	**P-Value**
Year	5	79.52	**< 0.001**	25.73	**< 0.001**	21.21	**< 0.001**
Sampling round	3	22.39	**< 0.001**	48.70	**< 0.001**	–	–
Delta temperature	1	0.14	0.704	1.02	0.314	6.90	**0.009**
Precipitation	1	8.41	**0.004**	7.50	**0.006**	–	–
Prop. ley meadows (LM)	1	0.21	0.651	0.83	0.363	0.12	0.727
- Prop. no conditioner within LM	1	0.09	0.770	1.24	0.265	0.48	0.489
- Prop. delayed mowing within LM	1	0.11	0.741	1.05	0.306	1.93	0.164
Prop. intensive permanent meadows (IPM)	1	0.27	0.603	0.02	0.901	0.24	0.628
- Prop. no conditioner within IPM	1	0.39	0.531	0.33	0.565	4.12	**0.042**
Prop. extensive permanent meadows (EPM)	1	0.14	0.708	2.05	0.152	0.10	0.756
- Prop. no conditioner within EPM	1	0.33	0.563	3.55	0.060	0.02	0.887
Prop. bee-friendly habitats (BFH)	1	1.62	0.203	2.51	0.113	0.28	0.595
Prop. bee-attractive crops	1	2.47	0.116	0.07	0.789	0.58	0.448
Prop. other crops	1	0.52	0.473	2.52	0.113	0.38	0.538
Prop. intensive pastures	1	1.22	0.270	5.37	**0.020**	0.42	0.515
Prop. extensive pastures	1	0.48	0.489	2.06	0.152	0.08	0.779
Year × Sampling round	15	186.25	**< 0.001**	104.04	**< 0.001**	–	–
Year × Prop. delayed mowing within LM	5	26.51	**< 0.001**	–	–	–	–
Year × Prop. bee-attractive crops	5	19.11	**0.002**	20.77	**0.001**	–	–
Year × Prop. no conditioner within EPM	5	–	–	21.77	**0.001**	–	–
Sampling round × Prop. BFH	3	10.80	**0.013**	19.43	**< 0.001**	–	–
Sampling round × Prop. other crops	3	11.46	**0.009**	14.19	**0.003**	–	–
Prop. BFH × Prop. no conditioner within EPM	1	9.65	**0.002**	5.69	**0.017**	5.30	**0.021**
Prop. no conditioner within LM × Prop. no conditioner within IPM	1	–	–	11.49	**0.001**	–	–
Prop. no conditioner within EPM × Prop. delayed mowing within LM	1	–	–	–	–	4.99	**0.025**

be abundant bee-friendly habitats in the surrounding area of the managed grasslands to promote bees, and beneficial effects are more likely to be achieved if multiple measures are combined. Importantly, refraining from a conditioner during mowing of extensively managed permanent meadows and an increased proportion of bee-friendly habitats was synergistically effective on all three response variables: wild bee abundance, bumblebee abundance, and bee species richness. Importantly, the effects of the no conditioner measure in extensive meadows and delayed mowing of ley meadows varied from year to year, making it difficult to infer overall positive effects on wild bees across years. It highlights the need for long-term monitoring of the effects of bee-promotion measures in agricultural landscapes.

4.1. Refraining from conditioners in extensive meadows only effective with surrounding bee-friendly habitats

Refraining from using a conditioner when mowing extensive meadows in combination with increased proportions of bee-friendly habitats in the surrounding landscapes, such as flower strips and hedgerows, benefitted wild bee abundance and richness synergistically. However, the positive effect of the no conditioner measure was lost if the proportion of bee-friendly habitats in the landscape was low. Indeed, in particular flower strips and hedgerows have been shown to benefit wild bees, being important for offering floral food resources, suitable nesting sites for both above and below ground nesting bees, as well as shelter (Kremen et al., 2019; Ganser et al., 2021; Maurer et al., 2022; Eeraerts and Isaacs, 2023). Such habitats are a key prerequisite for sustaining bee populations in intensively managed agricultural landscapes, and our study shows that, if they are lacking, bee-promotion measures focusing on management extensification in meadows appear to become ineffective. Similarly, a recent synthesis revealed a positive interaction between a biodiversity-promotion measure (crop diversification) and the proportion of semi-natural habitats in the landscape on pollinator diversity (Aguilera et al., 2020). While highly simplified landscapes likely have depleted source populations of pollinators, the ecological counteraction introduced by agro-ecological measures may not be significant enough to result in substantial effects. The positive impact of refraining from using a conditioner on pollinators is expected to increase with the amount of flower enhancement measures and landscape complexity, as the strongest beneficial effects are expected at intermediate landscape complexity (e.g., Kleijn et al., 2011; Scheper et al., 2013). Because the landscapes in the present study did not include highly complex landscapes, but rather ranged from highly simplified to intermediate complexity in terms of the availably of bee-friendly habitats, our findings are in agreement with theoretical predictions (Scheper et al., 2013). Beyond enhanced foraging resources offered by bee-friendly habitats, heterogeneity in vegetation cover and structure may be positively linked to nesting habitat quality for bees (Albrecht et al., 2023; Eeraerts and Isaacs, 2023). Old mammal burrows e.g., in permanent pastures, could potentially be important nesting habitats for certain bumblebee species, and may have contributed to the positive effect of intensive pastures on bumblebee abundance (Morandin et al., 2007; Liczner and Colla, 2019).

In Switzerland, extensively managed meadows are separated into two quality categories (quality I and II), based on the presence of a set of plant indicator species. For extensively managed meadows of quality II, the use of a conditioner during mowing is already prohibited by law,

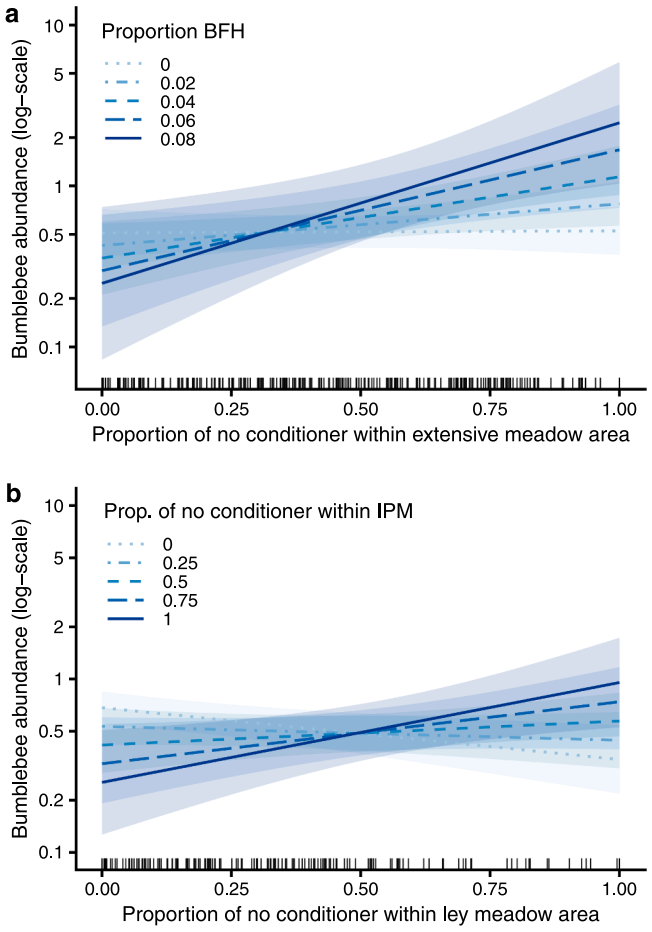


Fig. 4. Interactive effects of measures and land-use types on bumblebee abundance. a) Interactive effect of the proportions of no conditioner use within the total extensive permanent meadow area and bee-friendly habitats (BFH) in the 500 m landscapes on bumblebee abundance. The predictions are given as average across all study years. **b)** Interactive effect of the no conditioner measures within total ley meadow area and intensive permanent meadow (IPM) area on bumblebee abundance. Predictions and 95% confidence intervals (shaded areas) are based on a generalized linear mixed-effect model (Table 2).

whereas quality I meadows can still be mown with conditioning (Bundesrat, 2013). Encouraging farmers to refrain from conditioners also in extensively managed meadows of quality I, or even prohibiting their use, might be a relatively easy way to improve the situation for wild bees in grassland-dominated agricultural landscapes.

4.2. *Refraining from conditioners in intensive meadows effective given wide implementation*

While previous studies have shown that the use of conditioners might cause direct mortality of insects (Fluri and Frick, 2002; Humbert et al., 2010; Hecker et al., 2022), long-term negative consequences have not been found (Berger et al., 2024). Our findings did not reveal a strong consistent positive effect across years of the no conditioner measure in any of the meadow types. However, for bumblebee abundance, the effect of this measure varied between years with positive relationships in four out of six years (Supplementary Fig. 3). This pronounced variation suggests that a potential positive effect of the measure was too weak to be easily detected. Moreover, bumblebee abundance was only increased when the share of no conditioner use within leys *and* intensively managed permanent meadows was high (Fig. 4b). Bumblebees might therefore profit from this measure also in intensively managed meadows, given that farmers consistently refrain from conditioners

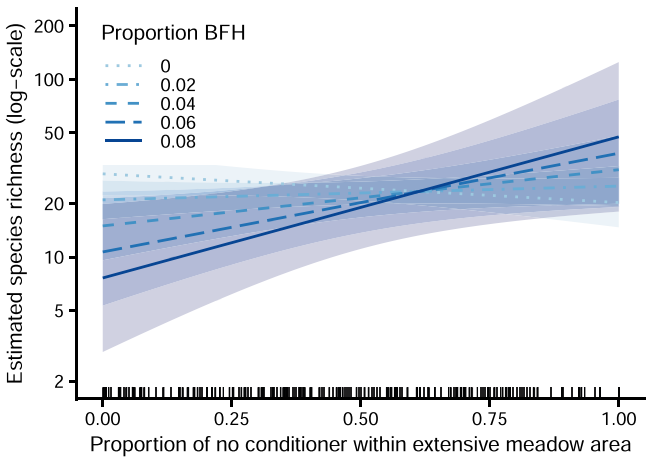


Fig. 5. Interactive effect of the proportions of no conditioner within the total extensive permanent meadow area and bee-friendly habitats (BFH) on estimated wild bee species richness. Predicted lines show the effect of the proportion of no conditioner within extensive permanent meadows at different levels of BFH in the 500 m landscapes. Predictions and 95% confidence intervals (shaded areas) are based on a generalized linear mixed-effect model (Table 2).

during mowing. Multiple species and high densities of bumblebees are found on ley meadows (e.g., Rundlöf et al., 2014; Riggi et al., 2021), and conditioners are expected to be harmful when used on this meadow type.

4.3. *Delayed mowing on ley meadows not effective, but with high year-to-year variation*

We could not find an overall positive effect of delayed mowing of ley meadows on wild bee and bumblebee abundance or on species richness, but rather that the effect on wild bee abundance appeared to vary from year to year (Supplementary Fig. 1). The effects of delayed mowing have so far been investigated in permanent meadows. Generally, delayed mowing had beneficial consequences for wild bees (Buri et al., 2014; Meyer et al., 2017), especially when the mowing regime was combined with a prohibition of fertilizer application (e.g., Albrecht et al., 2007). Delayed mowing of permanent hay meadows has been shown to increase the flowering period and diversity of flowering plants as a key driver for such positive effects on wild bees (e.g., Meyer et al., 2017; Johansen et al., 2019; Albrecht et al., 2023). While it might be assumed that prolonging the interval between cuts in ley meadows should similarly lead to a higher availability of floral food resources offered by clover, clear evidence for this has not been found so far. In our study, delayed mowing within the ley meadow area negatively affected wild bee species richness, when the share of no conditioner use in extensive meadows was high (Supplementary Fig. 7). Unfortunately, we are not able to provide a satisfactory explanation for this result. In another pilot project in northern Switzerland, farmers got financially compensated for implementing a similar measure in summer to prolong clover flowering in ley meadows by increasing mowing intervals to six weeks. The measure, however, did neither result in clearly detectable higher resource abundance nor in a positive effect on monitored bumblebees (A. Knauer, personal communication). Nevertheless, the colony fitness of *Bombus terrestris* increased with the amount of clover in the surrounding landscape, highlighting the potential of the measure if it succeeds in prolonging clover flowering during the time of most pronounced floral resource scarcity in early summer (Ammann et al., 2024). In our study, farmers received direct payments to postpone one cut of selected ley meadows between 1 June and 31 August until the start of the wilting of the leguminous flowers. However, compared to the no conditioner measure, the uptake of this measure was substantially

lower (see Table 1), resulting in smaller gradients and reduced statistical power to detect effects. Also, farmers could freely choose when to implement this measure within the prescribed period, which might have further impeded the chance of finding a positive effect on bees. If, for example, leys were mown late towards the end of the period, clovers would have flowered after the most pronounced floral resource scarcity in June and early July. To better match clover flowering to the time of highest resource scarcity in early summer, we recommend starting the time window of delayed mowing earlier, with a first cut between 10 and 31 May followed by one or two six-week intervals between cuttings (Agrofutura., 2023). The harvesting interval might be extended to more than six weeks, although tradeoffs between benefits for pollinators and disadvantages of decreasing fodder quality with longer harvesting intervals must be expected. Moreover, in the present study, it is possible that most meadows were cut around the same time rather than in a staggered manner, which would have resulted in a gap in resource availability despite prolonged flowering. Here, collaborative agri-environment schemes incentivizing regional coordination of grassland management among farmers could be a promising approach (e.g., Prager, 2015).

4.4. *Wild bee abundance fluctuates over years*

With the present data set covering six years, we found that the effectiveness of the two applied management measures was subject to significant year-to-year fluctuation, and overall direct positive effects over the entire study period were not evident. A variety of factors, such as weather conditions but also the inherent complexity of the analyzed landscapes, could have weakened the measures' impact. In contrast to experimental setups, the landscape composition in our study locations was subject to farmer's decisions and could change from year to year, for example, due to crop rotation in the case of measures implemented in ley meadows. The number of wild bees sampled showed a pronounced drop in 2021 and 2022, and slightly increased again in 2023. In fact, the year 2021 was characterized by substantially colder temperatures and higher precipitation during the sampling period compared to the other years, which was very likely the reason for the decreased bee numbers. Low numbers of sampled specimens due to unfavorable weather conditions will make it challenging to detect any effect of implemented measures and should be considered when interpreting the measures' effectiveness to promote wild bees.

Different sampling methods also have advantages and disadvantages. Transect walks can be a highly effective sampling method, as they often result in larger numbers of collected bee specimens and allow direct sampling of foraging insects within local land-use patches. However, to sample multiple meadows several times during the growing season within each of the 74 landscapes, and do so over six consecutive years, transect walks would have been far beyond the resources of this project. By using combi-traps it was possible to simultaneously sample bees for seven consecutive days per sampling round. Moreover, combi-traps, which combine passive sampling (large plexiglass windows that trap flying individuals) with large pan traps, have been shown to be highly effective for sampling insects in agricultural landscapes. The samples reflect bee and other flying insect communities beyond the immediate local sampling site (Duelli et al., 1999; Ammann et al., 2024), and sampling efficiency is less prone to the potential influences of the very local flower availability (Ammann et al., 2024). Similar to other commonly used sampling methods for bees (e.g., transect walks, pan trapping), combi-traps capture only active, foraging bees.

5. Conclusions and implications for management and policy

Our study highlights the critical role of the presence of bee-friendly habitats in agricultural landscapes so that bee-promoting management measures in meadows can be effective. It is therefore crucial to further maintain and promote such habitats via national agri-environment schemes. Further, our data suggest that the use of conditioners during mowing of extensively managed meadows should be avoided. When surrounded by bee-friendly habitats, high share of no conditioner use within the extensive meadow area was effective to promote wild bees. As farmers might be reluctant to delay mowing of ley meadows due to poorer forage quality and potentially lower quantity, this measure could be implemented by mowing different meadows in an area in a staggered manner. Being aware of the practical challenges of such approaches, the implementation of collaborative networks, in which farmers coordinate meadow management at the landscapes scale, should be encouraged. To increase the effectiveness of a delayed mowing measure in leys and better match clover flowering to the period of highest resource scarcity in early summer, we recommend setting the time window for this measure from the second half of May onwards. Finally, despite the complexities of multi-year studies, we encourage more long-term monitoring to assess the effectiveness of measures to promote pollinators and other aspects of biodiversity in agricultural landscapes.

CRediT authorship contribution statement

Janine M. Schwarz: Writing – original draft, Visualization, Formal analysis, Data curation. **Matthias Suter:** Writing – review & editing, Visualization, Formal analysis. **Stephanie Pettman:** Writing – review & editing, Data curation. **Christophe Praz:** Writing – review & editing, Resources, Methodology, Conceptualization. **Louis Sutter:** Writing – review & editing, Methodology, Conceptualization. **Yann-David Varennes:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Matthias Albrecht:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

The authors of this manuscript did not use any Generative AI and AI-assisted technologies during the manuscript preparation process.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Matthias Albrecht & Yann-David Varennes report financial support was provided by Fondation Rurale Interjurassienne. Matthias Albrecht & Yann-David Varennes report financial support was provided by ProConseil. Yann-David Varennes reports a relationship with Fondation Rurale Interjurassienne that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110796.

Data availability

The data used in this study are available at 10.5281/zenodo.18229536.

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