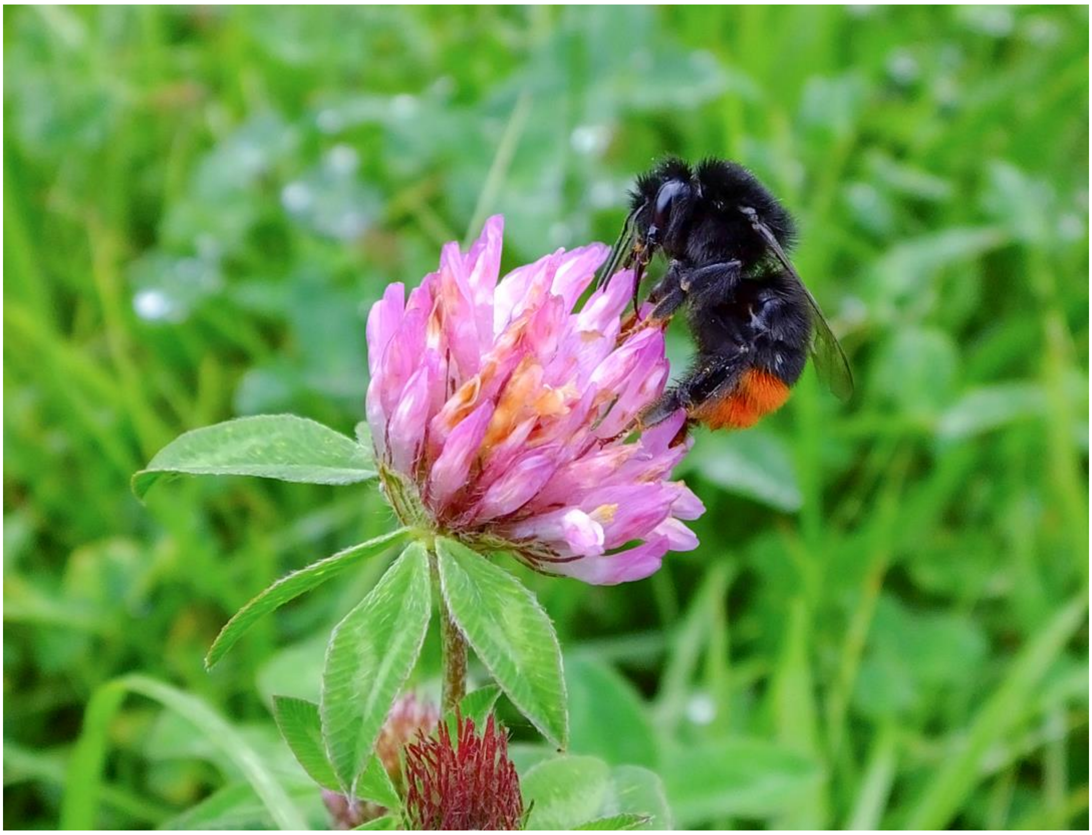
Wild Bee Abundance in Response to Grassland Area and Agricultural Conditioner Use in Switzerland



Stephanie Pettman

Université de Neuchâtel

Master of Science in Biology

Prof. Christophe Praz

Yann-David Varennes

June 20, 2022

Abstract

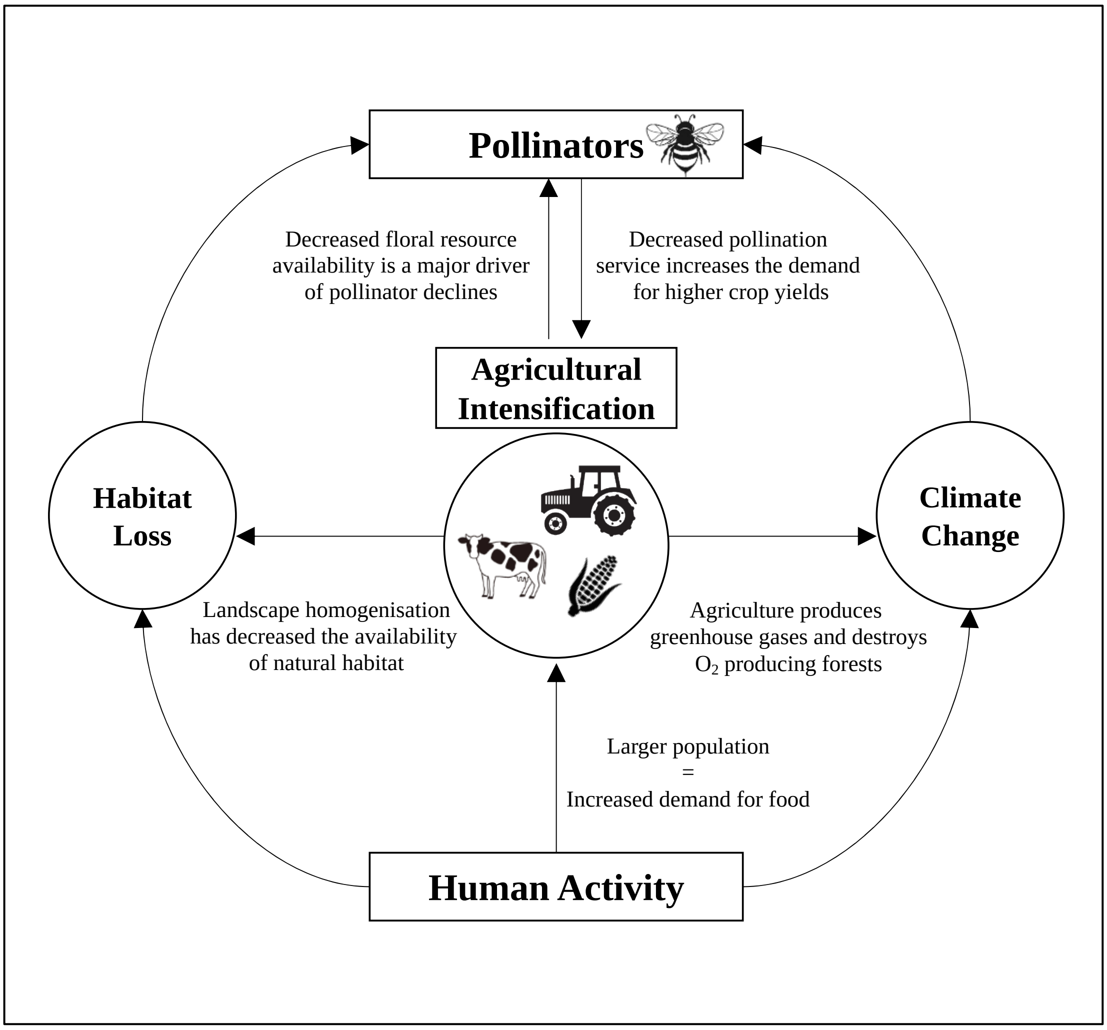
Pollinators, particularly bees, are essential for successful flowering plant reproduction, seed production and maintenance of ecological processes. Significant pollinator declines have been recorded for decades, primarily due to fragmented habitat, a lack of floral resources and insufficient nesting site availability driven by the conversion of natural habitat and traditional, extensive agricultural environments to homogenous intensive agricultural landscapes. Contemporary farming practices use different methods to improve crop yields which often involve operations that directly or indirectly lead to insect declines. Many farmers utilize a conditioner during meadow mowing which crushes grass to accelerate the drying process; animals, especially insects, are frequently killed during this procedure. We present a hypothesis that an increased area of meadows can support more abundant and diverse wild bee communities. We posit that the strength of this relationship will increase when meadows are permanent. We also hypothesize that reduced conditioner use in agricultural landscapes promotes greater wild bee abundance and diversity. The impact of each land use variable is considered for different bee classifications based on species' functional traits and foraging preferences. Our data indicates that areas where conditioner is used less extensively are associated with a higher abundance of wild bees. There was no impact of conditioner use on wild bee diversity. The effect of conditioner use was significant only from late June to early July, which corresponds to the primary time of mowing in the study area. Our study demonstrates how wild bee abundance can benefit from increased meadow area and changes in agricultural mowing regimes.

Keywords: Pollinators, agricultural intensification, conditioner, mowing, wild bees, land management, permanent meadows

Introduction

Pollinator Declines

Pollinators play a crucial role in flowering plant seed production and ecosystem functioning (Cunningham-Minnick et al., 2019; Rhodes, 2018; Vanbergen, 2013). Recent declines in pollinator populations are a major threat to sustainable crop production and maintenance of biodiversity services (Gallai et al., 2009; Klein et al., 2006; Potts et al., 2016; Rhodes, 2018). Worldwide research provides evidence of major losses in pollinator populations; a study in the USA revealed wild bee abundance declined by 23% in only 5 years (between 2008 and 2013) (Koh et al., 2016; Potts et al., 2010; Rhodes, 2018). Many factors have demonstrated negative influences on wild pollinators such as pathogens, pollution, climate change and pesticides (Kinney, 2018; Potts et al., 2010; Vanbergen, 2013; Van der Sluijs et al., 2013). More importantly, the major decline drivers of wild bee populations include reduced floral resources, lack of appropriate nesting habitat and increased population isolation due to habitat fragmentation (Everaars et al., 2018, Goulson et al., 2015; Potts et al., 2010). Increased human activity has directly or indirectly influenced all wild bee decline drivers (Cane and Tepedino, 2001; Marshman et al., 2019). Intensification of agriculture by way of human activity has completely altered land management practices and produced simplified habitats lacking the complexity necessary to support diverse wild bee populations (Box 1) (Dicks et al., 2021; Marshman et al., 2019; Potts et al., 2010).



Box 1. Pollinator decline driver interactions and the role of agricultural intensification. Human activity plays a direct or indirect role in all influential factors of pollinator declines. A growing human population drove the intensification of agriculture through a demand for increased crop production. Intensification of agriculture has converted many natural habitats and extensive agricultural environments to uniform landscapes, unsuitable for supporting diverse pollinator populations. Intensively farmed areas typically have few floral resources and limited nesting site availability, both of which are influential factors in pollinator declines. Increased pressure for high-yielding agriculture broadened the use of insecticides such as neonicotinoids which negatively influence pollinator foraging behaviour and disease susceptibility. The influence of agriculture on pollinators has a positive feedback effect since decreased pollination services leads to lower crop yields, which increases the demand for agriculture. Human activity by way of industry, agriculture, development, and overexploitation decreases the available areas of natural habitat. Less area of natural habitat means fewer flowering plants are present as foraging resources. Landscapes with limited resources are less biodiverse and can support fewer species. A growing human population and consumerism has led to increased waste production. Air pollution acts to trap heat in the Earth’s atmosphere and warmer temperatures can influence air pollution levels. A larger population with greater activity produces more CO_2 which advances climate change. Agricultural intensification has converted natural habitats into infertile regions with low biodiversity. Forest destruction reduces the production of O_2 and animal agriculture produces greenhouse gas emissions. Climate change forces range shifts in both plant and pollinator species which can alter the composition of a natural ecosystem. More intricate relationships exist between these variables, however only the interactions most directly connected to pollinator declines and agricultural intensification have been included.

Pollinators and Agriculture

Agricultural intensification has negatively impacted wild bee populations through habitat loss, fragmentation and disturbance (Hofmann et al., 2019, Potts et al., 2010). Before the 1950s, agricultural landscapes were composed of small polycultures and extensive grasslands rich in flowering resources (Robinson and Sutherland, 2002). Over time, agriculture became dominated by massive monocultures, intensive pastures and uniform, frequently mowed grasslands (Robinson and Sutherland, 2002; Mazoyer and Roudart, 2006; Vray et al., 2019). Homogenous and frequent mowing regimes limit the diversity of flowering plants which results in few floral resources for wild bees (Johansen et al., 2019). Due to the benefits of delayed mowing, many farmers have adopted a later first-cut date. An increase in the frequency of late-season mowing has led to shortages in late-season flowering resources (Johansen et al., 2019).

Disturbances such as: fertilizers, pesticides, and heavy machinery became common practice in pursuit of increased crop yields and efficiency (Hofmann et al., 2019; Kovács-Hostyánszki et al., 2017; Warren et al., 2008). Homogenous landscapes lacking diverse flowering resources and nesting habitats cannot support large and diverse wild bee communities (Everaars et al., 2018, Goulson et al., 2015). Findings indicate that low-intensity agriculture has a much higher capacity to support wild pollinators, though species' responses are highly dependent on their nesting behaviour, flight duration, reproductive strategy, and foraging preferences (De Palma et al., 2015; Knop et al., 2006; Meyer et al., 2017). Environmentally conscious farming practices promote higher biodiversity however, more research is still required to establish the most effective management practices (Buri et al., 2014; Knop et al., 2006).

Grasslands

Grasslands contribute a unique floral community and act as important foraging habitats for bees, particularly later in the season (Evans et al., 2018b; Mallinger et al., 2016). As grasslands can range greatly in their composition, their capacity to support pollinator communities through floral resources or nesting sites can vary greatly (Buchholz et al., 2020; Mallinger et al., 2016). Some are intensively managed areas with few grass species while others found in low-intensity areas often provide a wide range of flowering species (Buchholz et al., 2020; Mallinger et al., 2016). Intensification in grasslands has contributed to structural landscape simplification thereby reducing the diversity of nesting site availability (Ekroos et al., 2020; Vickruck et al., 2021). Changes in grassland size, complexity and configuration have significant effects on pollinator population diversity and pollination services (Vickruck et al., 2021).

Here we compare the influence of two types of grasslands: (1) meadows and (2) pastures. Meadows are a type of grassland typically managed to grow hay, require regular mowing and involve no grazing (Saarinen and Jantunen, 2005). Regular meadow mowing prevents vegetative succession and promotes plant diversity (Humbert et al., 2009). Pastures are grasslands which are used for grazing by domestic livestock (Saarinen and Jantunen, 2005). Grazing typically depletes flowering resources more rapidly than mowing (Saarinen and Jantunen, 2005).

Meadows can be temporary which typically exist for only a few years, whereas permanent meadows exist for many decades (Bretagnolle et al., 2018). Meadows provide resources and habitat for many species and findings indicate that permanent meadows have a positive impact on wild bee reproduction (Billaud et al., 2021; Van der Meersch et al., 2022). The undisturbed vegetation in permanent meadows provides protected hibernation sites and nesting resources which may be destroyed in temporary meadows due to increased intensity and plowing (Pfiffner and Luka, 2000). Since meadows are composed of a unique floral community, certain bee species are more likely to be found in these landscapes (Hatfield and LeBuhn, 2007; Mallinger et al., 2016). Flowers typical of meadows will attract species with specific functional traits and preferences (Goulson et al., 2005; Hatfield and LeBuhn, 2007; Jones et al., 2021; Mallinger et al., 2019).

Pastures are a type of grassland used for livestock grazing; pastures can be intensive which are typically flat and receive fertilizer or extensive which are usually sloped, receive little to no fertilizer and tend to dry out quickly during the summer due to low water retention (Harris and Ratnieks, 2021; Kruess and Tscharntke, 2002; Saarinen and Jantunen, 2005; Waser and Price, 2016). Evidence suggests pastureland may benefit wild bee abundance in agriculturally intensive landscapes where fields are typically homogenous, tilled crop fields (Morandin et al., 2007). However, research suggests native plant dominated grasslands such as prairies can support a bumble bee community with up to twice the richness of pasture sites (Rosenberger and Conforti, 2020). The potential for pastureland to benefit the wild bee community may also depend upon the species of grazing livestock. Research suggests bison pastures can support more abundant bee communities than cattle pastures; however, cattle pastures can support more diverse and abundant bee communities than sheep pastures (Cutter et al., 2021; Rosenberger and Conforti, 2020).

Flowers from the Asteraceae, Campanulaceae and especially the Fabaceae family are abundant in Swiss grasslands and act as important foraging resources for many bee species (Harris and Ratnieks, 2021; Swiss Bee Team, 2021). Temporal availability of nectar and pollen sources is greatest in varied landscapes where foraging resources follow varying seasonal patterns (Mandelik et al., 2012; Morandin et al., 2007). Temporal trends of floral resources and pollinator community composition are important considerations when evaluating the wild bee community response (Cutler et al., 2015; Duchenne et al., 2020).

Conditioner Use

Current crop harvesting techniques often implement stages to improve efficiency, including the conditioning stage, where grass is crushed to accelerate the drying process (Fluri and Frick, 2002; Humbert et al., 2009). These conditioners are typically fixed to the mower and operate through a crimping or rolling mechanism (Humbert et al., 2009). Research indicates that implementing conditioners can kill many insects, including bees (Fluri and Frick, 2002; Frick and Fluri, 2001; Hecker et al., 2022; Humbert et al., 2009). One study demonstrated that mowing with a conditioner increased arthropod mortality by at least 18% (Hecker et al., 2022). Another suggested mowing with a conditioner killed 53% - 62% of bees present in a white clover field (Frick and Fluri, 2001). As conditioners have been identified as a culprit for increased pollinator death, it is recommended that farmers avoid this technique to support wild bee abundance and diversity, and limit mowing where possible (Buri et al., 2014; Humbert et al., 2009; Humbert et al., 2010).

The Agriculture and Pollinators project (Agripol) associated with this study aims to establish the best farming management practices to support pollinator communities in agricultural landscapes. The Cantons of Vaud, Jura and Bern participate in Agripol in collaboration with Prométerre, Fondation Rurale Interjurassienne and the Federal Office of Agriculture (OFAG). Our study, in association with Agripol, focuses on how conditioner use management can influence wild bee abundance and diversity. We examine the relationships between wild bee abundance and the area of meadows mowed without a conditioner around the sampling points. In addition, we consider the effects of grassland landscape composition; specifically, we investigate how the area covered with permanent meadows, temporary meadows, ecological meadows and pastures is related to wild bee abundance. Based on the aim of our project, we tested the following hypotheses:

H1. Grasslands represent a particular agricultural cropland since they can, more than most other croplands, provide flowering and nesting resources for bees. Therefore, we expect areas with a high proportion of grasslands to host abundant and diverse bee communities.

H2. Grasslands vary in their structure, longevity and overall quality for pollinators. We expect meadows to have a more positive impact on wild bee abundance and diversity than pastures. However, in landscapes with low variation in land use and fewer meadows, a higher proportion of pastureland may support more abundant and diverse wild bee communities. We expect permanent meadows to have a greater overall positive impact on wild bee abundance and diversity than temporary meadows. We also expect ecological meadows (those following the Swiss agri-environment scheme (AES)) to host more diverse and abundant bee communities.

H3. With respect to meadows, the use of a conditioner during mowing kills significantly more bees than mowing practices without a conditioner. Therefore, we expect that areas with reduced conditioner use will host more diverse and abundant wild bee communities. We expect the impact of conditioner to be greater in meadow types which have the strongest positive impact on wild bee communities. Lastly, we expect the impact of conditioner to be strongest during peak mowing times (June/July) as compared to earlier (April/May) or later (August) in the season.

H4. Since not all bees depend on grasslands, we expect the response to grassland variables to be different across different bee guilds; responses are expected to be stronger for bees associated with grasslands (or those species foraging on host plants found in grasslands), than for bees associated with other habitat types. We expect this for variables linked to the use of conditioner, but also for other variables related to grasslands.

Methods

The Agriculture and Pollinators Project

The Agripol project which runs from 2018 to 2025, aims at offering farmers an opportunity to test agroecological measures which support pollinator communities, thus benefiting biodiversity and crop production through optimal pollination. A scientific team has been set up to evaluate the effect of such agroecological measures. To assess all aspects of the applied agroecological measures, the scientific team is organized into four teams: one for domestic bees, one for wild bees, a socio-anthropological team and an agronomical team. The project is funded by the federal office for agriculture and the Cantons of Bern, Jura and Vaud. Overall, a significant proportion of farmers participated in one or more measures. Our study focused on the agroecological measures applied in meadows, specifically those related to the use of conditioner during mowing.

Study Area

Sampling was conducted in western Switzerland, in the Cantons of Vaud, Jura and Bern from April to August for three successive years (2018 - 2020). The agricultural landscape of these three regions is characterized by a mosaic of diverse elements such as meadows, arable fields and forests (Lachat et al., 2010). Legumes (mainly: white clover, red clover and alfalfa) are an important source of nectar and pollen and are highly frequent in meadows. Swiss Agricultural Policy defines three types of meadows: temporary meadows, permanent meadows and ecological meadows. Temporary meadows are included in crop rotation and last up to five years before being replaced by crops. Permanent meadows last for long periods (several decades). These two meadow types receive fertilizer, are mowed two to five times per year and are occasionally used as pastures. Harvest dates and equipment are chosen independently by farmers. In contrast, mowing dates in ecological meadows are set in Swiss Agricultural Policy which dictates the first mow must occur after June 15 with no uncut refuge left behind (Buri et al., 2014). Moreover, ecological meadows receive little or no fertilizer.

Site Selection

Wild bee sampling sites were selected using several criteria: sites must be on agricultural land used by farmers as ecological meadows; sites must be 250 m away from any domestic bee colony and 100 m away from forest; sites must be at least 500 m away from each other. Farmer's consent was always asked prior to sampling (all requested farmers except one accepted sampling being performed on their meadows). Sampling sites were clustered in groups of three sites which fit into 2 km-radius circles, each circle being referred to as a "sector". Thirty sectors were defined: they were centered on 30 apiaries which were part of a research project on domestic bees. The selection of sectors was driven by the enrolment of volunteer beekeepers within the project. Recruitment of beekeepers occurred during information sessions and selection was based on the following criteria: beekeeper age under 70, apiary size of at least 10 colonies, distance to another selected beekeeper's apiary of at least 5 km. In total, 83 wild bee sampling sites were identified, grouped into 30 sectors (Figure 1). In 23 of the 30 sectors, three sampling sites were selected. In seven of the 30 sectors, only two sampling sites could be identified because of our selection criteria. Each of the 30 sectors were sampled during 2018. To minimize the impact of excessive bee sampling over the years, alternate sectors were sampled during one of the subsequent collection years, resulting in 15 sectors sampled during 2019 and 2020.

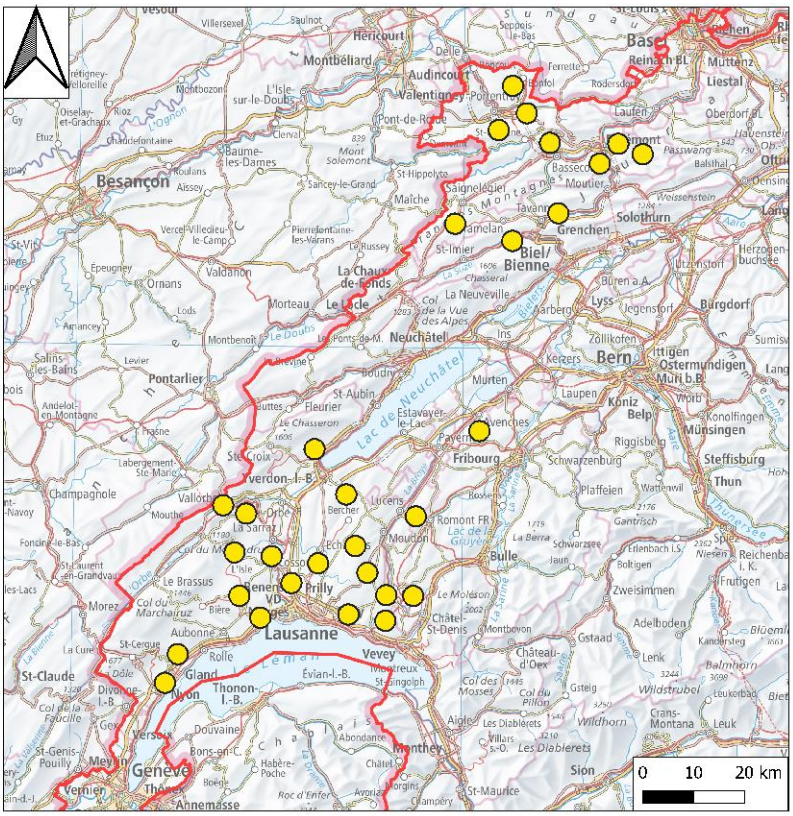


Figure 1. Locations (yellow dots) of the 30 monitored sectors across western Switzerland.

Farmers possessing meadows within the sectors were given the opportunity to apply agroecological measures which aimed to enhance resources for bees. On temporary meadows, three measures were implemented, alone or in combination: (i) to forego conditioner use when mowing; (ii) to leave a strip unmown during each of the mowing operations performed between June 1st and August 31st (time of legume flowering); (iii) to delay one mowing operation until legumes (white clover, red clover, alfalfa) had finished flowering. The combination of (ii) + (iii) was not allowed. On permanent meadows and ecological meadows, farmers were only allowed to forego conditioner use, the other measures were not allowed. On average, meadows represented ca. 300 ha per sector (24 % of total sector area; Table 1).

Table 1. List of grassland types, corresponding agroecological measures, average area occupied per sector in 2018 and codes used for analyses. Values in brackets indicate the average proportion of the total sector area occupied by each grassland type. The last column indicates how each type of grassland was coded in figures and models presented in results and supplementary material.

Grassland type	**Agroecological measure description**	**Area (average, in ha and in % of total sector area)**	**Code used in analyses**
Temporary Meadows	Temporary meadows without agroecological measures	97 ha (7.7%)	*pratemp00*
	Mowing without conditioner	18 ha (1.5%)	*pratemp29*
	Unmown floral strip	2 ha (0.1%)	*pratemp22*
	Delayed mowing	5 ha (0.4%)	*pratemp23*
	Combination of mowing without conditioner use and leaving an unmown strip	3 ha (0.3%)	*pratemp92*
	Combination of mowing without conditioner and delaying mowing	5 ha (0.4%)	*pratemp93*
Permanent Meadows	Permanent meadows without agroecological measures	78 ha (6.2%)	*praperm00*
	Mowing without conditioner	20 ha (1.6%)	*praperm29*
Ecological Meadows	Ecological meadow without agroecological measure	53 ha (4.2%)	*praecol00*
	Mowing without conditioner	7 ha (0.6%)	*praecol29*
Pastures	Intensive pastures	50 ha (3.9%)	*pastureintense*
	Pastures dedicated to the promotion of biodiversity and summer pasturing areas	97 ha (7.7%)	*pastureecol*

Bee Sampling

Specimens were sampled over three years, across four different sampling periods referred to as “rounds”, from late April until early August (Table 2). The traps were set for periods of 7 days, with at least 20 days between two sampling times; exact sampling dates vary between years.

Table 2. List of sampling dates for 2018 – 2020, organised by round.

Sampling Period	Sampling Time	Start Date	End Date
Round 1	Late April to Early May	26.04.18	03.05.18
		26.04.19	03.05.19
		04.05.20	11.05.20
Round 2	Late May to Early June	24.05.18	31.05.18
		27.05.19	03.06.19
		01.06.20	08.06.20
Round 3	Late June to Early July	22.06.18	29.06.18
		28.06.19	05.07.19
		29.06.20	06.07.20
Round 4	Late July to Early August	19.07.18	26.07.18
		26.07.19	02.08.19
		27.07.20	03.08.20

Bees were sampled using combi-traps, which consisted of a 43 cm insect-attracting yellow plastic bowl, filled with 2-3 L of water and a drop of detergent (Duelli et al., 1999). Transparent plastic pans (50 cm high, 42.5 cm wide) were placed on top of the bowl to catch insects by interception (Figure 2). During each sampling year, combi-traps were placed on sampling sites at the end of April and collected after seven days, in early May. Then combi-traps were inactivated for three weeks, and sampling occurred again for a period of seven days, and so on until the last round in early August. In total, four sampling rounds were performed. Collected material was stored in 70% ethanol at room temperature.

Figure 2. Combi-trap, in activated position. Corgémont, 2019.

In the lab, domestic bees were sorted out of the collected material and counted. Wild bees were washed, dried and pinned. Identifications were performed by Manuel Chalverat and Kilian Vaucher; each identification was verified by Christophe Praz. Species data was organized based on species' pollen specializations and red list species were identified based on the unreleased 2022 Swiss Red List (Müller and Praz, in prep).

Surrounding Land

Landscape data originated from various public sources. Forest, urban and water area information were obtained from Cantonal Services of Geographic Information (Geoportal SIT-Jura, Geoportal Canton de Berne, ASIT-VD catalogue). All agricultural land-use types were provided by Cantonal Services of Agriculture (Jura, Bern, Vaud, Fribourg). Agricultural data provided the following information: field location, crop type, surface area and whether agroecological measures had been implemented. These datasets were used to quantify the total surface area per land use, within the 2 km-radius sectors around the monitored apiaries. Geographic information was computed through QGIS (QGIS Development Team, 2021).

Land Use

A total of 12 grassland variables were included in our wild bee analysis (Table 1). The proportion of land area occupied by each grassland type was calculated for each 2 km-radius sector. Each sector was equal to 1260 ha which corresponds to 100% of the land area within one sector. Land use variables were sorted based on various characteristics to establish which characteristics are beneficial in supporting the wild bee community (Table 3). First, grasslands were sorted into meadows and pastures. Meadows were then arranged based on meadow age; permanent meadows exist for many decades and temporary meadows exist for a few years. Meadows were also arranged based on the use of conditioner which was reported by farmers; no conditioner meadows were mown without a conditioner and conditioner meadows were mown with a conditioner. Ecological meadows were analysed separately from other meadow types to prevent confounding between the various types of meadows. Pastures were composed of intensively managed pastures and ecological pastures.

Table 3. List of land use types, sorted by the type of grassland. Represents the type of land use utilized in analysis with the corresponding variables included within each grassland type.

Land Use Type			Variables Included
Grasslands	Meadows	Permanent	praperm00, praperm29
		Temporary	pratemp00, pratemp22, pratemp23, pratemp29, pratemp92, pratemp93
		No-conditioner	pratemp29, pratemp92, pratemp93, praperm29
		Conditioner	pratemp00, pratemp22, pratemp23, praperm00
		Ecological	praecol00, praecol29
	Pastures		pastureintense, pastureecol

Guild Classification

All sampled species were classified into functional guilds based on pollen collection preferences. These classifications were made to compare the impacts of conditioner use on different guilds of bee species. Asteraceae, Fabaceae and Campanulaceae were identified as important foraging resources in grasslands. Each bee species was assigned a ranking of 0 or 1 depending on whether they collected pollen from these plant families. Although they can be found in some grassland types, Apiaceae, Brassicaceae, Boraginaceae and Scrophulariaceae were not included as grassland resources in our case, since these plant families are typically absent in most grassland types investigated here, especially non-permanent grasslands. To create additional guilds, we ranked species on a scale of grassland habitat preference. Species received a rank of 0 if they never visited grasslands, a rank of 1 if they sometimes visited grasslands, a rank of 2 if they mostly visited grasslands and a rank of 3 if they were considered a parasitic species; the "grassland guild" included species with a rank of 1 or 2. Rankings were determined through consideration of each species' pollen specializations from the three plant families Asteraceae, Fabaceae and Campanulaceae. Specific pollen preferences within each plant family were considered in relation to flowering plant prevalence in grasslands. All species were sorted into the forest guild or non-forest guild based on their association with forests (and the expert opinion of Christophe Praz). Bee species foraging on grassland plant families will hereinafter be referred to as grassland bees, bee species foraging on Fabaceae flowers will hereinafter be referred to as Fabaceae bees and bee species associated with forests will hereinafter be referred to as forest bees. We posit that forest bees will not respond to the use of conditioner during mowing.

Data Analysis

Cantonal services provided land use data for geographic composition and agricultural land use. Land use data was assembled for each sampling year (2018, 2019, 2020) to account for changes in land use between years. Each land use variable correlates to a specific habitat type and degree of agricultural management (Table S1). Kendall's rank correlation was used to test for confounding between land use variables. Kendall's rank correlation was selected as it is a non-parametric test and is generally more robust than Spearman's rank correlation.

Climate data was extracted from MétéoSuisse for each of the participating plots at specific sampling dates (MétéoSuisse, 2022). Relative daily sunshine, mean daily temperature and mean daily rainfall were selected as our climate variables to evaluate the potential confounding influence of weather.

All 30 sectors were sampled during 2018; however, to avoid excessive bee sampling, only half (15) of the sectors were sampled during 2019 and 2020. Consequently, the 2019 and 2020 datasets have half the sample size of 2018, which provides a less accurate representation of the actual population and provides more room for error. All analyses were completed for each year and round; however, the 2018 dataset will be the focus of this study as we have more confidence with a larger sample size.

We analysed wild bee community response variables including diversity, abundance, red list species diversity and abundance of the species in each guild. All data was analysed in R studio to examine relationships between land use variables and wild bee abundance and diversity (R Core Team, 2021). Autocorrelation function plots (ACF) were used to test for autocorrelations between variables. For each variable, a Shapiro-Wilk test was used to assess distribution normality, a Fligner-Killeen test was used to analyze the homogeneity of the variance since data has a non-normal distribution, and a skewness test revealed directional skew. We first established relationship significance using linear regression models (LM) in the R package MASS. We selected linear regression models (LM) as all our dependent and independent variables are quantitative and our data follows a linear trend. Data had a non-normal distribution; however, a normal distribution is not necessary in linear regression model analysis. Log transformations had minimal influence on data skew therefore, our scatter plots and LMs utilized the untransformed dataset. The effect of each land use variable was tested against wild bee abundance, wild bee diversity, the number of red list species, and the abundance of species in each guild. These variables are referred to as wild bee community response variables. The effect of each climate variable (relative sunshine, temperature, and rainfall) was also tested against the wild bee community response variables. All analyses were repeated for each individual year and round to evaluate temporal trends in the data. All mentioned effect sizes were rounded to whole numbers for clarity. Effect sizes were compared to the average number of individuals sampled during the corresponding round.

A linear mixed-effect model (LMER) was selected to compare the influence of multiple fixed effects since both our dependent and independent variables are quantitative and our data follows a linear trend. Linear mixed-effect models (LMER) were analysed using the R package lme4 to compare the simultaneous effect of multiple variables. Fixed effects included area of grasslands, meadows, pastures, permanent meadows, temporary meadows, ecological meadows, meadows mowed without a conditioner, meadows mowed with a conditioner, year, round and sun with the sector as a random effect. LMERs were assessed overall and for each year. In accordance with statistical parsimony, a simplified minimum adequate model (MAM) was established by dropping non-significant variables using a likelihood ratio test (ANOVA).

Results

Overview

First, land use and wild bee community response variables were tested for normality using a Shapiro-Wilk test which indicated a non-normal distribution for all variables. The homogeneity of variance was tested for each variable using the Fligner-Killeen test. When we obtained a p-value > 0.05, we could conclude there were no significant differences between the sampled variances. Autocorrelation function plots (ACF) were used to test for autocorrelations between variables. Each of these tests were considered in relation to model assumptions to ensure appropriate models were selected. The non-normal distribution of our data is also an important consideration for interpretation. All relationships between land use variables and wild bee community response variables were first assessed using linear regression models (LMs) (Table 4) and scatter plots to visualize the effect. Linear mixed effect models (LMERs) were then used to compare the effect of multiple independent variables. For our LMER analysis, our dependant variable was log-transformed to improve data distribution. Relationships were evaluated at various time scales to establish temporal trends.

Table 4. Indicates the relationship between variables based on linear regression models (LM). Analysis completed using the 2018 dataset. Colour represents the direction of the relationship; grey cells indicate positive relationships and white cells indicate negative relationships. Statistical significance levels: blank = no statistical significance, * = 0.05 - 0.01, ** = 0.01 - 0.001, *** < 0.001.

	Area of grasslands	Area of meadows	Area of pastures	Area of permanent meadows	Area of temporary meadows	Area of meadows mown without conditioner	Area of ecological meadows
Abundance	*	**		**			
Diversity							
Grassland guild abundance		**		**			
Fabaceae guild abundance		*		*			
Forest guild abundance							

Land Use

All land use variables were evaluated based on their cumulative and individual impacts to better identify underlying patterns. To assess potential confounding, Kendall's rank correlation was used to test correlation significance between land use variables (Table 5). Significant correlations were present between many variables, as some types of grasslands were included in multiple variables. However, some of the confounding variables provide important insight into the potential influences of other types of land use. The proportion of meadows mowed without a conditioner are significantly, positively correlated with total pasture area and significantly, negatively correlated with ecological meadow area. The correlations present between land use variables are important considerations for result interpretation.

Table 5. Correlations between land use variables based on Kendall's rank correlation. Colour represents the direction of the relationship; grey cells indicate positive correlations and white cells indicate negative correlations. Significance levels: blank = no significance, * = 0.05 - 0.01, ** = 0.01 - 0.001, *** < 0.001.

	Total grassland area	Total meadow area	Total area mowed without conditioner	Total area mowed with conditioner	Total area permanent meadows	Total area temporary meadows	Total area ecological meadows	Total pasture area	Propotion of meadow mowed without conditioner	Propotion of meeadow that is permanent
Total grassland area		***	***	***	***	***		***	***	***
Total meadow area	***		***	***	***	***	***			***
Total area mowed without conditioner	***	***			***	***		***	***	**
Total area mowed with conditioner	***	***			***	***	***		*	***
Total area permanent meadows	***	***	***	***		*	**	***	*	***
Total area temporary meadows	***	***	***	***	*				*	
Total area ecological meadows		***		***	**			***	**	
Total pasture area	***		***		***		***		***	***
Proportion of meadow mowed without conditioner	***		***	*	*	*	**	***		
Proportion of meadow that is permanent	***	***	**	***	***			***		

Wild Bee Specimens

A total of 5,598 wild bee specimens were sampled from 2018 – 2020 across the 83 sampling sites (Table 6). Wild bees belonged to all six bee families present in Switzerland: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae and Melittidae, and to 20 genera including: *Andrena, Anthidium, Anthophora, Bombus, Chelostoma, Colletes, Eucera, Halictus, Heriades, Hoplitis, Hylaeus, Lasioglossum, Megachile, Melitta, Nomada, Osmia, Sphecodes, Stelis, Trachusa* and *Xylocopa* (Table S2).

Table 6. Total number of wild bees sampled during each round and year, indicates wild bee abundance, diversity, grassland guild abundance, Fabaceae guild abundance and number of red list species. All 30 sectors were sampled in 2018, while only half of the sectors (15) were sampled during 2019 and 2020.

Round 1					
Year	Abundance	Diversity	Grassland	Fabaceae	Red list
2018	324	52	292	102	3
2019	399	54	342	79	3
2020	121	33	113	36	3
Round 2					
Year	Abundance	Diversity	Grassland	Fabaceae	Red list
2018	522	68	498	279	4
2019	333	61	319	127	4
2020	121	30	111	49	0
Round 3					
Year	Abundance	Diversity	Grassland	Fabaceae	Red list
2018	1959	77	1946	1060	9
2019	213	48	202	126	4
2020	341	30	339	154	2
Round 4					
Year	Abundance	Diversity	Grassland	Fabaceae	Red list
2018	519	52	512	275	4
2019	682	55	668	207	3
2020	64	20	61	26	0

Grasslands

To investigate the impact of grassland area on the wild bee community response variables, we analysed our data using LMs for each year and round (Figure S1). The total area occupied by grasslands ranged from 13.8% to 70.5% per sector during 2018 (Table 7). No significant relationships were found between the area of grasslands and wild bee diversity for any year, round or overall ($R^2 < 0.001$, $F(1, 221) = 0.14$, $p = 0.71$). No significant relationships were found between any land use variable and wild bee diversity or the number of red list species; therefore, the remaining analyses will focus solely on the response of wild bee abundance. The total area occupied by grasslands was significantly related with wild bee abundance for 2018 overall ($R^2 = 0.04$, $F(1, 107) = 4.14$, $p = 0.044$) and for round 4, 2018 ($R^2 = 0.32$, $F(1, 28) = 13.07$, $p = 0.001$) (Figure 3). For round 4, 2018 our LM indicated approximately one more wild bee individual could be found for each 20 ha area of grasslands. This represents a 47.8% increase in wild bee abundance per 50% coverage of grasslands as compared to the average number of individuals sampled at round 4, 2018 (17 individuals). At round 4 of 2018, the total area of grasslands was significantly related with grassland bee abundance ($R^2 = 0.31$, $F(1, 28) = 12.62$, $p = 0.001$) and Fabaceae bee abundance ($R^2 = 0.50$, $F(1, 28) = 27.93$, $p < 0.001$), while no significant relationship was observed between grassland area and forest bee abundance ($R^2 = 0.08$, $F(1, 28) = 2.55$, $p = 0.121$) (Figure S2). We tested a LMER which included the area of grasslands in addition to round, year and daily sunshine plus sector as a random effect. Overall, only sunshine had predictive power for wild bee abundance ($b = 0.01$, $SE = 0.004$, $t = 2.68$). A LMER for 2018 indicated the predictive power of the area of grasslands for wild bee abundance ($b = 1.99$, $SE = 0.59$, $t = 3.38$).

Table 7. Indicates the minimum and maximum coverage per sector of land use variables for 2018.

Land Use Variable	Minimum Coverage per Sector (%)	Maximum Coverage per Sector (%)
Grasslands	13.8%	70.5%
Meadows	8.5%	53.4%
Pastures	3.6%	34.4%
Intensive Pastures	0.2%	10.0%
Ecological Pastures	0.0%	29.1%

Wild Bee Abundance vs Area of Grasslands – 2018

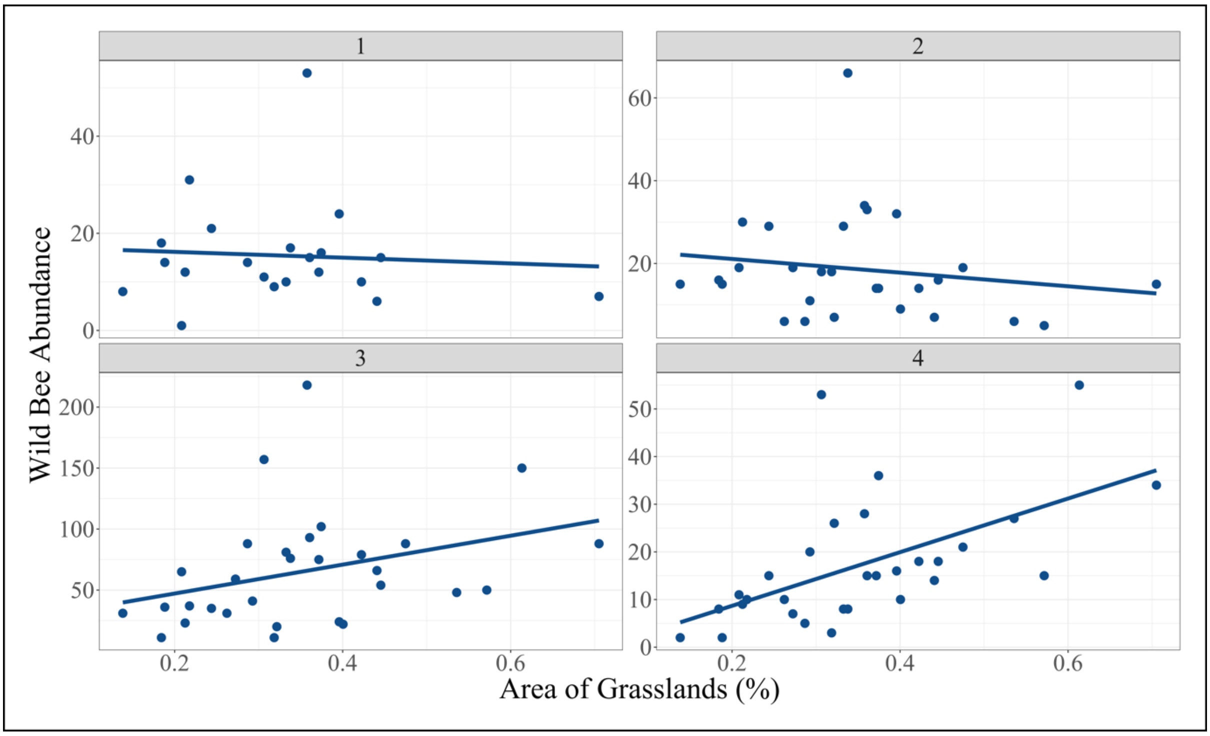


Figure 3. Relationship between wild bee abundance and the total area occupied by grasslands per sector. Based on the 2018 dataset, fitted lines based on linear regression models (LM).

Grasslands can vary greatly in their composition; therefore, we consider how changes in wild bee abundance relate to the area of meadows and pastures (Figure 4). The relationship between meadow area and wild bee abundance was significant for 2018 overall (R^2 = 0.08, F(1, 107) = 8.92, p = 0.003), round 3, 2018 (R^2 = 0.21, F(1, 28) = 7.52, p = 0.011) and round 4, 2018 (R^2 = 0.39, F(1, 28) = 17.92, p < 0.001). For round 3 of 2018, our LM suggests approximately two more wild bee individuals could be found for each 10 ha area of meadow coverage. This represents a 91.9% increase in wild bee abundance per 50% coverage of meadows as compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals). During 2018, the area of meadows was significantly related with grassland bee abundance (R^2 = 0.08, F(1, 107) = 9.12, p = 0.003) and Fabaceae bee abundance (R^2 = 0.05, F(1, 107) = 5.30, p = 0.023) whereas no significant relationship was found between the area of meadows and forest bee abundance ($R^2 = 0.02$, $F(1, 107) = 1.94$, $p = 0.167$).

Total area of pasturelands was not significantly related with wild bee abundance for any round or year. When intensive pastures were analysed individually, a significant relationship was found between wild bee abundance and the area of intensive pastures overall ($R^2 = 0.05$, $F(1, 221) = 11.45$, $p < 0.001$), for 2018 ($R^2 = 0.07$, $F(1, 107) = 8.07$, $p = 0.005$), for round 3, 2018 ($R^2 = 0.27$, $F(1, 28) = 10.52$, $p = 0.003$) and for round 4, 2018 ($R^2 = 0.2$, $F(1, 28) = 7.00$, $p = 0.013$). For round 3 of 2018, our LM indicated about eight more wild bee individuals could be found for each 10 ha coverage of intensive pastures. This represents a 91.9% increase in wild bee abundance per 10% coverage of intensive pastures compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals). During 2018, the area of intensive pastures was significantly related with grassland bee abundance ($R^2 = 0.07$, $F(1, 107) = 7.69$, $p = 0.007$) and Fabaceae bee abundance ($R^2 = 0.04$, $F(1, 107) = 4.09$, $p = 0.046$) whereas no significant relationship was found between the area of intensive pastures and forest bee abundance ($R^2 = 0.001$, $F(1, 107) = 0.14$, $p = 0.714$). No significant relationships were found between the area of ecological pastures and wild bee abundance for any round or year. A LMER for the 2018 dataset including meadow area, pasture area, round and daily sunshine with sector as a random effect indicated total meadow area had predictive power for wild bee abundance ($b = 3.07$, $SE = 0.78$, $t = 3.92$), while total pasture area did not ($b = 0.35$, $SE = 0.99$, $t = 0.36$), Wild Bee Abundance vs Area of Meadows and Pastures – 2018

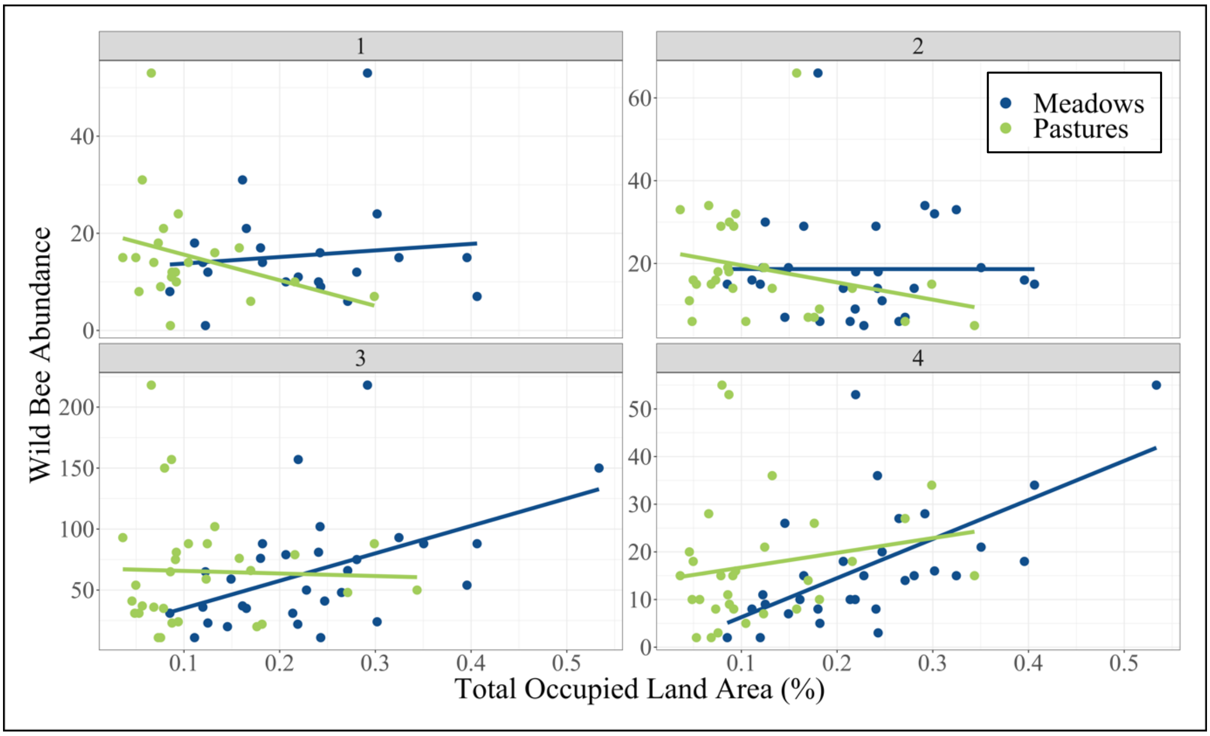


Figure 4. Abundance of wild bees in relation to the area per sector occupied by meadows and pastures. Based on the 2018 dataset with fitted lines based on linear regression models (LM).

Permanent and Temporary Meadows

To further investigate how characteristics of meadows can influence the wild bee community, we analysed the relationship between the area of permanent meadows and wild bee abundance (Figure S3). The total area occupied by permanent meadows ranged from 1.1% to 37.6% per sector during 2018 (Table 8). Positive effects were evidenced between the area of permanent meadows and wild bee abundance during 2018 for round 3 (R^2 = 0.20, F(1, 28) = 7.11, p = 0.013) and round 4 (R^2 = 0.48, F(1, 28) = 25.57, p < 0.001) (Figure 5). Wild bee abundance and the area of permanent meadows were significantly related for 2018 overall (R^2 = 0.07, F(1, 107) = 8.65, p = 0.004) and for round 3 of all years (R^2 = 0.08, F(1, 57) = 4.84, p = 0.032). Our LM for round 3 of 2018 indicated that two more wild bee individuals could be found for each additional 10 ha of permanent meadows which represents an 84.6% increase in wild bee abundance per 30% coverage of permanent meadows compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals). During round 4 of 2018, one wild bee individual could be found for every additional 10 ha of permanent meadows which represents a 144% increase in wild bee abundance per 30% coverage of permanent meadows as compared to the average number of individuals sampled per site during round 4 of 2018 (17 individuals). During 2018, the area of permanent meadows was significantly related with grassland bee abundance (R^2 = 0.07, $F(1, 107) = 8.41$, $p = 0.005$) and Fabaceae bee abundance (R^2 = 0.06, $F(1, 107)$ = 6.58, $p = 0.012$) whereas no significant relationship was found between the area of permanent meadows and forest bee abundance (R^2 = 0.006, $F(1, 107) = 0.73$, $p = 0.395$).

Table 8. Indicates the minimum and maximum coverage per sector of land use variables for 2018.

Land Use Variable	Minimum Coverage per Sector (%)	Maximum Coverage per Sector (%)
Permanent Meadows	1.1%	37.6%
Praperm00 (permanent meadows with no agroecological measures)	0.9%	34.1%
Praperm29 (permanent meadows mowed without a conditioner)	0.0%	7.0%
Temporary Meadows	3.7%	19.2%
Pratemp00 (temporary meadows with no agroecological measures)	2.0%	16.4%
Pratemp22 (temporary meadows with a floral strip)	0.0%	0.9%
Pratemp23 (temporary meadows with delayed mowing)	0.0%	2.3%

Wild Bee Abundance vs Area of Permanent Meadows – 2018

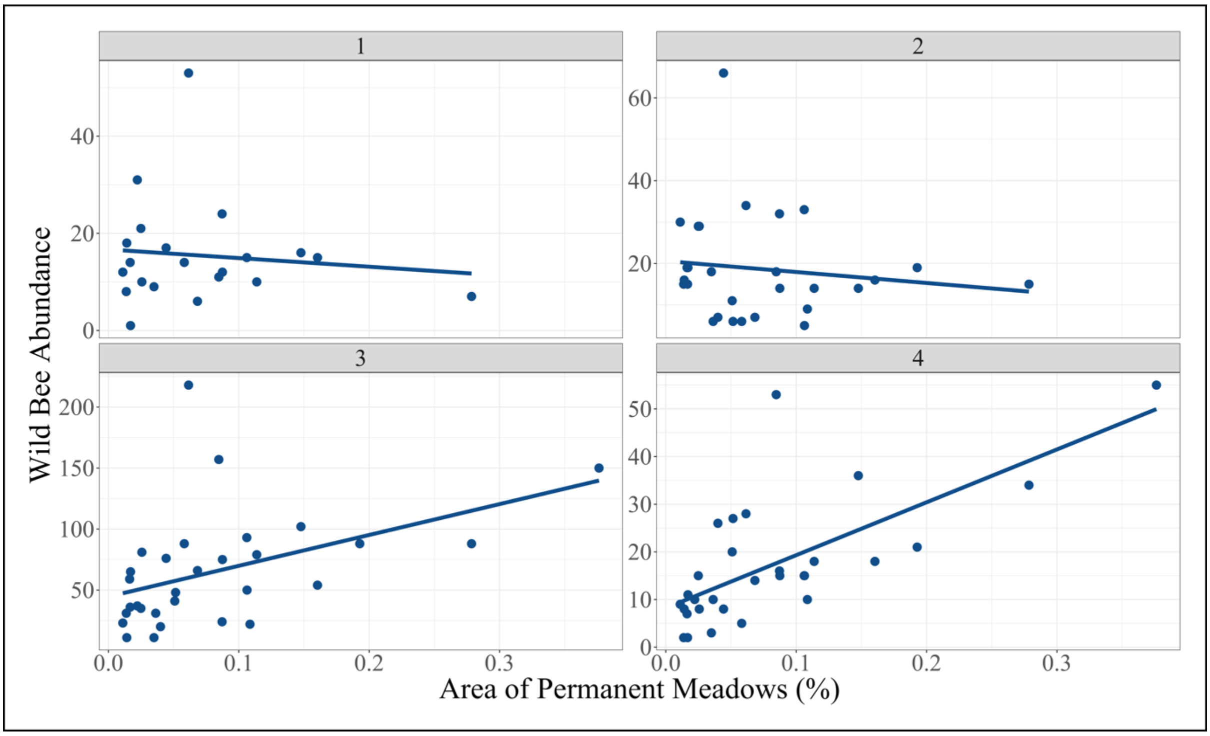


Figure 5. Abundance of wild bees in relation to the area of permanent meadows per sector (linear regressions model (LM)). Based on the 2018 dataset and organized by round.

To further investigate the specific influence of permanent meadow area on wild bee abundance, each type of permanent meadow was analyzed individually (Figure 6). During round 3 of 2018, wild bee abundance was significantly related with the area of permanent meadows mowed with a conditioner (praperm00) (R^2 = 0.17, F(1, 28) = 5.92, p = 0.022) and permanent meadows mowed without a conditioner (praperm29) (R^2 = 0.15, F(1, 28) = 4.99, p = 0.034). During round 4 of 2018, a significant relationship was present between wild bee abundance and the area of praperm00 (R^2 = 0.51, F(1, 28) = 28.99, p < 0.001) but not with the area of praperm29 (R^2 = 0.09, F(1, 28) = 2.89, p = 0.101). The LM for round 3 of 2018 indicated there were about eight more wild bee individuals found for every additional 10 ha area of permanent meadows mowed without a conditioner. This represents a 53.5% increase in wild bee abundance per 5% area covered with permanent meadows mowed without a conditioner as compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals). The LM indicated about two more wild bees were found for every additional 10 ha area of permanent meadows mowed with a conditioner. This represents a 14.4% increase in wild bee abundance per 10% coverage of praperm00 as compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals).

Wild Bee Abundance vs Area of Permanent Meadows – 2018

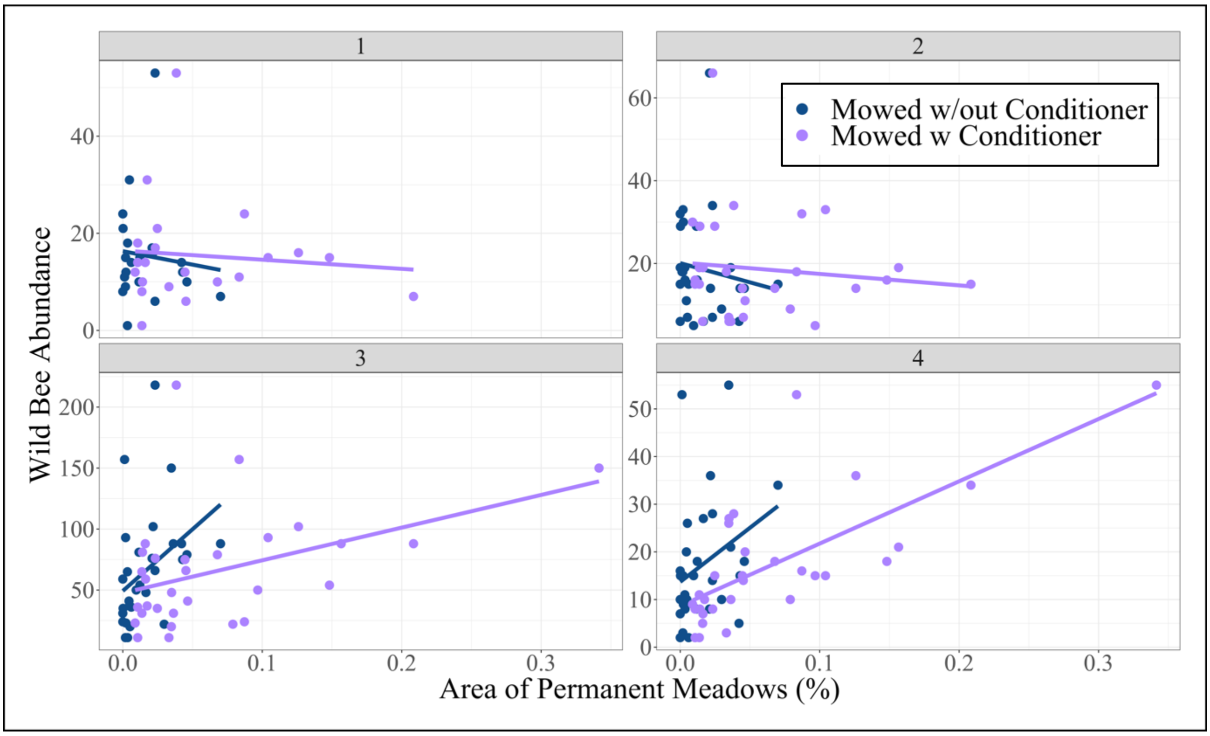


Figure 6. Relationship between wild bee abundance and the area of permanent meadows per sector in 2018, based on linear regression models (LM) and organized by round.

To better assess the influence of meadow permanence, we investigated the relationship between wild bee abundance and the area of temporary meadows (Figure 7). Overall, no significant relationships were found between the total area of temporary meadows and wild bee abundance for any round or year (Figure S4). We then analyzed each type of temporary meadow individually to determine what each variable contributed on its own. Temporary meadows mowed without a conditioner will be discussed under the conditioner use section. A significant relationship was found between wild bee abundance and the area of temporary meadows with a floral resource strip (pratemp22) for round 2, 2018 (R^2 = 0.18, $F(1, 26) = 5.79$, $p = 0.023$) and round 3, 2019 ($R^2 = 0.30$, $F(1, 12) = 5.16$, $p = 0.042$). However, it is important to note that pratemp22 occupied a maximum of 0.9% of the total sector area.

Wild Bee Abundance vs Area of Meadows - 2018

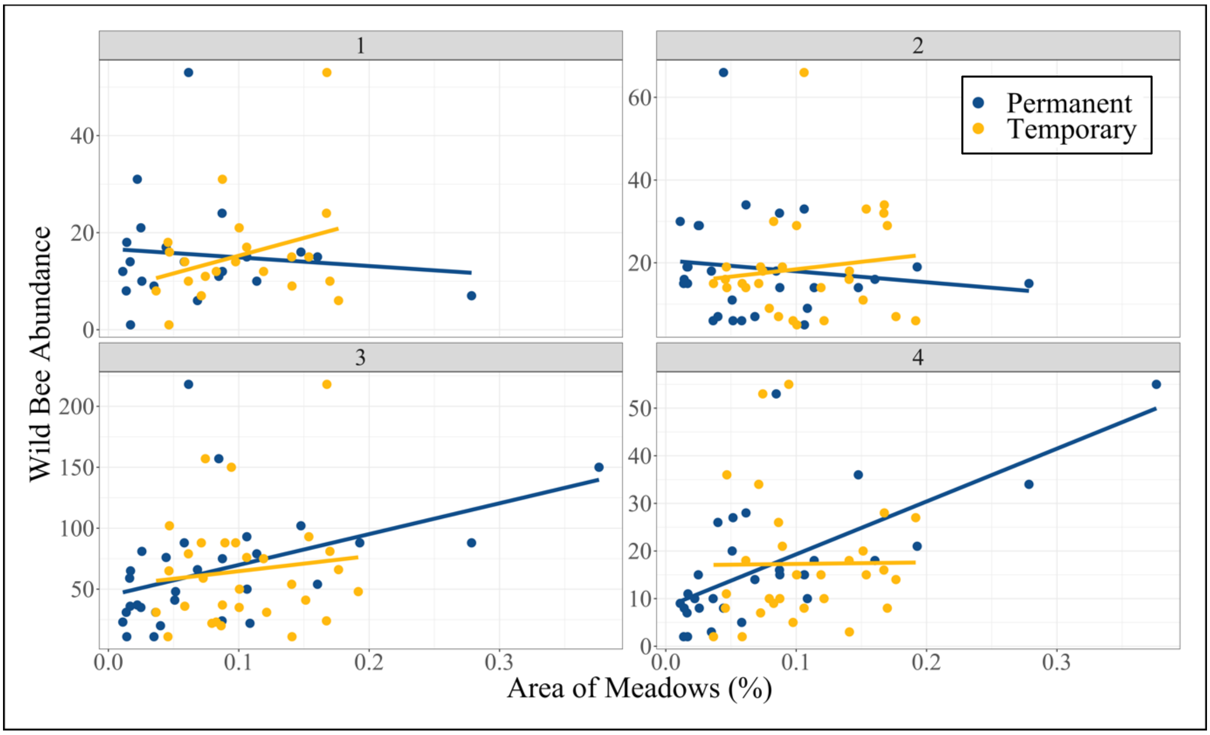


Figure 7. Abundance of wild bees in relation to the area of permanent and temporary meadows. Created using the 2018 dataset, with fitted lines based on linear regression models (LM).

To compare the influence of multiple independent variables on wild bee abundance, we analysed our data using LMERs. Our model included the area of permanent meadows in addition to the area of temporary meadows, round, year and sunshine plus sector as a random effect. Overall, only sunshine had predictive power for wild bee abundance (b = 0.01, SE = 0.004, t = 2.69). A LMER based only on the 2018 dataset revealed the predictive power of permanent meadows (b = 3.51, SE = 0.96, t = 3.66). Temporary meadows had no predictive power in any model.

Ecological Meadows

The overall area of ecological meadows did not have a significant relationship with wild bee abundance. The total area occupied by ecological meadows ranged from 1.9% to 9.5% per sector during 2018 (Table 9). The area of ecological meadows mowed with a conditioner (praecol00) had a significant relationship with wild bee abundance for 2018 overall (R^2 = 0.04, F(1, 107) = 4.23, p = 0.042) and at round 3, 2018 (R^2 = 0.17, F(1, 28) = 5.57, p = 0.026) (Figure S5). Our LM indicated about 10 more wild bee individuals could be found for every additional 10 ha area of ecological meadows (praecol00) during round 3 of 2018. This represents a 40.5% increase in wild bee abundance per 7.5% coverage of praecol00 compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals). During round 3 of 2018, the area of ecological meadows (praecol00) was significantly related with grassland guild abundance (R^2 = 0.17, F(1, 28) = 5.54, p = 0.026), Fabaceae guild abundance (R^2 = 0.14, F(1, 28) = 4.66, p = 0.040) but not forest guild abundance (R^2 = 0.002 F(1, 28) = 0.04, p = 0.836). No significant relationship was found between wild bee abundance and the area of ecological meadows mowed without a conditioner (praecol29) for any round or year. The total area of ecological meadows did not have predictive power in any of the LMERs based on both the cumulative and yearly datasets.

Table 9. Indicates the minimum and maximum coverage per sector of land use variables for 2018.

Land Use Variable	Minimum Coverage per Sector (%)	Maximum Coverage per Sector (%)
Ecological Meadows	1.9%	9.5%
Praecol00 (ecological meadows mowed with a conditioner)	1.7%	7.5%
Praecol29 (ecological meadows mowed without a conditioner)	0.0%	2.0%

Conditioner Use

To investigate the effect of conditioner use, we analysed the response of wild bee abundance to changes in meadow area mowed without a conditioner for each year and at the round scale to establish temporal trends (Figure S6). The total area occupied by meadows mowed without a conditioner ranged from 0.0% to 9.9% per sector during 2018 (Table 10). The area mowed without a conditioner was significantly related with wild bee abundance during round 3, 2018 (R^2 = 0.18, F(1, 28) = 6.31, p = 0.018) (Figure 8). Our LM for round 3 of 2018 suggests there were about five more wild bee individuals found for every 10 ha area mowed without a conditioner. This represents a 57.4% increase in wild bee abundance per 10% area per sector mowed without a conditioner as compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals).

Table 10. Indicates the minimum and maximum coverage per sector of land use variables for 2018.

Land Use Variable	Minimum Coverage per Sector (%)	Maximum Coverage per Sector (%)
Meadows mowed without a conditioner	0.0%	9.9%
Pratemp29 (temporary meadows mowed without a conditioner)	0.0%	5.3%
Pratemp92 (temporary meadows with a floral strip and mowed without a conditioner)	0.0%	1.8%
Pratemp93 (temporary meadows with delayed mowing and mowed without a conditioner)	0.0%	2.5%
Praperm29 (permanent meadows mowed without a conditioner)	0.0%	7.0%
Meadows mowed with a conditioner	5.0%	43.2%

Wild Bee Abundance vs Area Mowed Without Conditioner – 2018

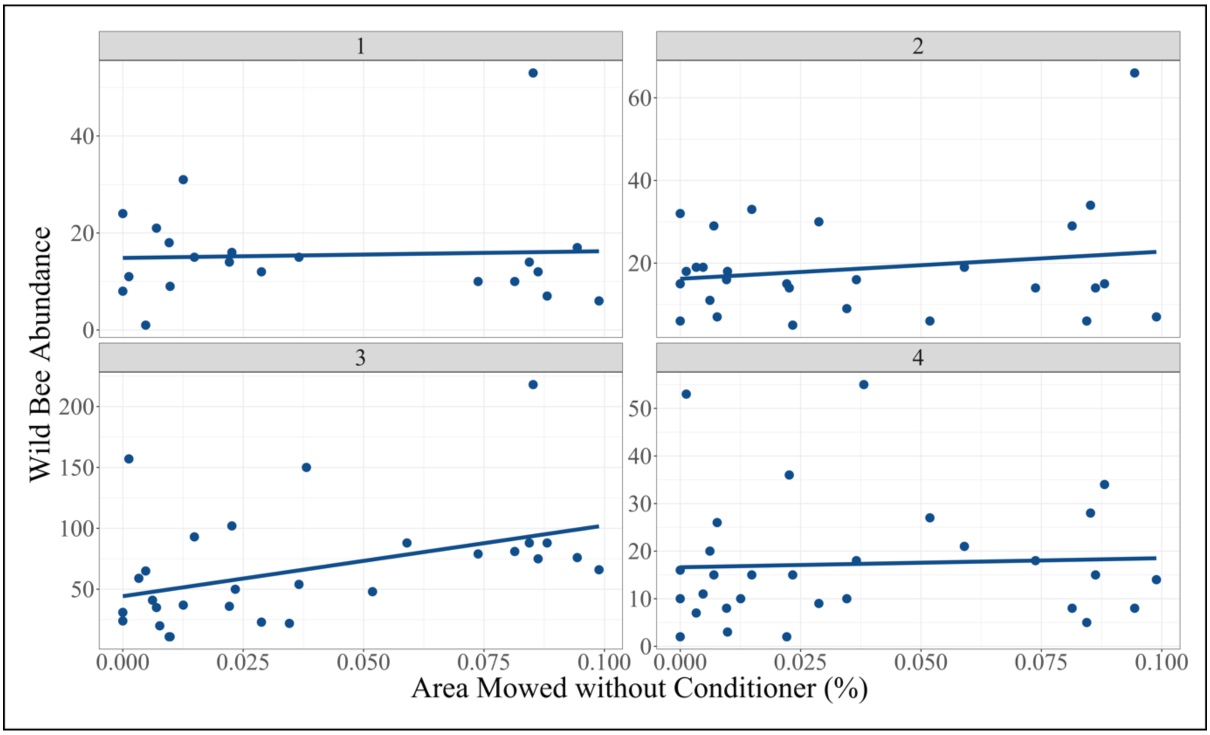


Figure 8. Wild bee abundance vs area mowed without a conditioner per sector. Created using the 2018 dataset, organised by round. Fitted lines based on linear regression models (LM).

To further investigate the influence of conditioner use, we analysed the impact on wild bee guild abundance (Figure 9). We explored the relationships between the area mowed without conditioner and the abundance of different wild bee guilds, namely grassland bees, forest bees, and bees associated with specific plant families using LMs. Grassland bee abundance and Fabaceae bee abundance were greater in areas with reduced conditioner use during round 3 of 2018; our LM indicated grassland guild abundance to be the most related with the area mowed without a conditioner (R^2 = 0.18 , F(1, 28) = 6.18, p = 0.019). The relationship between the area mowed without conditioner and Fabaceae guild abundance was also significant (R^2 = 0.14, F(1, 28) = 4.47, p = 0.044). No significant relationships were detected between the area mowed without conditioner and abundance of the Asteraceae (R^2 = 0.08, F(1, 28) = 2.54, p = 0.122), Campanulaceae (R^2 = 0.05, F(1, 28) = 1.48, p = 0.233) or forest guilds (R^2 = 0.02, F(1, 28) = 0.48, p = 0.494).

Wild Bee Abundance vs Area Mowed Without Conditioner – Round 3, 2018

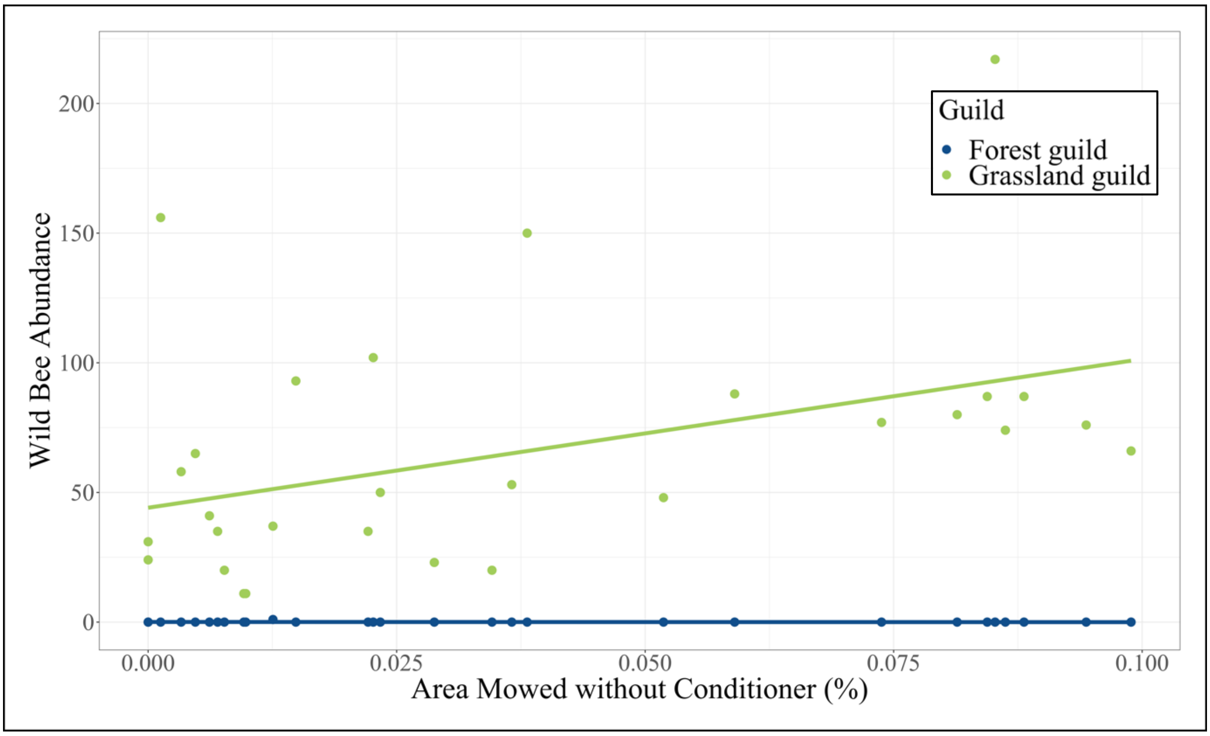


Figure 9. Relationship between wild bee abundance organised by guild and proportion of the total land area per sector mowed without a conditioner. Sampling data from round 3, 2018 with fitted lines based on linear regression models (LM).

To better understand the influence of conditioner use on wild bee abundance, we individually evaluated the effect of each of the meadow types included in the no conditioner measure (Figure S7). For round 2 of 2018, a significant relationship was found between wild bee abundance and the area of pratemp93, a temporary meadow with delayed mowing and no conditioner use ($R^2 = 0.37$, $F(1, 26) = 15.52$, $p < 0.001$). Assuming a direct effect, our LM for round 2, 2018 suggests about 10 more wild bees could be supported for each 10 ha area of temporary meadows with delayed mowing and no conditioner use. This represents a 140.5% increase in wild bee abundance per 2.5% area of pratemp93 as compared to the average number of individuals sampled during round 2 of 2018 (19 individuals).

The area of permanent meadows mowed without a conditioner (praperm29), had a strong relationship with wild bee abundance during round 3 of 2018 ($R^2 = 0.15$, $F(1, 28) = 4.99$, $p = 0.034$) (Figure 10). The area of permanent meadows mowed without a conditioner (praperm29) produced a greater effect size on wild bee abundance than the total area of meadows mowed without a conditioner. The LM for round 3 of 2018 indicated there were about eight more wild bee individuals found for every additional 10 ha area of permanent meadows mowed without a conditioner. This represents a 53.5% increase in wild bee abundance per 5% area of praperm29 as compared to the average number of individuals sampled per site during round 3 of 2018 (65 individuals). Therefore, the area of permanent meadows mowed without a conditioner had a strong relationship with wild bee abundance during late June to early July.

During 2019, a significant relationship was found for round 3 between wild bee abundance and the area of pratemp92, temporary meadows with a floral resource strip, mowed without a conditioner ($R^2 = 0.64$, $F(1, 12) = 21.27$, $p < 0.001$). Our LM suggests that about 12 more wild bees could be found for every 10 ha area of temporary meadows with a floral resource strip and no conditioner use (pratemp92). This represents a 165.3% increase in wild bee abundance per 2% area of pratemp92 as compared to the average number of individuals sampled during round 3, 2019 (15 individuals).

Wild Bee Abundance vs Area Mowed Without Conditioner – Round 3, 2018

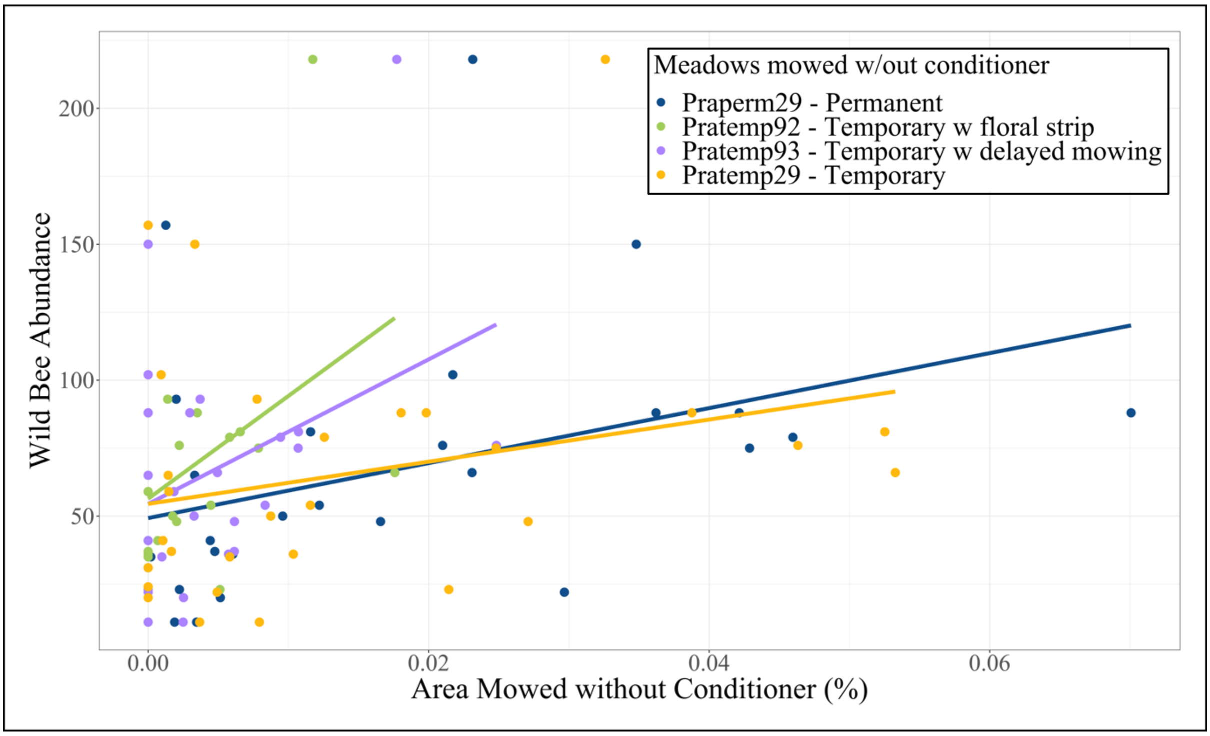


Figure 10. Relationship between wild bee abundance and the area of each meadow type mowed without a conditioner. Based on the 2018 dataset with fitted lines based on linear regression models (LM).

To directly assess the influence of conditioner use, we analysed the relationship between wild bee abundance and the proportion of grasslands mowed without a conditioner (Figure 11). During round 3 of 2018, the proportion of grasslands mowed without a conditioner was significantly related with wild bee abundance (R^2 = 0.10, F(1, 28) = 4.24, p = 0.048). No significant relationship was found between wild bee abundance and the proportion of grasslands mowed without a conditioner for any other round. This indicates the important influence of mowing time in relation to the impact of conditioner use on wild bee abundance.

Wild Bee Abundance vs Proportion of Grasslands Mowed without Conditioner - 2018

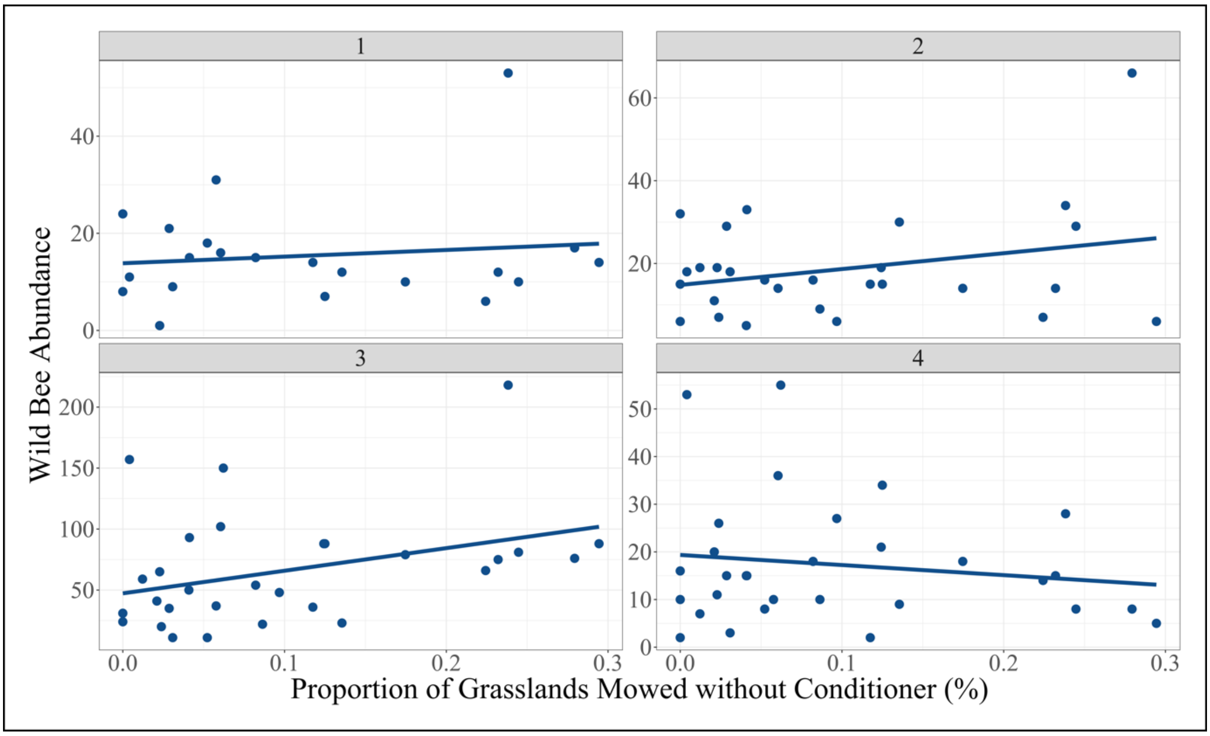


Figure 11. Relationship between wild bee abundance and the proportion of grasslands mowed without a conditioner. Data from 2018 with fitted lines based on linear regression models (LM).

Next, we compared the response of wild bee abundance to the area of meadows mowed with a conditioner (Figure 12). The area of each meadow type mowed with a conditioner was summed as a variable to test the effect of mowing with a conditioner. A similar variable was created for the meadow types mowed without a conditioner. The area of meadows mowed with a conditioner was significantly related with wild bee abundance during round 4 of 2018 (R^2 = 0.43, F(1, 28) = 21.34, p < 0.001). Our LM suggests a 10 ha area of meadows mowed with a conditioner can support one more wild bee individual, which represents a 31.8% increase in wild bee abundance per 20% area of meadows mowed with a conditioner as compared to the average number of wild bees sampled during round 4 of 2018 (17 individuals). See supplementary data for change in conditioner use over time (Figure S8).

Wild Bee Abundance vs Area of Meadows – 2018

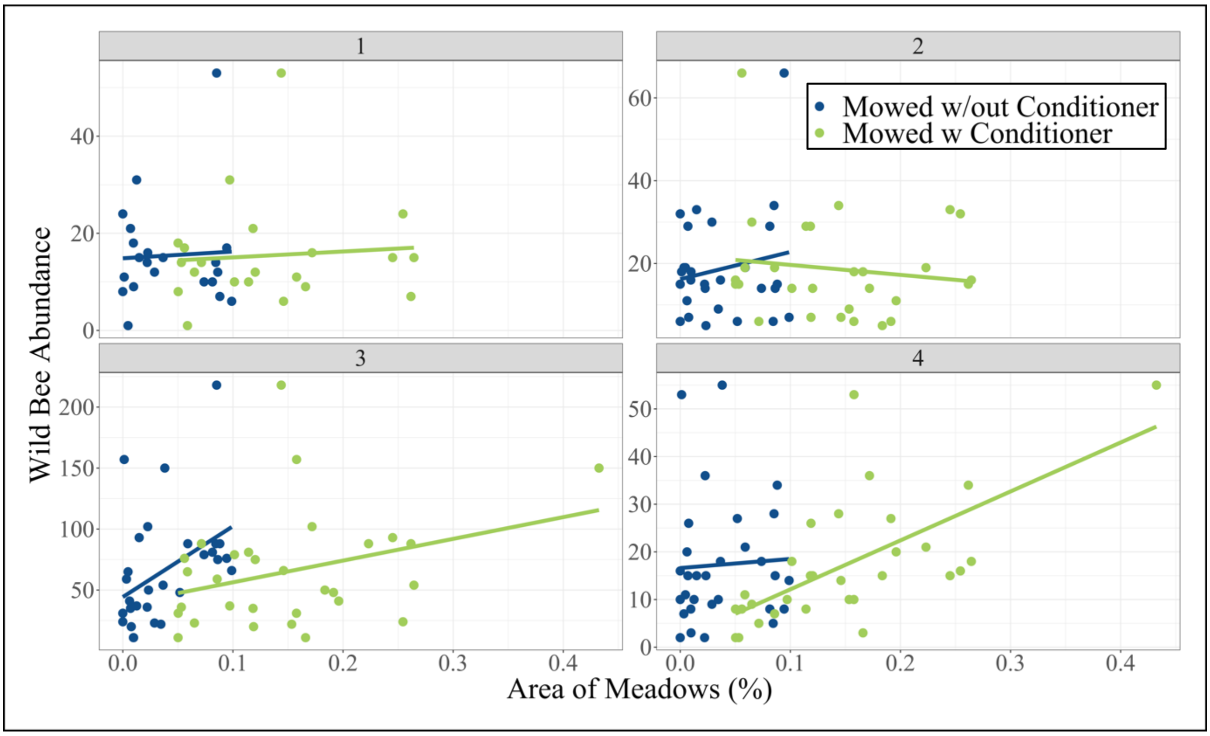


Figure 12. Abundance of wild bees in relation to the area of meadows mowed with and without a conditioner. Based on the 2018 dataset with linear regression models (LM) for fitted lines.

Finally, to simultaneously compare the influence of multiple independent variables on wild bee abundance, we analysed our data using LMERs. The first model was based on all sampled years (2018-2020) and included the area mowed without a conditioner in addition to round, year and sunshine plus sector as a random effect. The only variable with overall predictive power for wild bee abundance was daily sunshine (b = 0.01, SE = 0.004, t = 2.63). A LMER based only on the 2018 dataset demonstrates the predictive power of mowing without a conditioner (b = 6.44, SE = 2.28, t = 2.83). Additional models were created including the area of grasslands, meadows, pastures, permanent meadows, temporary meadows, meadows mowed with and without a conditioner, ecological meadows, round, year and sunshine as fixed effects. Our maximum likelihood estimation using ANOVA revealed our MAM included the area of meadows, round, year and sunshine plus sector as a random effect.

Weather Data

To investigate the influence of weather, we analyzed 2018, 2019 and 2020 climate data obtained from MétéoSuisse for the specific coordinates of each sector and sample dates of each round (MétéoSuisse, 2022). We created LMs for each of the climate variables: daily relative sunshine, daily rainfall and daily mean temperature. Daily sunshine was significantly related with abundance ($R^2 = 0.06$, $F(1, 221) = 13.19$, $p < 0.001$), diversity ($R^2 = 0.06$, $F(1, 221) = 14.11$, $p < 0.001$) and the number of red list species ($R^2 = 0.05$, $F(1, 221) = 11.42$, $p < 0.001$) based on the full dataset (Figure S9). Daily rainfall was significantly related with abundance ($R^2 = 0.03$, $F(1, 221) = 6.19$, $p = 0.014$), diversity ($R^2 = 0.08$, $F(1, 221) = 19.17$, $p < 0.001$) and the number of red list species ($R^2 = 0.03$, $F(1, 221) = 7.87$, $p = 0.005$) based on the full dataset (Figure S10). Each weather variable was significantly related with wild bee abundance at the round level for one round each. A significant relationship was found between temperature and abundance for round 4, 2018 ($R^2 = 0.15$, $F(1, 28) = 4.81$, $p = 0.037$). A significant relationship was found at round 3, 2019 between daily sunshine and wild bee abundance ($R^2 = 0.49$, $F(1, 12) = 11.52$, $p = 0.005$). Daily rainfall was significantly related with abundance during round 3, 2020 ($R^2 = 0.39$, $F(1, 13) = 8.28$, $p = 0.013$). The cumulative influence of sunshine and rainfall was much greater than at the round level. Due to its strong predictive power, sunshine was included as a fixed effect in all LMERs. Sunshine had predictive power in every model based on the cumulative and yearly datasets.

Discussion

Overview

In this study, we examined the impact of multiple land use variables in relation to wild bee abundance; we investigated the impact of (1) grassland area and the response of various bee guilds, (2) meadow and pasture area, (3) permanent and ecological meadow area, (4) area mowed without a conditioner and (5) temporal data trends. Our results suggest that an increased area of grasslands can host more abundant wild bee communities; meadows are more advantageous for wild bee abundance than pastures. Our findings indicate an increased area of permanent meadows is more beneficial for wild bee abundance than an increased area of temporary meadows. Our study shows that mowing without a conditioner positively influences wild bee abundance, specifically during peak mowing times (June/July). Bee species foraging on grassland plant families (grassland bees) and bee species foraging on Fabaceae flowers (Fabaceae bees) are identified as the bee groups most influenced by conditioner use and changes in grassland area. Bee species associated with forests (forest bees) were unaffected by changes in grassland area and conditioner use. Our evidence demonstrates the relevance of temporal trends in the efficacy of various pollinator friendly agricultural measures. Wild bee diversity, community composition, pollinator services and flowering resource community composition vary temporally which may explain the response variation in wild bee abundance between rounds (Cutler et al., 2015; Duchenne et al., 2020; Lautenbach et al., 2012). Our findings should be considered for future research and conservation policy concerning wild bee responses to agricultural practices.

Land Use

As our study is observational, potential confounding between land use variables may distort the true association present between a specific type of land use and the wild bee community response. An important consideration in our study is the strong positive correlation present between the proportion of meadows mowed without a conditioner and the total area of pastures. Areas where conditioner use is less widespread also tend to have a higher proportion of pasturelands. It is therefore difficult to isolate how each land use variable influences wild bee abundance. There is also a strong negative correlation present between the proportion of meadows mowed without a conditioner and the total area of ecological meadows. Areas where conditioner use is less widespread tend to have a lower proportion of ecological meadows. To account for the effects of confounding, we compared the influence of land use variables with their counterparts; for example, we compared the influence of changes in area of temporary and permanent meadows, and changes in the area of meadows mowed with and without a conditioner.

Grasslands

Our results demonstrate that an increased area of grasslands is related with greater wild bee abundance; the strength of this relationship increases later in the season. This is consistent with our expectations as wild bees tend to be more reliant on grasslands later in the season when floral resources are less abundant (Evans et al., 2018b). Our findings are in agreement with the first part of our hypothesis H1, that an increased proportion of grasslands could support a more abundant wild bee community. No significant relationship was observed between the area of grasslands and wild bee diversity. This may be explained by the range of species which can benefit from grasslands. Grassland bee abundance was significantly related with grassland area during round 4, 2018 and our data indicates that 98.5% of species sampled at this time were grassland bee species. Therefore, the diversity of bees that grasslands can support is limited by the foraging preferences of bees. This may explain why we observed significant differences in wild bee abundance but not diversity as the same species of bees will tend to visit grasslands. Grasslands can only provide a certain range of floral resources for bees; therefore, to positively influence wild bee diversity, it is important to diversify the landscape composition to maximize flowering plant diversity (Isbell et al., 2017). Fabaceae bee abundance was most significantly related with the area of grasslands, which highlights grasslands as an important host for Fabaceae foraging wild bee species (Harris and Ratnieks, 2021; Swiss Bee Team, 2021). The strong relationship present between grassland area and Fabaceae bee abundance suggests that grasslands are rich in flowering legumes and are therefore important habitats for wild bees who prefer Fabaceae flowering resources.

Meadows and Pastures

Grasslands can vary greatly in their structure and composition, which alters their capacity to support wild bee communities through floral resources or nesting sites (Buchholz et al., 2020; Mallinger et al., 2016). We demonstrate that meadows can support more abundant wild bee communities than pastures. This may be explained by the differences in land management as grazing in pastures tends to deplete more flowering resources than mowing in meadows (Saarinen and Jantunen, 2005). Increased meadow area is most related with wild bee abundance during later rounds (June-August). It is known that late-flying bee populations are most at risk of declines and extinction, primarily due to a lack of floral resources (Hofmann et al., 2019; Scheper et al., 2015). Therefore, it is relevant to know that meadows can act as important foraging habitats for bees during this time.

The overall area of pastureland was not significantly related with wild bee abundance, however when we assessed the pasture variables individually, we found wild bee abundance responded very differently to the area of intensive pastures and ecological pastures. Ecological pastures were negatively related with wild bee abundance while intensive pastures were significantly, positively related with wild bee abundance. Intensive pastures are usually flat and receive fertilizer which are ideal conditions for white clover growth (Harris and Ratnieks, 2021; Kruess and Tscharntke, 2002). Such conditions promote stable soil water content which allows for nectar production during drought-like conditions (Waser and Price, 2016). Since pasturelands remain untilled, there is typically high availability of habitat for nesting sites such as old burrows, hollows in twigs, grass or holes in dirt (Morandin et al., 2007). The combined impact of floral resources (especially clovers), lower vegetation height and high nesting structure availability can make intensive pastures a valuable habitat for wild bees, particularly when other such habitats are limited (Kruess and Tscharntke, 2002). Extensive pastures are often composed of a few grasses and dicotyledons, are usually sloped and tend to dry out quickly during the summer due to low water retention (Waser and Price, 2016). Such drought-like conditions may limit floral density and nectar production. Previous findings indicate no differences in wild bee abundance or diversity in areas with intensive vs extensive pastures which suggests local differences in foraging resource availability plays a more influential role (Sárospataki et al., 2009). Overall, we found that an increased area of intensive pastures could host more abundant wild bee communities which is consistent with the first part of our hypothesis, H2. Our results suggest that an increased area of intensive pastures may host more abundant wild bee communities than meadows, however this finding may be a result of the confounding between the area of intensive pastures and the area of meadows mowed without a conditioner. No significant relationship was observed between wild bee diversity and the area of pastures or the area of meadows.

Permanent and Temporary Meadows

Our findings suggest that an increased area of permanent meadows can positively influence wild bee abundance. Previous research illustrates the benefits of permanent meadows for the biodiversity of beetles, molluscs, bees and wasps (Billaud et al., 2021; Van der Meersch et al., 2022). Permanent meadows may also be important to offset some bee declines caused by meadow-to-crop conversion that occurred years ago (Le Provost et al., 2021). An increased area of permanent meadows is positively related with greater wild bee abundance during late June to early August of 2018. It is expected that this relationship be strongest later in the season, at a time when meadows act as a more valuable foraging resource for bees (Evans et al., 2018b; Mallinger et al., 2016). Our results demonstrate that a greater area of permanent meadows is significantly related with increased wild bee abundance. The strength of this relationship increases when meadows are mowed without a conditioner during peak mowing times. Both permanent meadows and no conditioner use have demonstrated a positive influence on bee abundance (Frick and Fluri, 2001; Humbert et al., 2009; Van der Meersch et al., 2022). Our evidence demonstrates that mowing without a conditioner in permanent meadows may have synergistic positive effects on wild bee abundance. Our findings are consistent with the first part of our hypothesis H2, that temporary and permanent meadows can be beneficial for wild bee abundance, but permanent meadows are more advantageous. No significant relationship was found between permanent meadows and wild bee diversity.

When all temporary meadows were analysed together, no significant relationships with wild bee abundance were found. When assessed individually, certain types of temporary meadows were related with wild bee abundance at specific rounds. Our findings suggest that temporary meadows are more impactful when multiple measures are combined; the implementation of floral resource strips or mowing without a conditioner was necessary to encourage wild bee abundance in temporary meadows. Previous research reveals the benefits of floral resource strips and mowing without a conditioner for the bee community (Frick and Fluri, 2001; Humbert et al., 2009; Ouvrard et al., 2018; Scheper et al., 2015). Further research should be done to optimize the combination of pollinator promoting ecological measures.

Ecological meadows

Ecological meadows receive no fertilizer and must follow the Swiss agri-environment scheme (AES) which dictates no mowing prior to June 15 (Buri et al., 2014; Bruppacher et al., 2016). Some research demonstrates the effectiveness of AES schemes for promoting biodiversity (Boetzl et al., 2021; Crowther and Gilbert, 2020). However, there are concerns that increased participation in AES schemes may promote landscape homogenization due to identical mowing regimes (Buri et al., 2014; Littlewood et al., 2012; Garibaldi et al., 2014). To effectively promote biodiversity, landscape heterogeneity should be prioritized for ecological agricultural schemes (Buri et al., 2014; Littlewood et al., 2012). Our results suggest that an increased area of praecol00, ecological meadows, can positively impact wild bee abundance. Our findings do not indicate a relationship between wild bee abundance and praecol29, ecological meadows mowed without a conditioner. However, the total area covered by ecological meadows mowed without a conditioner is very low (average coverage per sector is 0.6%) (Table S3). Since both AES schemes and no conditioner use have previously demonstrated a positive influence on the bee community, it is probable that mowing without a conditioner in ecological meadows would be beneficial for the wild bee community (Boetzl et al., 2021; Crowther and Gilbert, 2020; Fluri and Frick, 2002; Humbert et al., 2010). Future studies must be done to determine the impact of combining ecological meadows and no conditioner use. Overall, our findings lend support to previous work which demonstrates the positive contribution of ecological meadows for biodiversity (Boetzl et al., 2021; Crowther and Gilbert, 2020; Tonietto and Larkin, 2018). Our finding is consistent with the first part of our hypothesis H2, that a greater area of ecological meadows can host more abundant wild bee communities. No significant relationship was found between wild bee diversity and the area of ecological meadows.

Conditioner Use

Our findings indicate that mowing without a conditioner in meadows, particularly during late June and early July, can promote a more abundant wild bee community. During round 3, the overall area of grasslands and the area of meadows mowed with a conditioner are not significantly related with wild bee abundance. Meadows mowed with a conditioner are not beneficial to wild bee communities when mowing frequency is high. This highlights the importance of mowing without a conditioner during June and July to promote wild bee abundance.

Our results highlight the temporal effects of mowing. Typical mowing regimes of Swiss meadows can explain why a significant, positive relationship is present between the area of meadows mowed without a conditioner and wild bee abundance during round 3, 2018. For most farmers, the initial mow occurs in May or early June with subsequent mowing every four to five weeks depending on weather conditions (Knop et al., 2006; Kolecka et al., 2018). During the first mow in May or early June, there are often few flowering resources. By the time of the second mow, there are typically many more clovers, and therefore increased foraging resources for bees (Evans et al., 2018b; Mallinger et al., 2016). Samplings made during round 3, which runs from late June to early July, would consequently be after the second mow in most meadows. Increased floral coverage at this time could provide floral resources for a much larger bee community. Therefore, mowing with a conditioner would likely result in the killing of more wild bees (Mallinger et al., 2019). This is demonstrated in our results, as mowing without a conditioner has the strongest relationship with wild bee abundance during round 3 in 2018.

Our findings are consistent with the first part of our initial hypothesis, H3; wild bee abundance is greater is areas with reduced conditioner use, specifically during late June and early July when mowing frequency is high. No significant relationship was found between wild bee diversity and the area of meadows mowed without a conditioner. When a meadow is mowed with a conditioner, many bees present will be killed (Humbert et al., 2010). The selection of bees present during mowing will be influenced by the time of year and the type of floral resources available in the meadow (Hofmann et al., 2019; Mallinger et al., 2019).

However, we can assume the random selection of bees present should be a good representation of the current local bee community. Therefore, since death by conditioner occurs by chance, it is reasonable that conditioner use affects wild bee abundance but not diversity. Similar previous findings have demonstrated the positive effects of mowing regime changes on wild bee abundance and not diversity (Buri et al., 2014).

By organising bee species into guilds based on foraging preferences, we were able to analyze the specific impact of conditioner use on different groups of bees. Positive effects were most evident between grassland bee abundance and the area mowed without a conditioner. Positive effects were also detected between the area mowed without a conditioner and Fabaceae bee abundance while forest bee abundance was unaffected by conditioner use. The grassland guild includes species which frequently collect nectar or pollen from flowers typical of grasslands. Presumably, the majority of bees present in a grassland would be those who prefer grassland associated flowering resources. Therefore, in fields with reduced conditioner use, we would expect to sample more wild bee individuals who prefer grassland flowers, which is precisely what we found. Fabaceae flowers are typical in many grasslands which explains the significant impact of conditioner use on Fabaceae bee abundance (Harris and Ratnieks, 2021; Swiss Bee Team, 2021). Wild bees who collect foraging resources typical of forests, would rarely be found in grasslands. Our guild findings support the probable direct effect of conditioner use on wild bee abundance. This outcome is consistent with our initial hypothesis H4, as the response to mowing without a conditioner is strongest for grassland bees.

The area of each meadow type mowed without a conditioner was considered individually to establish their respective impacts on wild bee abundance. Our results demonstrate the potential benefits for wild bee abundance of implementing delayed mowing and no conditioner use as a combined measure (pratemp93), specifically in late May to early

June. Our findings also suggest combining floral resource strips and mowing without a conditioner (pratemp92) in the same meadow may provide additional benefits for wild bee abundance, specifically during late June to early July. For 2018, pratemp93 occupied a maximum of 2.5% of the total land area per sector and for 2019 pratemp92 occupied a maximum of 2.2% of the total land area per sector; therefore, to better investigate the potential benefits of combining no conditioner use with additional agroecological measures, future studies should be conducted with a larger land area. Previous findings highlight the benefits of delayed mowing, especially for providing additional floral resources earlier in the season (Buri et al., 2014; Humbert et al., 2012). Research identifies the implementation of floral resource strips as an effective method to support pollinator populations (Ouvrard et al., 2018; Scheper et al., 2015). Our findings suggest that combined measures including mowing without a conditioner are required for temporary meadows to positively influence wild bee abundance.

Positive effects were also evidenced between wild bee abundance and the area of praperm29, a permanent meadow mowed without a conditioner. Previous research highlights the important influence of permanent meadows on local biodiversity (Billaud et al., 2021; Van der Meersch et al., 2022). Our results demonstrate the value of permanent meadows mowed without a conditioner, particularly during late June to early July. Of all the meadow types mowed without a conditioner, praperm29 produced the greatest effect size on wild bee abundance. Since permanent meadows exist for many years, more wild bees could have the opportunity to discover and forage from such a meadow (Van der Meersch et al., 2022). Permanent meadows mowed without a conditioner are the most advantageous for wild bee abundance. Our results are consistent with our hypothesis H3, as the impact of conditioner use is greatest in meadow types which have the strongest positive impact on wild bee abundance.

Our evidence illustrates that reducing the proportion of grasslands mowed with a conditioner during late June to early July can increase wild bee abundance. A 30% reduction in the proportion of grasslands mowed with a conditioner could double local wild bee abundance. This is an important finding as the proportion of grasslands mowed without a conditioner is independent from the remaining land use variables. Our findings lend support to previous studies that recommend the reduction of conditioner use (Buri et al., 2014; Humbert et al., 2009; Humbert et al., 2010) particularly during peak mowing times.

Our results demonstrate that greater meadow area is related with higher wild bee abundance. The strength of this relationship increases when meadows are mowed without a conditioner. Temporal trends play an important role in the influence of conditioner use in meadows. The area of meadows mowed without a conditioner is most related with wild bee abundance in late June and early July, whereas the area of meadows mowed with a conditioner is most related with wild bee abundance in late July and early August, possibly explained by reduced mowing frequency at this time. The area of meadows mowed without a conditioner occupies one quarter of the total area occupied by meadows mowed with a conditioner. Despite this, mowing without a conditioner had a greater impact on the sampled number of wild bee individuals. This indicates the importance of mowing without a conditioner, especially in late June and early July, to support the pollinator community. Conditioner use research highlights the strategy of mowing during times of low arthropod richness to minimize mortality rates (Hecker et al., 2022; New, 2019). This study supports previous findings that indicate mowing with a conditioner in meadows is detrimental to pollinator community health and should be avoided when possible (Fluri and Frick, 2002; Hecker et al., 2022; Humbert et al., 2009; Humbert et al., 2010).

If our result is a true direct impact of conditioner use, we can deduce that meadows mowed without a conditioner have greater wild bee survival rates during mowing. Increased wild bee survival should correlate to greater wild bee abundance. Longer term studies should be conducted to assess how conditioner use can influence future wild bee populations. However, we must consider that our findings could result from an indirect effect of conditioner use. It is possible that mowing without a conditioner destroys less flowers than meadows mowed with a conditioner. In this case, the increased floral coverage may attract more wild bees. As previously discussed, it is also possible that confounding between the land use variables could have influenced our results. Future studies should avoid an observational approach to better evaluate how mowing with a conditioner influences wild bee abundance and diversity.

Weather Data

To evaluate the influence of weather during each round, we analysed the impact of daily temperature, daily relative sunshine and daily precipitation. Weather can have important impacts on bee foraging ability and also plays a significant role in wild bee behaviour (Peat and Goulson, 2005; Soroye et al., 2020; Tuell and Isaacs, 2010). Overall, daily rainfall and daily sunshine have greater predictive power for the wild bee community than daily temperature. Weather is more impactful overall than at the round level which is expected as there would be minimal variation in weather conditions within one round. If one round was much more impacted by weather conditions than another, this would be relevant for evaluating the effect of the land use variables, however this is not what we found. It is especially relevant that weather data be included in our LMERs to accurately establish each variable’s predictive power. Weather data should always be considered in ecological research to investigate the potential impact on your population of study (Tuell and Isaacs, 2010).

Limitations

Scientific research always has potential sources of error and areas for improvement. One of the major limitations of our study is that sample sizes differed between years. All 30 sectors were sampled during 2018, whereas only 15 sectors were sampled during both 2019 and 2020. By sampling sites every other year, the impact on the wild bee community should be lessened. The dataset from 2018 exhibits a more accurate representation of the actual population. Most of the significant relationships between land use variables and wild bee abundance are found in 2018. However, we cannot accurately determine if the varying trends we observe across years are due to actual differences in the population or simply a lack of adequate information due to a lower sample size.

Our study was observational as we analyzed wild bee communities in relation to local land use where agroecological measures were applied by farmers for financial compensation. This is a limitation in our study as confounding between land use variables may distort the true association between a type of land use and the response of the wild bee community. To account for confounding variables in our study we analysed the correlation present between land use variables which was considered in our interpretation. We also matched and compared the influence of opposite land use variables; for example, we compared how wild bee abundance related to the area of meadows mowed with and without a conditioner.

Another limitation of our study are the considerable differences in the proportions of land use variables. Some variables covered a very small percentage of the total land area per sector. Land use variables such as praecol29, ecological meadows mowed without a conditioner, have an average coverage of 0.6 %. Such low proportions of land coverage will be unlikely to produce any statistically significant effects. It is also less relevant to compare the impacts of land use variables with extremely different proportions of coverage.

There are many methods commonly used to sample bees, all of which have their advantages and disadvantages. Our project used yellow combi-traps which evidence indicates can encounter many problems such as varied success with different colours and sizes and contents being spilled or degraded (Prendergast et al., 2020). This sampling method is biased towards only catching low-flying, slow and small bees (Giles and Ascher, 2006; Prendergast et al., 2020). Combi-traps are shown to sample the highest number of individuals, but the lowest diversity (McCravy and Ruholl, 2017). This bias may have played a role in our results, as no significant relationships were found between the area of any land use variable and wild bee diversity.

Future Research

All samplings were made in the cantons of Vaud, Jura and Bern, Switzerland; therefore, similar studies should be conducted in various climates to determine how land use impacts may differ. Pollinator responses to land use changes, weather conditions, climate change, pathogens and invasive species can vary worldwide which is an important consideration for future studies to better represent global pollinator trends (Aizen et al., 2008; Osterman et al., 2021). Considering that we have evaluated all types of land use, we can have confidence that our findings reflect true relationships between land use and the wild bee community. However, land use can indirectly affect parasite prevalence, floral resources and nesting site availability (Evans et al., 2018a; Papanikolaou et al., 2017). Future research should work to quantify the indirect effects of land use to understand the mechanisms by which they influence the wild bee community. It is important for future studies to consider how changes in land use or mowing regimes can impact certain species differently, such as those using the habitat for feeding vs nesting purposes (Meyer et al., 2017).

Previous research indicates pollinator populations benefit from the implementation of nesting structures, delayed mowing, mowing without a conditioner and floral resource strips (Fortel et al., 2016; Humbert et al., 2010; Knop et al., 2006; Ouvrard et al., 2018; Scheper et al., 2015). Our findings indicate that combinations of these measures may provide more substantial positive impacts for the wild bee community. Future research should attempt to optimize the combination of measures to improve the efficacy of pollinator promoting agroecological measures.

Major differences in land use proportions make it difficult to accurately compare their influence. Further research regarding the impacts of land use on wild bees should consider land use proportions when selecting sampling locations. Our findings and previous research suggest permanent meadows may provide more benefits to the wild bee community than temporary meadows (Van der Meersch et al., 2022). Therefore, future studies should include meadow age as a covariate to determine the optimal meadow age for assisting pollinator populations. Our study is composed of data sampled over three years (2018 – 2020) and is therefore focused on the short-term impacts of land use. Future research should investigate the long-term impacts of land use to see how changes in agricultural management can influence future pollinator populations.

Conclusions

Our study demonstrates that grasslands, particularly meadows, can act as important habitats for wild bees. Permanent meadows can support more abundant wild bee communities than temporary meadows (Billaud et al., 2021; Van der Meersch et al., 2022). Since agricultural intensification is a major driver of pollinator declines (Dicks et al., 2021; Potts et al., 2010; Vanbergen, 2013), it is essential to identify measures which can reduce the negative impacts of agriculture. Our research suggests that mowing meadows without a conditioner can promote wild bee abundance, specifically during peak mowing times in late June and early July. Mowing without a conditioner is most beneficial when implemented in permanent meadows or in combination with other agroecological measures such as floral resource strips or delayed mowing. Varied pollinator friendly mowing regimes across a heterogeneous landscape will ensure the availability of various resources across time and space (Buri et al., 2014; Littlewood et al., 2012). Our evidence contributes valuable considerations for future studies of agricultural management and pollinator conservation practices.

Acknowledgements

I am incredibly grateful to everyone who contributed to the completion of my thesis. I would like to express my deepest gratitude to Christophe Praz for his invaluable feedback and supervision of my project. This endeavor would not have been possible without the support of Yann-David Varennes and his contributions to project design and methodology. I am deeply grateful to Jan Hattendorf for his guidance and advice regarding statistical analyses. A special thanks to Louis Sutter and Matthias Albrecht for their contributions to result interpretations and wild bee discussions. My deepest thanks to Pamela Pettman, Sherry Agellon and Luis B. Agellon for their valued advice and feedback. This study would not have been possible without the support of the “Agriculture et Pollinisateurs” project. I am very grateful to the Université de Neuchâtel for allowing me to conduct my research. Finally, I wish to thank my friends and family for their support and encouragement throughout my study.

Supplementary Data

Wild Bee Abundance vs Area of Grasslands

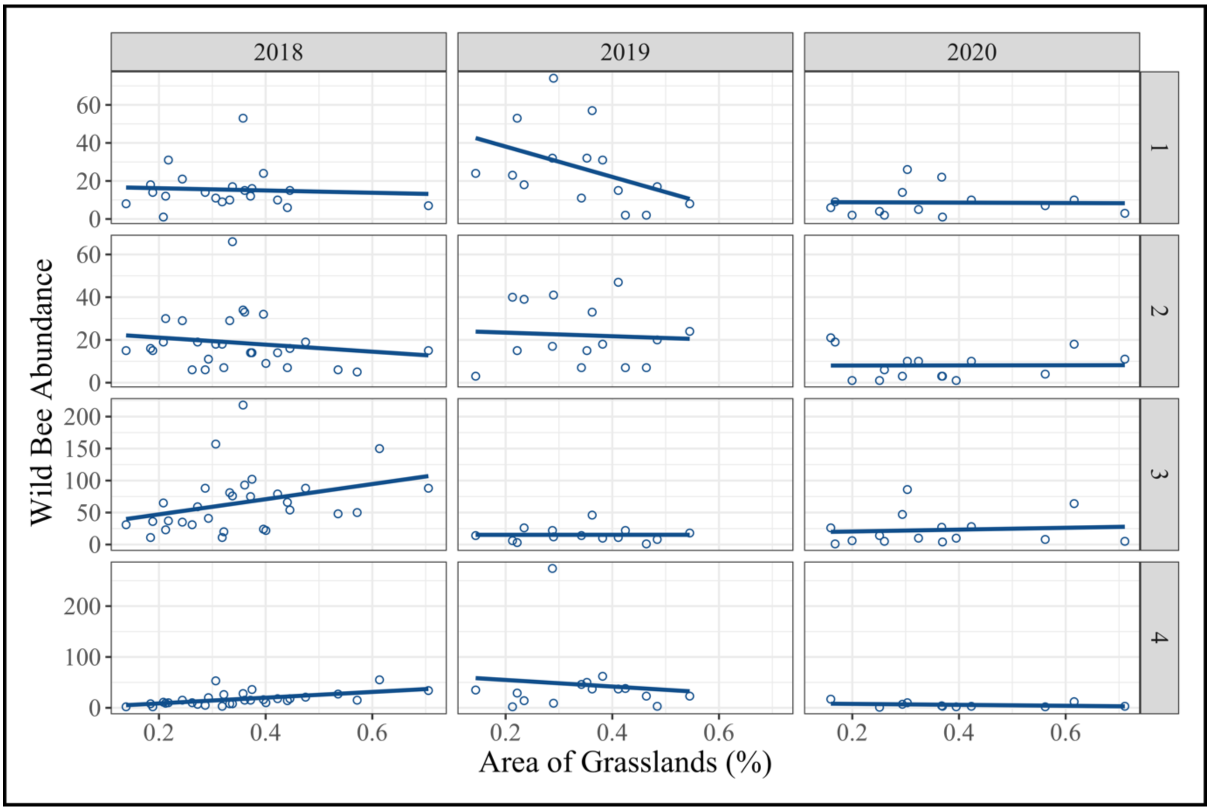


Figure S1. Abundance of wild bees in relation to the total area of grasslands. Organized by year and round, fitted lines based on linear regression models (LM).

Wild Bee Abundance vs Area of Grasslands – Round 4, 2018

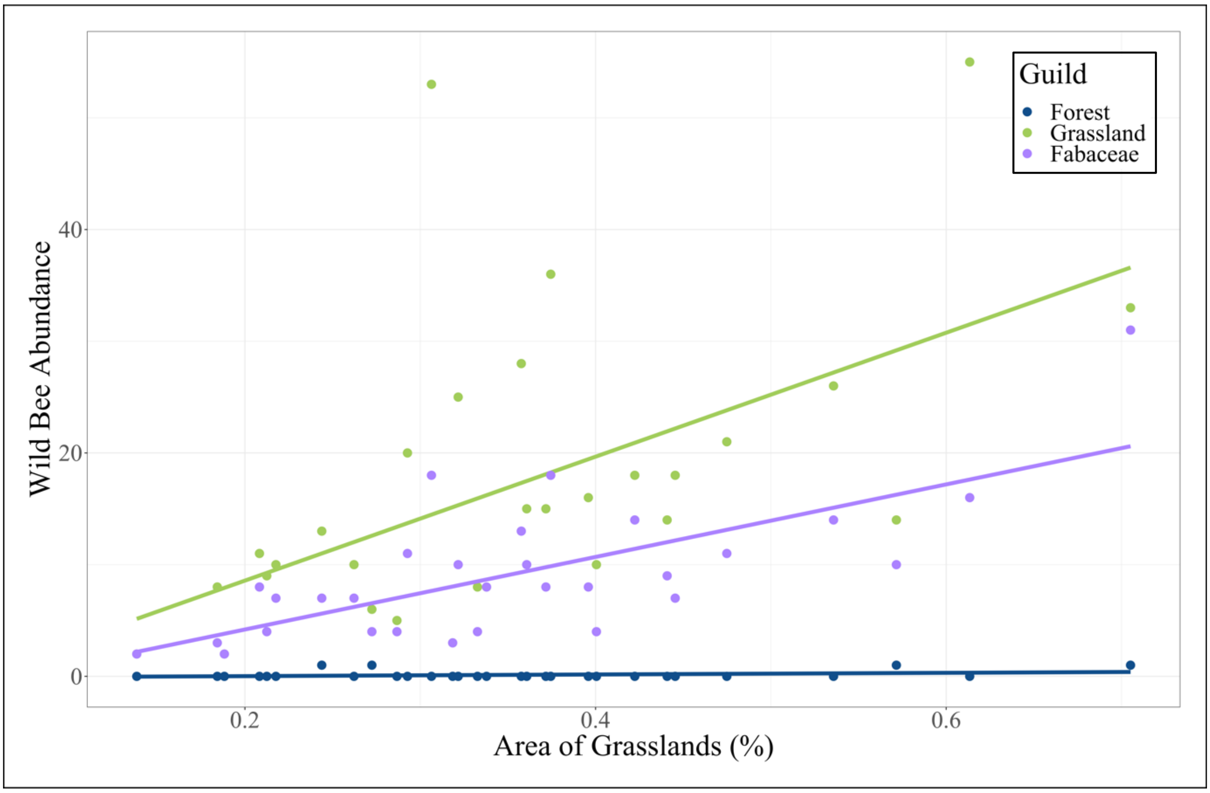


Figure S2. Relationship between the abundance of forest bees, grassland bees and Fabaceae bees and the area of grasslands. Sample data from round 4 of 2018 with fitted lines based on linear regression models (LM).

Wild Bee Abundance vs Area of Permanent Meadows

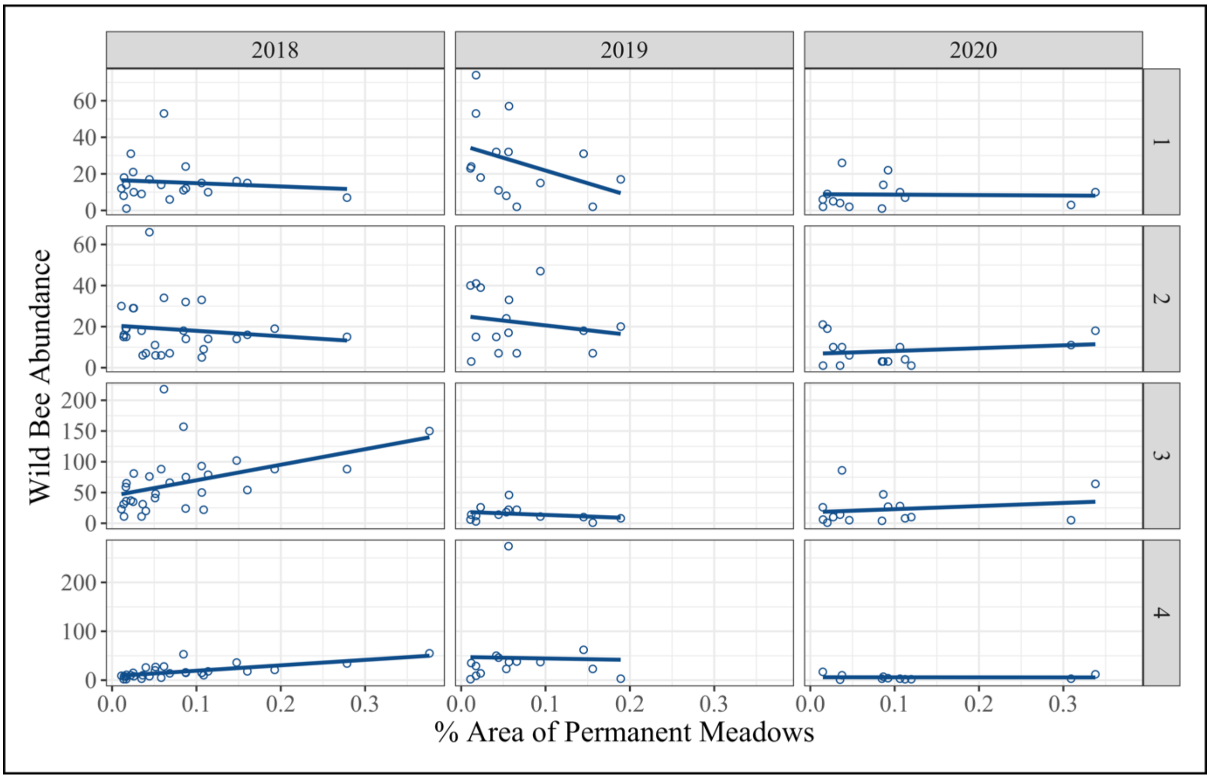


Figure S3. Wild bee abundance in relation to the area of permanent meadows per sector. Organized by year and round, fitted lines based on linear regression models (LM).

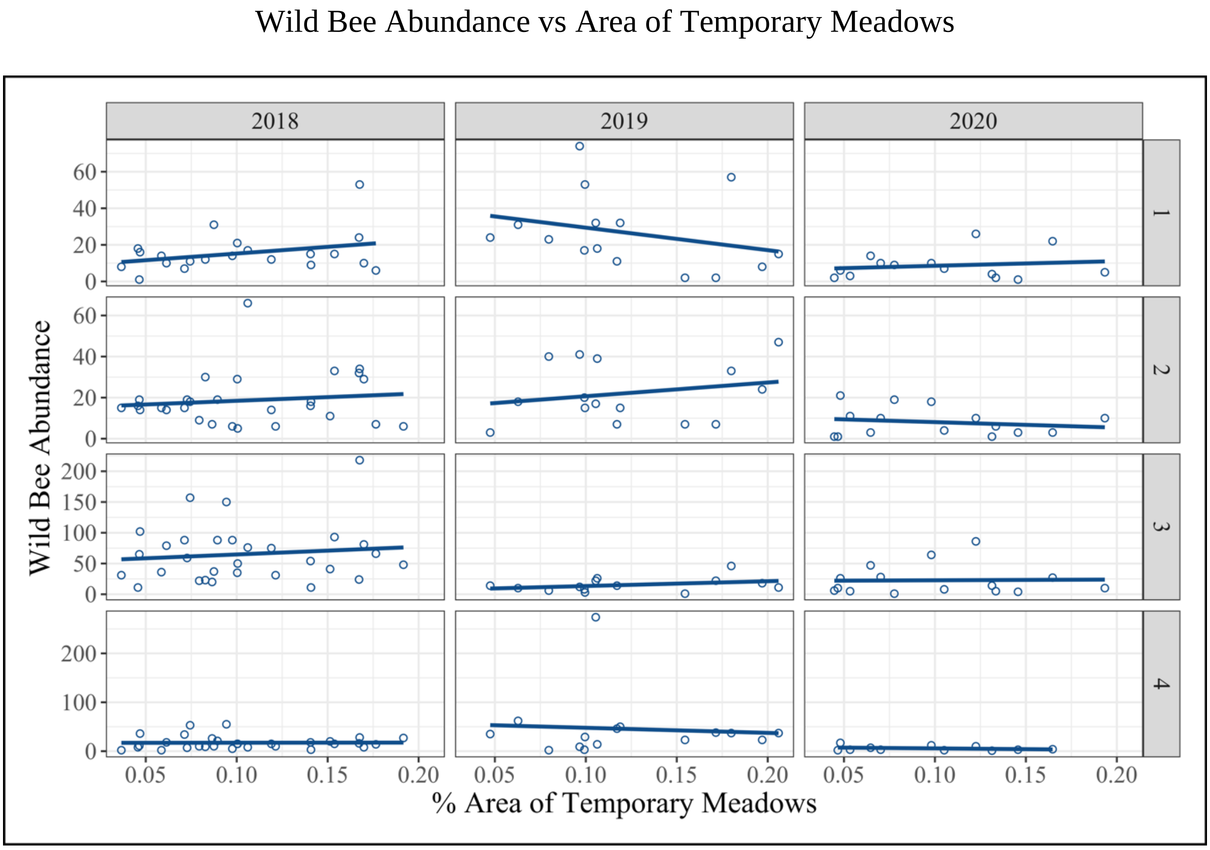


Figure S4. Relationship between wild bee abundance and the area of temporary meadows. Organized per round, created using full dataset (2018-2020). No significance found for any round based on linear regression models (LM).

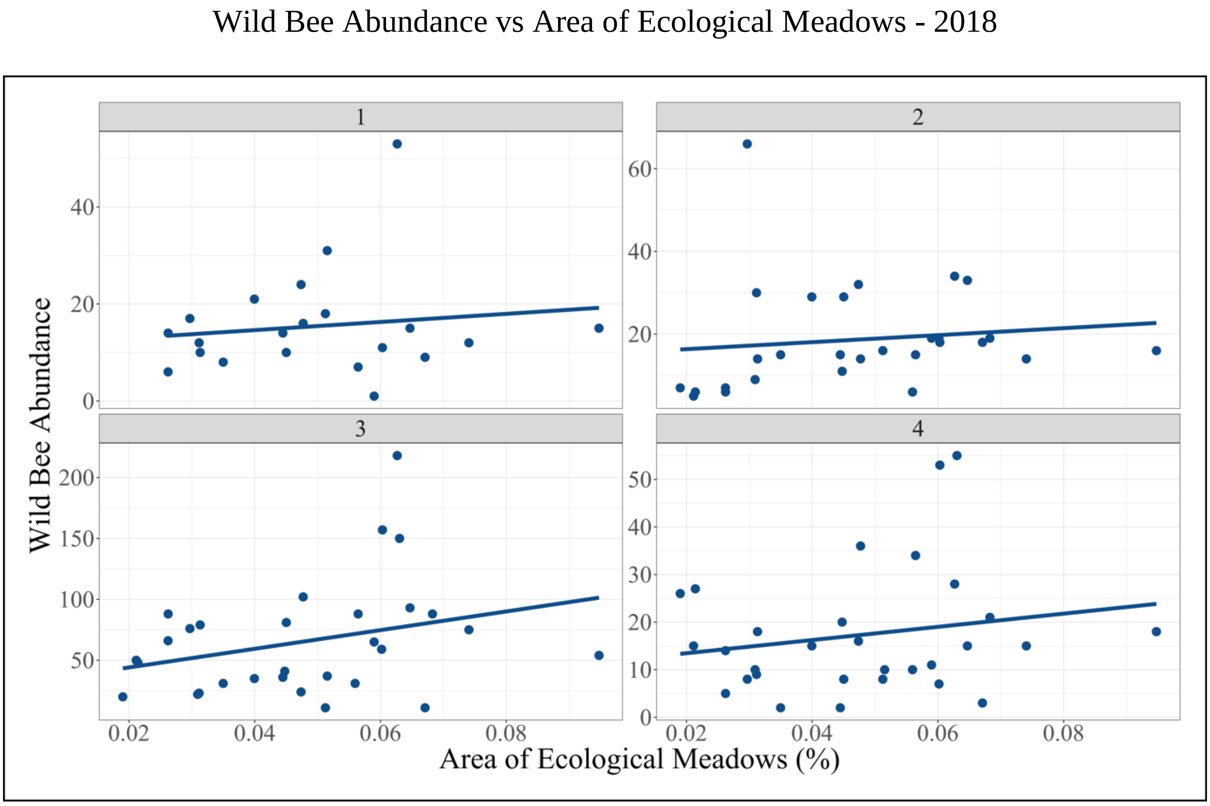


Figure S5. Wild bee abundance in relation to the area of ecological meadows for 2018. Organized by round, with fitted lines based on linear regression models (LM).

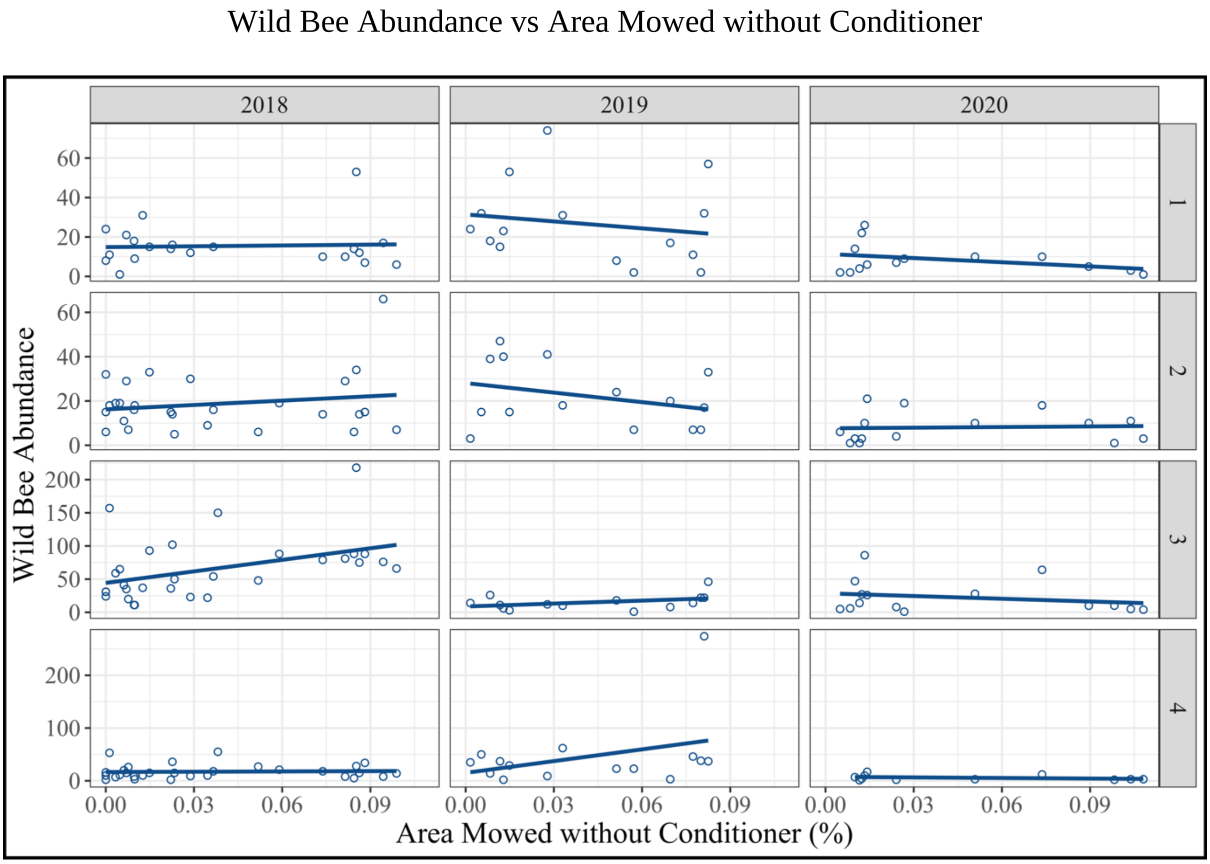


Figure S6. Relationship between wild bee abundance and the area mowed without a conditioner. Organized by round and year, with fitted lines based on linear regression models (LM).

Figure S7. Abundance of wild bees in relation to the area mowed without conditioner per sector. Compares the linear regression models (LM) of four types of meadows mowed without a conditioner. Organised by round and year, based on the full dataset (2018-2020).

Wild Bee Abundance vs Change in Area Mowed without Conditioner 2018 – 2019/20

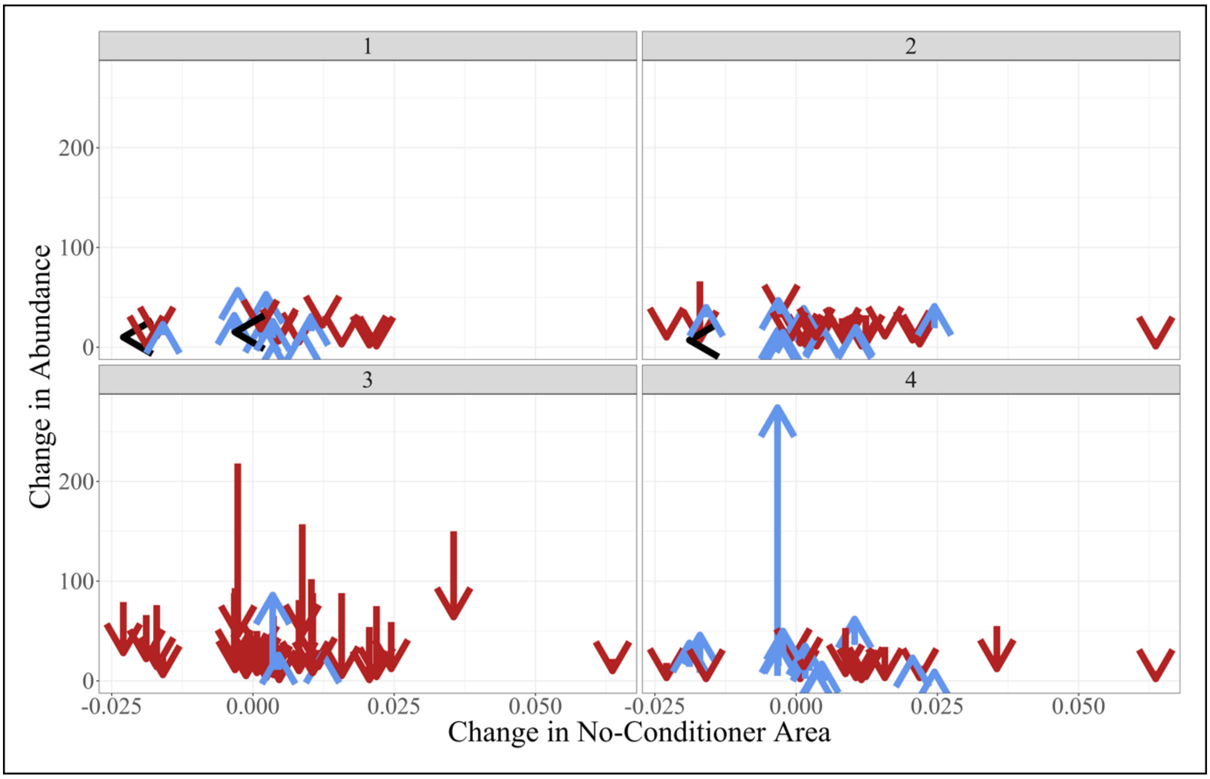


Figure S8. Change in wild bee abundance compared to change in area mowed without a conditioner. Illustrates the change in abundance and conditioner use over time between 2018 - 2019/20.

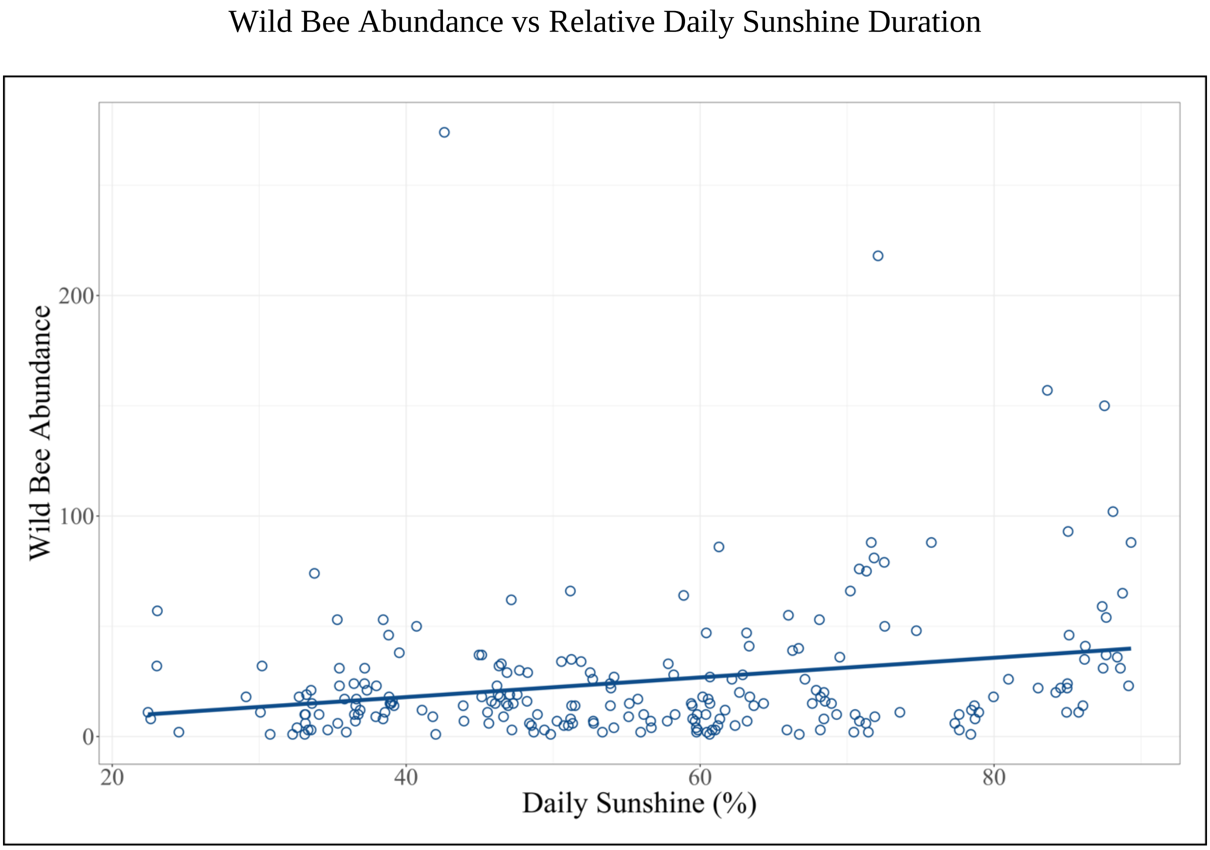


Figure S9. Abundance of wild bees in relation to daily sunshine duration. Created using the full dataset for all years, 2018 - 2020 (linear regression model (LM)).

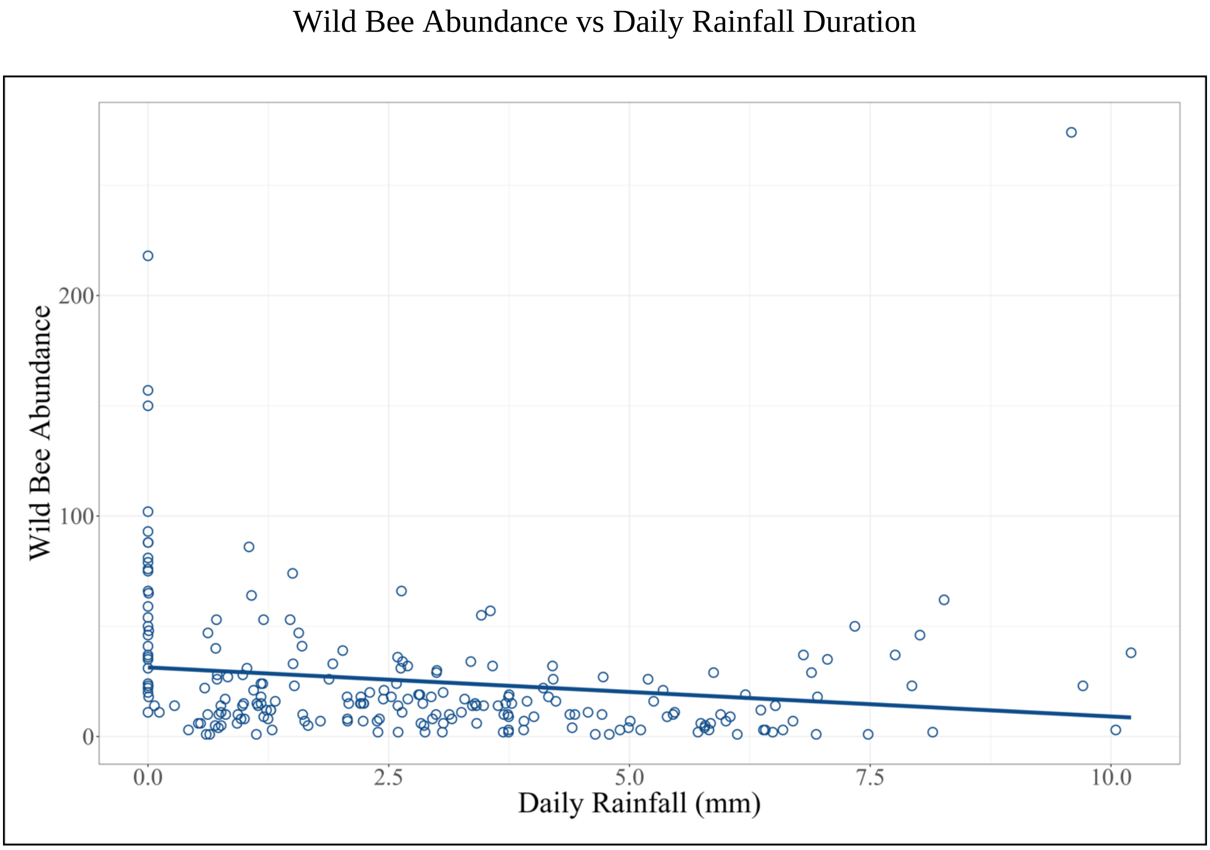


Figure S10. Relationship between wild bee abundance and average daily rainfall (mm). Created using the full dataset (2018 – 2020) with fitted line based on a linear regression model (LM).

Table S1. Description of all land use variables which occupy each sector.

Variables in landuse	Description
pratemp22	Temporary meadows w. AP-M n°22 "floral ressource strip"
pratemp23	Temporary meadows w. AP-M n°23 "delayed mowing"
pratemp29	Temporary meadows w. AP-M n°29 "mowing w.out conditionner"
pratemp92	Temporary meadows w. AP-Ms n°29 and n°22 combined on the same meadow
pratemp93	Temporary meadows w. AP-Ms n°29 and n°23 combined on the same meadow
pratemp00	Temporary meadows w. no AP-M
praperm29	Permanent meadows w. AP-M n°29 "mowing w.out conditionner"
praperm00	Permanent meadows w. no AP-M
praecol29	Ecological meadows w. AP-M n°29 "mowing w.out conditionner"
praecol00	Ecological meadows w. no AP-M
cereal21	Cereals (wheat, oats, triticale, all cereals except barley) w. AP-M n°21 "legume undersowing"
cereal00	Cereals (wheat, oats, triticale, all cereals except barley) w. no AP-M
barley24	Barley w. AP-M n°24 "no neonic seed coating"
barley00	Barley w. no AP-M
colza26	Oilseed rape (= colza) w. AP-M n°26 "no insecticide spraying"
colza00	Oilseed rape (= colza) w. no AP-M
sunflower26	Sunflower w. AP-M n°26 "no insecticide spraying"
sunflower00	Sunflower w. no AP-M
potato27	Potato w. AP-M n°26 "no insecticide spraying"
potato00	Potato w. no AP-M
floweringcrop26	Various flowering crops (soy bean, peas, etc, excepted oilseed rape and sunflower) w. AP-M n°26
floweringcrop00	Various flowering crops (soy bean, peas, etc, excepted oilseed rape and sunflower) w. no AP-M
beetroot25	Sugarbeet w. AP-M n°25 "no neonic seed coating"
beetroot00	Sugarbeet w. no AP-M
maize	Corn (silage and grain)
nonflowercrop	Various non-flowering crops
othercrops	Crops that do not fall into any other category
ecol_herb	Agricultural herbaceous areas for the promotion of biodiversity (fallow parcels, floral strips, litter meadows
pastureintense	Intensive pastures
pastureecol	Pastures dedicated to the promotion of biodiversity and summer pasturing areas. This was used as "buffering"
orchard	Commercial orchards (does not include high-stem fruit trees dedicated to the promotion of biodiversity)
vineyards	Vineyards
ecol_ligneous	Hedgerows, small parcels of woody habitats dedicated to the promotion of biodiversity
forest	Forest
waters	Lakes, rivers, bassins
urban	Urban areas, buildings, roads, railways

Table S2. Wild bee specimen data. Indicates the number of individuals sampled, organised by family, genus and species.

Family	Genus	Species	# of Individuals
Andrenidae	*Andrena*	*agilissima*	2
		alfkenella	1
		bicolor	8
		bucephala	17
		carantonica	30
		chrysosceles	26
		cineraria	121
		curvungula	11
		dorsata	16
		flavipes	247
		fucata	1
		fulva	18
		fulvago	3
		fulvata	5
		gelriae	1
		gravida	30
		haemorrhoa	200
		helvola	20
		humilis	34
		labialis	16
		labiata	3
		lagopus	5
		minutula	29
		minutuloides	3
		mitis	1
		nigroaenea	4
		nigroolivacea	5
		nitida	118
		ovatula	64
		pandellei	19
		proxima	1
		schencki	11
		semilaevis	1
		sp.	1
		tibialis	6
		trimmerana	5
		vaga	2

		ventralis	1
		wilkella	38
Apidae	*Anthophora*	*aestivalis*	2
	Bombus	*barbutellus*	6
		bohemicus	6
		campestris	3
		hortorum	55
		humilis	32
		hypnorum	3
		lapidarius	72
		lucorum	17
		pascuorum	44
		pratorum	42
		ruderarius	2
		ruderatus	3
		rupestris	5
		soroeensis	3
		sp.	4
		sylvarum	65
		sylvestris	4
		terrestris	317
		vestalis	2
		veteranus	1
		wurflenii	1
	Eucera	*longicornis*	6
		nigrescens	9
	Nomada	*armata*	1
		bifasciata	1
		fabriciana	1
		flava	4
		flavopicta	4
		hirtipes	1
		marshamella	1
		moeschleri	1
		ruficornis	1
	Xylocopa	*valga*	1
Colletidae	*Colletes*	*cunicularius*	11
		daviesanus	1
	Hylaeus	*communis*	3
		confusus	12
		dilatatus	1
		gredleri	4

		hyalinatus	1
		taeniolatus/pictipes	1
Halictidae	*Halictus*	*carinthiacus*	3
		eurygnathus	1
		langobardicus	1
		maculatus	19
		rubicundus	6
		scabiosae	147
		sexcinctus	8
		simplex	118
		subauratus	5
		tumulorum	247
	Lasioglossum	*albipes*	17
		calceatum	76
		costulatum	1
		fulvicorne	44
		glabriusculum	117
		griseolum	17
		interruptum	17
		laevigatum	1
		laticeps	474
		lativentre	200
		leucopus	3
		leucozonium	41
		lineare	4
		malachurum	182
		minutissimum	1
		morio	224
		nigripes	8
		nitidulum	9
		pallens	4
		parvulum	2
		pauxillum	763
		politum	106
		punctatissimum	5
		pygmaeum	1
		sp.	3
		subhirtum	1
		tricinctum	6
		villosulum	13
		zonulum	680
	Sphecodes	*crassus*	4

		ephippius	14
		ferruginatus	1
		gibbus	4
		hyalinatus	2
		majalis	2
		monilicornis	3
Megachilidae	*Anthidium*	*oblongatum*	1
	Chelostoma	*campanularum*	2
		florisomne	37
		rapunculi	3
	Heriades	*truncorum*	3
	Hoplitis	*adunca*	1
		leucomelana	7
		ravouxi	1
		tridentata	1
	Megachile	*centuncularis*	2
		circumcincta	6
		willughbiella	1
	Osmia	*bicornis*	27
		caerulescens	3
		cornuta	2
		leaiana	1
		xanthomelana	1
	Stelis	*breviuscula*	1
		ornatula	2
	Trachusa	*byssina*	1
		byssinum	1
Melittidae	*Melitta*	*leporina*	11

Table S3. Average area of land use per sector (%), organized by year.

Year	ecological mead	seminatural	no cond	intensive gras	pratemp22
2018	4.98%	7.70%	4.11%	16.95%	0.14%
2019	4.39%	7.88%	4.10%	19.12%	0.11%
2020	5.29%	8.05%	3.94%	19.39%	0.10%
Year	**pratemp23**	**pratemp29**	**pratemp92**	**pratemp93**	**pratemp00**
2018	0.41%	1.67%	0.32%	0.50%	7.21%
2019	0.41%	1.79%	0.29%	0.59%	9.09%
2020	0.42%	1.54%	0.12%	0.38%	7.83%
Year	**praperm29**	**praperm00**	**praecol29**	**praecol00**	**cereal21**
2018	1.61%	5.43%	0.60%	4.38%	0.30%
2019	1.44%	5.12%	0.54%	3.84%	0.67%
2020	1.91%	7.56%	0.89%	4.40%	0.67%
Year	**cereal00**	**barley24**	**barley00**	**colza26**	**colza00**
2018	12.41%	0.58%	2.20%	0.03%	3.55%
2019	10.99%	0.34%	2.27%	0.07%	2.83%
2020	11.26%	NA	2.77%	0.04%	3.30%
Year	**sunflower26**	**sunflower00**	**potato27**	**potato00**	**floweringcrop26**
2018	0.00%	0.95%	0.16%	0.51%	0.04%
2019	0.01%	0.79%	0.00%	0.33%	0.05%
2020	0.00%	0.93%	0.23%	0.68%	0.10%
Year	**floweringcrop00**	**beetroot25**	**beetroot00**	**maize**	**nonflowercrop**
2018	1.49%	0.07%	1.99%	4.70%	0.01%
2019	1.36%	0.17%	1.33%	4.09%	0.05%
2020	1.45%	0.27%	1.67%	4.24%	0.04%
Year	**othercrops**	**ecol_herb**	**pastureintense**	**pastureecol**	**orchard**
2018	0.39%	0.50%	3.77%	6.58%	0.46%
2019	0.32%	0.48%	4.38%	6.78%	0.41%
2020	0.46%	0.35%	3.48%	7.15%	0.27%
Year	**vineyards**	**ecol_ligneous**	**forest**	**waters**	**urban**
2018	1.56%	0.62%	22.33%	0.78%	11.75%
2019	1.82%	0.61%	25.48%	0.62%	10.52%
2020	0.34%	0.55%	22.87%	0.74%	10.99%

References

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2008). Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Current biology*, *18*(20), 1572-1575. https://doi.org/10.1016/j.cub.2008.08.066

Billaud, O., Vermeersch, R. L., & Porcher, E. (2021). Citizen science involving farmers as a means to document temporal trends in farmland biodiversity and relate them to agricultural practices. *Journal of Applied Ecology*, *58*(2), 261-273. DOI: 10.1111/1365-2664.13746

Boetzl, F.A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S., ... & Steffan-Dewenter, I. (2021). A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *Proceedings of the National Academy of Sciences, 118*(10). https://doi.org/10.1073/pnas.2016038118

Bretagnolle, V., Berthet, E., Gross, N., Gauffre, B., Plumejeaud, C., Houte, S., ... & Gaba, S. (2018). Towards sustainable and multifunctional agriculture in farmland landscapes: lessons from the integrative approach of a French LTSER platform. *Science of the Total Environment*, *627*, 822-834. https://doi.org/10.1016/j.scitotenv.2018.01.142

Bruppacher, L., Pellet, J., Arlettaz, R. & Humbert, J.Y. (2016). Simple modifications of mowing regime promote butterflies in extensively managed meadows: evidence from field-scale experiments. *Biological Conservation*, *196*, 196-202.

Buchholz, S., Gathof, A.K., Grossmann, A.J., Kowarik, I. & Fischer, L.K. (2020). Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. *Landscape and Urban Planning*, *196*, 103731. https://doi.org/10.1016/j.landurbplan.2019.103731

Buri, P., Humbert, J.Y. & Arlettaz, R. (2014). Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. *PloS one*, *9*(1), e85635. https://doi.org/10.1371/journal.pone.0085635

Cane, J.H. & Tepedino, V.J. (2001). Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conservation Ecology*, *5*(1). https://www.jstor.org/stable/26271794

Crowther, L.I. & Gilbert, F. (2020). The effect of agri-environment schemes on bees on Shropshire farms. *Journal for Nature Conservation*, *58*, 125895. https://doi.org/10.1016/j.jnc.2020.125895

Cunningham-Minnick, M.J., Peters, V.E. & Crist, T.O. (2019). Nesting habitat enhancement for wild bees within soybean fields increases crop production. *Apidologie*, *50*(6), 833-844. https://doi.org/10.1007/s13592-019-00691-y

Cutler, G.C., Nams, V.O., Craig, P., Sproule, J.M. & Sheffield, C.S. (2015). Wild bee pollinator communities of lowbush blueberry fields: Spatial and temporal trends. *Basic and Applied Ecology*, *16*(1), 73-85. https://doi.org/10.1016/j.baae.2014.11.005

Cutter, J., Geaumont, B., McGranahan, D., Harmon, J., Limb, R., Schauer, C. & Hovick, T. (2021). Cattle and sheep differentially alter floral resources and the native bee communities in working landscapes. *Ecological Applications*, *31*(7), e02406. https://doi.org/10.1002/eap.2406

De Palma, A., Kuhlmann, M., Roberts, S.P., Potts, S.G., Börger, L., Hudson, L. N., ... & Purvis, A. (2015). Ecological traits affect the sensitivity of bees to land-use pressures in E uropean agricultural landscapes. *Journal of Applied Ecology*, *52*(6), 1567-1577. https://doi.org/10.1111/1365-2664.12524

Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., ... & Potts, S.G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, *5*(10), 1453-1461. https://doi.org/10.1038/s41559-021-01534-9

Duchenne, F., Thébault, E., Michez, D., Gérard, M., Devaux, C., Rasmont, P., ... & Fontaine, C. (2020). Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Global Change Biology*, *26*(12), 6753-6766. https://doi.org/10.1111/gcb.15379

Duelli, P., Obrist, M.K. & Schmatz, D.R. (1999). Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems & Environment*, *74*(1-3), 33-64. https://doi.org/10.1016/S0167-8809(99)00029-8

Ekroos, J., Kleijn, D., Batáry, P., Albrecht, M., Báldi, A., Blüthgen, N., ... & Smith, H. G. (2020). High land-use intensity in grasslands constrains wild bee species richness in Europe. *Biological Conservation*, *241*, 108255. https://doi.org/10.1016/j.biocon.2019.108255

Evans, A.N., Llanos, J.E., Kunin, W.E. & Evison, S.E. (2018). Indirect effects of agricultural pesticide use on parasite prevalence in wild pollinators. *Agriculture, Ecosystems & Environment*, *258*, 40-48. https://doi.org/10.1016/j.agee.2018.02.002

Evans, E., Smart, M., Cariveau, D. & Spivak, M. (2018). Wild, native bees and managed honey bees benefit from similar agricultural land uses. *Agriculture, Ecosystems & Environment*, *268*, 162-170. https://doi.org/10.1016/j.agee.2018.09.014

Everaars, J., Settele, J. & Dormann, C.F. (2018). Fragmentation of nest and foraging habitat affects time budgets of solitary bees, their fitness and pollination services, depending on traits: results from an individual-based model. *PloS one*, *13*(2), e0188269. https://doi.org/10.1371/journal.pone.0188269

Fluri, P. & Frick, R. (2002). Honey bee losses during mowing of flowering fields. *Bee world*, *83*(3), 109-118. DOI: 10.1080/0005772X.2002.11099550

Fortel, L., Henry, M., Guilbaud, L., Mouret, H. & Vaissiere, B.E. (2016). Use of human-made nesting structures by wild bees in an urban environment. *Journal of Insect Conservation*, *20*(2), 239-253. https://doi.org/10.1007/s10841-016-9857-y

Frick, P. & Fluri, P. (2001). Bee losses during mowing with rotary mowers. *Bee losses during mowing with rotary mowers, 8*, 196-201.

Gallai, N., Salles, J.M., Settele, J. & Vaissière, B.E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological economics*, *68*(3), 810-821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., ... & Winfree, R. (2014). From research to action: enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, *12*(8), 439-447. doi:10.1890/130330

Giles, V. & Ascher, J.S. (2006). A survey of the bees of the Black Rock Forest preserve, New York (Hymenoptera: Apoidea). *Journal of Hymenoptera research*, *15*(2), 208-231.

Giriens, S. (2015). *Bombus lapidarius* worker on *Trifolium pratense* (Cheyres, FR). Info fauna. https://species.infofauna.ch/groupe/1/portrait/130

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005). Causes of rarity in bumblebees. *Biological Conservation*, *122*(1), 1–8. https://doi.org/10.1016/j.biocon.2004.06.017

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E.L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957. DOI: 10.1126/science.1255957

Hatfield, R.G. & LeBuhn, G. (2007). Patch and landscape factors shape community assemblage of bumble bees, Bombus spp.(Hymenoptera: Apidae), in montane meadows. *Biological Conservation*, *139*(1-2), 150-158. https://doi.org/10.1016/j.biocon.2007.06.019

Harris, C. & Ratnieks, F.L. (2021). Clover in agriculture: combined benefits for bees, environment, and farmer. *Journal of Insect Conservation*, 1-19. https://doi.org/10.1007/s10841-021-00358-z

Hecker, L.P., Wätzold, F., Yang, X. & Birkhofer, K. (2022). Squeeze it or leave it? An ecological-economic assessment of the impact of mower conditioners on arthropod populations in grassland. *Journal of Insect Conservation*, 1-13. https://doi.org/10.1007/s10841-022-00392-5

Hofmann, M.M., Constantin, Z.M. & Renner, S.S. (2019). Narrow habitat breadth and late-summer emergence increases extinction vulnerability in Central European bees. *Proceedings of the Royal Society B, 286*(1898). DOI: https://doi.org/10.1098/rspb.2019.0316

Humbert, J.Y., Ghazoul, J. & Walter, T. (2009). Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment*, *130*(1-2), 1-8. https://doi.org/10.1016/j.agee.2008.11.014

Humbert, J.Y., Ghazoul, J., Sauter, G.J. & Walter, T. (2010). Impact of different meadow mowing techniques on field invertebrates. *Journal of Applied Entomology*, *134*(7), 592-599. https://doi.org/10.1111/j.1439-0418.2009.01503.x

Humbert, J.Y., Pellet, J., Buri, P. & Arlettaz, R. (2012). Does delaying the first mowing date benefit biodiversity in meadowland?. *Environmental Evidence*, *1*(1), 1-13. https://doi.org/10.1186/2047-2382-1-9

Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., ... & Scherer-Lorenzen, M. (2017). Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology*, *105*(4), 871-879. https://doi.org/10.1111/1365-2745.12789

Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C. M., Kallioniemi, E. & Lennartsson, T. (2019). Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. *Global Ecology and Conservation*, *18*, e00619. https://doi.org/10.1016/j.gecco.2019.e00619

Jones, L., Brennan, G.L., Lowe, A., Creer, S., Ford, C. R. & de Vere, N. (2021). Shifts in honeybee foraging reveal historical changes in floral resources. *Communications biology*, *4*(1), 1-10. https://doi.org/10.1038/s42003-020-01562-4

Kinney, P.L. (2018). Interactions of climate change, air pollution, and human health. *Current environmental health reports*, *5*(1), 179-186. https://doi.org/10.1007/s40572-018-0188-x

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2006). Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, *274*(1608), 303-313. https://doi.org/10.1098/rspb.2006.3721

Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J. & Ricketts, T.H. (2016). Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences*, *113*(1), 140-145. https://doi.org/10.1073/pnas.1517685113

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C. & Dicks, L.V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, *20*(5), 673-689. https://doi.org/10.1111/ele.12762

Knop, E.V.A., Kleijn, D., Herzog, F. & Schmid, B. (2006). Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of applied ecology*, *43*(1), 120-127. https://doi.org/10.1111/j.1365-2664.2005.01113.x

Kolecka, N., Ginzler, C., Pazur, R., Price, B. & Verburg, P.H. (2018). Regional scale mapping of grassland mowing frequency with sentinel-2 time series. *Remote Sensing*, *10*(8), 1221. https://doi.org/10.3390/rs10081221

Kruess, A. & Tscharntke, T. (2002). Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological conservation*, *106*(3), 293-302. https://doi.org/10.1016/S0006-3207(01)00255-5

Lachat, T., Pauli, D., Gonseth, Y., Klaus, G., Scheidegger, C., Vittoz, P. & Walter, T. (2010). Evolution de la biodiversité en Suisse depuis 1900. Avons-nous touché le fond? *Bristol-Schriftenreihe, 29*. https://www.dora.lib4ri.ch/wsl/islandora/object/wsl:10030

Lautenbach, S., Seppelt, R., Liebscher, J. & Dormann, C.F. (2012). Spatial and temporal trends of global pollination benefit. *PLoS one*, *7*(4), e35954. https://doi.org/10.1371/journal.pone.0035954

Le Provost, G., Badenhausser, I., Violle, C., Requier, F., D'ottavio, M., Roncoroni, M., ... & Gross, N. (2021). Grassland-to-crop conversion in agricultural landscapes has lasting impact on the trait diversity of bees. *Landscape ecology*, *36*(1), 281-295. https://doi.org/10.1007/s10980-020-01141-2

Littlewood, N.A., Stewart, A.J. & Woodcock, B.A. (2012). Science into practice–how can fundamental science contribute to better management of grasslands for invertebrates?. *Insect Conservation and Diversity*, *5*(1), 1-8. https://doi.org/10.1111/j.1752-4598.2011.00174.x

Mallinger, R.E., Franco, J.G., Prischmann-Voldseth, D.A. & Prasifka, J.R. (2019). Annual cover crops for managed and wild bees: Optimal plant mixtures depend on pollinator enhancement goals. *Agriculture, ecosystems & environment*, *273*, 107-116. 10.1016/j.agee.2018.12.006

Mallinger, R.E., Gibbs, J. & Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape ecology*, *31*(7), 1523-1535. https://doi.org/10.1007/s10980-015-0332-z

Mandelik, Y., Winfree, R., Neeson, T. & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, *22*(5), 1535-1546. https://doi.org/10.1890/11-1299.1

Marshman, J., Blay-Palmer, A. & Landman, K. (2019). Anthropocene crisis: climate change, pollinators, and food security. *Environments*, *6*(2), 22. https://doi.org/10.3390/environments6020022

Mazoyer, M. & Roudart, L. (2006). A history of world agriculture: from the neolithic age to the current crisis. NYU Press.

McCravy, K.W. & Ruholl, J.D. (2017). Bee (Hymenoptera: Apoidea) diversity and sampling methodology in a Midwestern USA deciduous forest. *Insects*, *8*(3), 81. https://doi.org/10.3390/insects8030081

MétéoSuisse. (2022). Swiss Confederation: Federal office of meteorology and climatology MétéoSuisse.

Meyer, S., Unternährer, D., Arlettaz, R., Humbert, J.Y. & Menz, M.H.M. (2017). Promoting diverse communities of wild bees and hoverflies requires a landscape approach to managing meadows. *Agriculture, Ecosystems and Environment, 239*, 376–384. https://doi.org/10.1016/j.agee.2017.01.037

Morandin, L.A., Winston, M.L., Abbott, V.A. & Franklin, M.T. (2007). Can pastureland increase wild bee abundance in agriculturally intense areas?. *Basic and Applied Ecology*, *8*(2), 117-124. https://doi.org/10.1016/j.baae.2006.06.003

Müller, A., Praz, C. in prep. Rote Liste der Bienen. Gefährdete Arten der Schweiz. Bundesamt für Umwelt (BAFU) und Info Fauna.

New, T.R. (2019). Grassland Management for Insect Conservation: Grazing, Mowing, and Fire. In *Insect Conservation and Australia's Grasslands* (pp. 179-234). Springer, Cham. https://doi.org/10.1007/978-3-030-22780-7_10

Osterman, J., Aizen, M.A., Biesmeijer, J.C., Bosch, J., Howlett, B.G., Inouye, D.W., ... & Paxton, R.J. (2021). Global trends in the number and diversity of managed pollinator species. *Agriculture, Ecosystems & Environment*, *322*, 107653. https://doi.org/10.1016/j.agee.2021.107653

Ouvrard, P., Transon, J. & Jacquemart, A.L. (2018). Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. *Biodiversity and Conservation*, *27*(9), 2193-2216. https://doi.org/10.1007/s10531-018-1531-0

Papanikolaou, A.D., Kühn, I., Frenzel, M., Kuhlmann, M., Poschlod, P., Potts, S.G., ... & Schweiger, O. (2017). Wild bee and floral diversity co-vary in response to the direct and indirect impacts of land use. *Ecosphere*, *8*(11), e02008. https://doi.org/10.1002/ecs2.2008

Peat, J. & Goulson, D. (2005). Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, Bombus terrestris. *Behavioral Ecology and Sociobiology*, *58*(2), 152-156. https://doi.org/10.1007/s00265-005-0916-8

Pfiffner, L. & Luka, H. (2000). Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment*, *78*(3), 215-222. https://doi.org/10.1016/S0167-8809(99)00130-9

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, *25*(6), 345-353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J. & Vanbergen, A.J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

Prendergast, K.S., Menz, M.H., Dixon, K.W. & Bateman, P.W. (2020). The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere*, *11*(5), e03076. https://doi.org/10.1002/ecs2.3076

QGIS Development Team. (2021). QGIS Geographic Information System (3.16.1-Hannover). Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Core Team. (2021). R: A language and environment for statistical computing (Version 1.4.1717). R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rhodes, C.J. (2018). Pollinator decline–an ecological calamity in the making? *Science Progress*, *101*(2), 121-160. https://doi.org/10.3184/003685018X15202512854527

Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of applied Ecology*, *39*(1), 157-176. https://doi.org/10.1046/j.1365-2664.2002.00695.x

Rosenberger, D.W. & Conforti, M.L. (2020). Native and agricultural grassland use by stable and declining bumble bees in Midwestern North America. *Insect Conservation and Diversity*, *13*(6), 585-594. https://doi.org/10.1111/icad.12448

Saarinen, K. & Jantunen, J. (2005). Grassland butterfly fauna under traditional animal husbandry: contrasts in diversity in mown meadows and grazed pastures. *Biodiversity & Conservation*, *14*(13), 3201-3213. DOI 10.1007/s10531-004-0387-7

Sárospataki, M., Báldi, A., Batáry, P., Józan, Z., Erdős, S. & Rédei, T. (2009). Factors affecting the structure of bee assemblages in extensively and intensively grazed grasslands in Hungary. *Community Ecology*, *10*(2), 182-188.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P., ... & Kleijn, D. (2015). Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, *52*(5), 1165-1175. https://doi.org/10.1111/1365-2664.12479

Soroye, P., Newbold, T. & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, *367*(6478), 685-688. DOI: 10.1126/science.aax8591

Swiss Bee Team. (2021). Atlas en ligne des abeilles sauvages de Suisse. InfoFauna. www.swisswildbees.ch.

Tonietto, R.K. & Larkin, D.J. (2018). Habitat restoration benefits wild bees: A meta-analysis. *Journal of Applied Ecology*, *55*(2), 582-590. https://doi.org/10.1111/1365-2664.13012

Tuell, J.K. & Isaacs, R. (2010). Weather during bloom affects pollination and yield of highbush blueberry. *Journal of economic entomology*, *103*(3), 557-562. https://doi.org/10.1603/EC09387

Vanbergen, A.J. (2013). Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*(5), 251-259. https://doi.org/10.1890/120126

Van der Meersch, V., Billaud, O., San Cristobal, M., Vialatte, A. & Porcher, E. (2022). Landscape floral resources provided by rapeseed correlate with next-year reproduction of cavity-nesting pollinators in a national participatory monitoring program. *Landscape Ecology*, *37*(2), 551-565. https://doi.org/10.1007/s10980-021-01353-0

Van der Sluijs, J.P., Simon-Delso, N., Goulson, D., Maxim, L., Bonmatin, J.M. & Belzunces, L.P. (2013). Neonicotinoids, bee disorders and the sustainability of pollinator services. *Current opinion in environmental sustainability*, *5*(3-4), 293-305. https://doi.org/10.1016/j.cosust.2013.05.007

Vickruck, J., Purvis, E.E., Kwafo, R., Kerstiens, H. & Galpern, P. (2021). Diversifying Landscapes for Wild Bees: Strategies for North American Prairie Agroecosystems. *Current Landscape Ecology Reports*, *6*(3), 85-96. https://doi.org/10.1007/s40823-021-00066-z

Vray, S., Rollin, O., Rasmont, P., Dufrêne, M., Michez, D. & Dendoncker, N. (2019). A century of local changes in bumblebee communities and landscape composition in Belgium. *Journal of Insect Conservation*, *23*(3), 489-501. https://doi.org/10.1007/s10841-019-00139-9

Warren, J., Lawson, C.S. & Blecher, K. (2008). The Agri-Environment. Cambridge, United Kingdom. 1–232 p.

Waser, N.M. & Price, M.V. (2016). Drought, pollen and nectar availability, and pollination success. *Ecology*, *97*(6), 1400-1409.