Nesting incidence of ground-nesting bees in Swiss lowland perennial wildflower strips

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Abstract

The implementation of perennial wildflower strips is becoming increasingly common in agricultural landscapes. The positive effect of these wildflower strips has already been demonstrated for wild bee abundance and diversity, mostly due to an increased provision of floral feeding resources. Nevertheless, wild bees not only depend on floral resources but also on suitable nesting habitat. In this study, we investigated the vegetation and soil characteristics that explain the nesting incidence of ground-nesting wild bee species within perennial wildflower strips. The study was carried out in spring 2020 within twelve wildflower strips located in the Swiss lowlands. Nests from ground-nesting wild bees (n = 86) were found at five of the twelve study sites. 67 individuals were caught from these nests, belonging to the genera *Lasioglossum* (n = 59), *Halictus* (n = 4), *Andrena* (n = 1), and to the parasitic genus *Sphecodes* (n = 3). The mean number of flowering plant species per 10 m^2 was the best predictor of wildflower strip probability of colonization (i.e. presence of a wild bee nest) although it was not statistically significant. Within colonized strips, the percentage of bare ground cover (at 1 x 1 m scale) positively affected wild bees' presence, whereas grass cover had a negative influence. In order to promote ground-nesting wild bees, wildflower strips should thus offer a variety of floral resources, be heterogeneously structured and harbour patches of bare ground. Dense vegetation, in particular high grass cover, should be prevented, but it is not yet clear how this can be achieved.

Introduction

In the last decades, the population and diversity of insect pollinators, including wild bees, strongly declined in several regions of Europe (Biesmeijer *et al.* 2006). Agricultural intensification, comprising land-use changes and the loss of many natural and semi-natural habitats, is one of the major causes of the decline of farmland biodiversity in general (Bakker & Berendse 1999, Stoate *et al.* 2001), and wild bee abundance and species richness in particular (Winfree *et al.* 2009, Potts *et al.* 2010, Hoffmann *et al.* 2018). Since around 90 % of all flowering plants depend on animal pollination (Ollerton *et* al. 2011) honey bees together with wild bees provide an important ecosystem service (Garibaldi *et al. 2013,* Kleijn *et al.* 2015, IPBS 2016). In Switzerland, 45% of the wild bee species are red-listed (Amiet 1994). In this context, agri-environment schemes (AES) have been introduced in the early 1990s by most European countries, which provide incentives to farmers to practice environmentally friendlier agriculture (Kleijn & Sutherland 2003) and to promote biodiversity on their land. Similarly, in Switzerland, at least 7% of the farmland has to be managed as Swiss AES, which includes extensively managed grasslands, hedgerows, high-stem fruit trees, and sown wildflower strips (BLW 2020). It has been shown that increasing habitat richness and landscape composition diversity positively influence bee species richness and functional diversity (Papanikolaou *et al.* 2017*b*). Semi-natural areas and green infrastructure elements within agricultural landscapes, such as wildflower strips, might even mitigate the negative effects of increasing temperatures on wild bee species richness and total abundance (Papanikolaou *et al.* 2017*a*) and increase the local bee abundance and richness (Greenleaf & Kremen 2006, Balzan *et al.* 2014, Scheper *et al.* 2015, Sutter *et al.* 2017, Bartual *et al.* 2019). Thus, these measures may become even more important also under the predicted climate change.

Wildflower strips (hereafter WFS) represent a part of the European AES developed to promote farmland biodiversity in agricultural landscapes. They are arable sown fields of a seed mixture with ruderal plant species. Insect abundance and diversity have been shown to be higher on such WFS than on arable fields, as well as in sown grass margins and naturally regenerated field margins (Meek *et al.* 2002, Marshall *et al.* 2006, Pywell *et al.* 2007, Kohler *et al.* 2008, Haaland *et al.* 2011, Rollin *et al.* 2013, Sutter *et al.* 2018). They provide abundant nectar and pollen, which attract flower-visiting insects, especially bees (Haaland *et al.* 2011). The importance of floral resources and plant species diversity for solitary bees and bumblebees has already been shown (e.g. Steffan-Dwenter & Tscharntke 2001, Scheper *et al.* 2015, Papanikolaou *et al.* 2017*b*). However, mainly common and polylectic species seem to benefits from wildflower strip (Meek *et al.* 2002, Pywell *et al.* 2005, Grundel *et al.* 2010, Aviron *et al*. 2011, Korpela *et al*. 2013) and it remains unclear whether flowering semi-natural habitats could enhance the entire bee population in agricultural landscapes (Albrecht *et al*. 2020, Ganser *et al*. 2021) or if they only increase the local species abundance and richness of pollinators by attracting them from the surroundings. Consequently, flowering semi-natural habitats would simply contribute to a spatial re-distribution of foraging pollinators what would not enhance the local pollinator populations and the potential benefits for pollination services may remain limited (Klein *et al*. 2009).

As summarized above, until now the research focus was more on the effect of floral resources as a driver of local wild bees' abundance and diversity rather than on the role of nesting habitat (e.g. Potts *et al*. 2003, Bartual *et al*. 2019, Ganser 2019). However, to complete their life cycle, wild bees critically depend on suitable nesting and overwintering habitats and not only on good feeding habitats and resources (Tscharntke *et al*. 1998, Potts *et al*. 2005, Harmon-Threatt 2020). Gathmann & Tscharntke (2002) and Potts *et al*. (2003) assumed already that nest sites might be even more limiting than foraging places for solitary bees of different nesting guilds. In Potts *et al*. (2005) the importance of nesting structures and resources for wild bee communities was highlighted, whereby the structure was influenced by several soil and vegetation characteristics of the field.

Over half of all central European wild bees are nesting in the ground (Amiet & Krebs 2012, Zurbuchen & Müller 2012), many of them with particular conservation concern (Nieto *et al*. 2014). Ground-nesting bees mainly live solitary in self-constructed nests, where females dig a tunnel into the ground. Depending on the species the depth of the nest varies between some centimeters up to half a meter and can be constructed as a single tunnel or with many branches (Amiet & Krebs 2012, Wuellner 1999). Some species nest close to each other in aggregations (e.g. Cane 1991, Potts & Willmer 1997), and from species of the genera *Lassioglosum* and *Halictus* a social life history with a queen and workers is known (Amiet & Krebs 2012, Westrich 2019). This said, the exact nesting needs remain unknown from most species. Breeding time depends also on species. In Central Europe, the earliest species start breeding in March, whereas some species are active in late summer or autumn. However, the main breeding time of most species is between March and June. After the mating, the females lay each egg separately in a brood cell, with pollen and nectar as food storage. The offspring of most species hibernate as a prepupa or imago in their underground brood cell (Amiet & Krebs 2012, Westrich 2019).
The main goal of this study was: (i) to assess the potential of wildflower strips as a nesting habitat for ground-nesting wild bees; (ii) to investigate the role of vegetation traits such as vegetation cover and floral resource availability and diversity on the nesting incidence of ground-nesting bees; as well as

(iii) to examine the influence of the soil properties such as texture, humus amount and bulk density on the nesting incidence of ground-nesting bees.

It can be assumed that most ground-nesting wild bees prefer habitats with a high amount of bare ground and steep slopes with direct insolation (Potts & Willmer 1997, Potts *et al*. 2005, Sardiñas & Kremen 2014, Sardiñas *et al*. 2016, Carrié *et al*. 2018). Similarly, Bossart (2020) found higher nest abundance with increasing bare ground and moss cover, but lower abundance with increasing grass cover and vegetation height on meadows in the same study region of the Swiss Plateau. Previous studies showed in respect to soil characteristics that some ground-nesting wild bees prefer a high proportion of sand (Cane 1991, Potts & Willmer 1997, Polidori *et al*. 2010, Bossart 2020) and lower organic content (Osgood Jr. 1972, Grundel *et al*. 2010, Polidori *et al*. 2010). Results concerning other soil characteristics are contrarious and species-specific. For example, some studies found a preference for soft (e.g. Potts & Willmer 1997, Sardiñas & Kremen 2014), whereas others more for compact soil (e.g. Osgood Jr. 1972, Wuellner 1999, Potts *et al*. 2005, Polidori *et al*. 2010). Further uncertainty exists regarding the soil moisture (e.g. Osgood Jr. 1972, Wuellner 1999, Julier & Roulston 2009).
Besides such general tendencies, nesting habitat characteristics are often species-specific (Kim *et al*. 2006) and nesting rates depends also on the spatial distribution of these nesting resources (Sardiñas & Kremen 2014). However, the exact environmental drivers of nesting preferences and requirements of ground-nesting bees remains unknown. In particular in what extent WFS can provide those nesting habitat requirements. The difficulty to detect and quantify nests of ground-nesting bees in the landscape might be one reason for the relative scarcity of knowledge about nesting preferences of ground-nesting bees and the potential of specific land-use types and AES as nesting habitat for these bees. Although different approaches have been used in the past, we still lack a standard and universally applied method to quantify the nesting incidence of ground-nesting bees. Some studies have used emergency traps to quantify nesting incidence of ground-nesting bees and to assess the identity of the nesting bee species (e.g. Sardiñas & Kremen 2014, Sardiñas *et al*. 2016), while others trapped potentially nesting bees by covering patches of bare soil with a row cover fabric (Kim *et al*. 2006). Other methods have tried to indirectly quantify nesting incidence of bees through assessments of habitat (e.g. vegetation or soil) properties, without a direct sampling of nests (e.g. Potts et al. 2005), which may or may not correlate with actual nest presence. In this study, we, therefore, built on existing sampling methods of visually detecting and thus directly quantifying nests of ground-nesting bees (e.g. Venturini *et al*. 2017, Bossart 2020, Ullmann *et al*. 2020), and further developed and validated this methodology.

Materials and Methods

The study was conducted in the Swiss plateau (cantons Zürich and Aargau). This region is characterized by a relatively small-scale mosaic of arable crops, grasslands, and forest fragments. Data was collected on twelve perennial wildflower strips, which represent a part of the Swiss agri-environmental scheme. They are sown with a mixture of 24 resp. 35 annual and mostly perennial plant species on arable fields and stay for at least two to maximal eight years at the same place (BLW 2018). After the second year, an annual alternated mowing of half of the strip is allowed. Pesticides and fertilizers are not permitted and herbicides only for specific problematic plants (AGRIDEA 2018, BLW 2020). Appropriate study sites were searched based on existing maps and GIS analyses using the program ArcGIS. The WFS were selected (see Fig. 1) according to the following selection criteria: (i) WFS had to be separated by at least 1'000 m, which is a distance considered to be larger than the estimated average foraging ranges of solitary wild bees, which are considered to be a few hundred meters on average (Greenleaf *et al*. 2007); (ii) WFS had to be at least 50 m away from forest edges to avoid shadowing and (iii) they had a minimum area of 500 m^2, corresponding to the sampling area for nest sampling on each WFS. From the resulting list of possible study sites, twelve were selected based on accessibility and logistic reasons.

Nest and wild bee sampling

Nests of ground-nesting bees were sampled between 24th March and 24th June 2020. This period represents the main breeding season of most ground-nesting wild bee genera (personal communication of M. Albrecht). Every study site was visited four times i.e. during four sampling rounds (first: 24.03. – 09.04.2020, second: 14.04 - 24.04.2020, third: 07.05 - 20.05.2020, fourth: 26.05 - 24.06.2020). Fieldwork was only conducted on days without precipitation and at least two days after rainfall (to ensure that washed away tumuli at the nest entrances are rebuilt by the bees and thus detectable). In each sampling round nests of ground-nesting wild bees were searched within an area of 500 m^2. To facilitate the nest detection the sampling area was divided into 10 belt transects (1 m width). If this was not possible, due to the field shape, the length of the transect was adapted, so that the total area of the sampled belt transects always was the same. Further, the plot was always placed at least one meter beside the field edge, in order to prevent influences from the neighboring field. This was the only criterion for the location of the sampling area; within the WFS area the location of the sampling area was chosen randomly excluding edges.

Every nest of ground-nesting bees was recorded focusing on species with recognizable tumuli (e.g. Cane 2003, Venturini *et al*. 2017; Fig. 2) by walking the 1 m belt transects within the 500 m^2 sampling area in each WFS. To prevent double counts of nests (between sampling rounds), each detected nest was marked with a small wooden stick (with Nest ID), and additionally, the GPS point of each nest location was recorded.

To sample and identify nesting bees, emergence traps consisting of a transparent plastic container attached to a transparent plastic funnel mounted with three nails above the nest entrance were used (Fig. 3). A wooden stick inside the emergence trap helped the bee to reach the container filled with propylene glycol (60%) for preservation. Traps were placed in the morning before the bees start to fly (before 8:30 am, suggested by the personal experience of M. Albrecht) and were removed after at least more than 24 hours. Sampled wild bees were preserved in ethanol and later pinned for the identification to species level (using identification keys by Amiet *et al*. 2010). Identified bees were controlled by the bee taxonomic expert Mike Herrmann.

Assessment of vegetation characteristics

To estimate the cover, composition, and height of the vegetation, 10 randomly 1 x 1 m control plots were placed in the nest sampling area of each WFS in every sampling round (Fig. 4). This included an assessment of the cover (percentage area covered) by grasses (Poaceae, Cyperaceae, Juncaceae), forbs (including legumes), moss, litter, bare ground, and stones (> 2 cm) within each plot. The mean vegetation height in every 1 x 1 m plot was measured with a folding meter stick. To make the measurement easier the plot was divided into four quarters. Then the mean of the measures of each quarter was calculated. Furthermore, floral abundance (% cover of flowering plants) and diversity (number of flowering plant species) were always assessed in each plot and sampling round.

Soil sampling and analysis

The influence of soil composition and texture on nesting incidence was investigated by measuring bulk density, soil organic matter content (SOM) as well as soil texture (proportion of sand, silt, and clay). The samples were taken once per WFS from the end of June to the beginning of July 2020 from the top five centimeters of the soil with a soil cutter (100 ml cylinder; Fig. 5). For this six control soil samples were taken in each WFS, at least 1 m apart to field edge to prevent the influence of surrounding fields. Then additionally up to six “nest” soil samples immediately adjacent to a nest (ca. 2 cm away from the nest entrance) were taken. Thus, a total of 72 control and nest soil samples were taken. Distance between samples was always at least 2 m. Subsequently, the soil samples were stored in the fridge until the analysis.

First, the absolute bulk density was measured, which gives a measure of soil compaction, by following the reference method of the Swiss Federal Research Stations (1996). Samples were weighed and dried for at least 24 hours in a dry cabinet at 105 °C (Bender + Hobein, Trockenschrank). Afterward, the dry weight was taken. Bulk density was calculated as followed:

Bulk density (g/cm^3) = dry matter weight (g) / cylinder volume (100 cm^3)

To minimize the effort of the following time-consuming analysis the control samples, as well as the nest samples of the same WFS, were each aggregated. To analyse the soil texture the samples were sieved to 2 mm. For the analysis of the SOM measured a fraction of the samples were finely grounded. Soil texture and SOM were analysed by the labor of Dr. Thomas Keller at Agroscope following the Swiss standard protocols (Swiss Federal Research Stations 1996). Sedimentation analysis was performed to assess clay and silt content in water suspension aliquots. Sand was then measured as the difference to 100%. Wet combustion technique was conduct to determine soil organic content (SOC) i.e. by the oxidation of the bound carbon with a mixture of potassium dichromate and sulfuric acid and following titration of the residual potassium dichromate with ammonia ferrous sulfate. SOM (hereafter humus) was then obtained by multiplying SOC with the factor of 1.725.

Finally, the mean slope and exposition of each site were recorded with a compass. Information about the age and the management (e.g. mowing, weeding, herbicides, seed mixture) of the wildflower strip were obtained from the farmer. However, the management did not really differ between sites and was therefore no longer consider in the analysis.

Detection probability

We compared my detection probability with three other observers with diverse experience in nest searching. The same three transects were scanned by all observers. Then the total number of detected nests per transect was compared across observers. For each nest detected by an observer, it was confirmed whether the nest was correctly identified as a nest of a ground-nesting bee or not according to expert knowledge of experienced observers. The detection probability for each observer was then calculated by the average of each transect. My detection probability was highest with around 80% compared to the other observer (70%, 30% resp. 10%).

Statistical analysis

The main drivers of nesting incidence (binary response variable: nest present or absent) at a specific study site and sampling round were analyzed with general mixed-effects models using the package lme4 with a binomial error distribution. Effects of the potential drivers of nesting incidence were analysed at two different spatial scales: (i) the site (WFS) scale, testing for variation of drivers between sites, and (ii) the plot (1 x 1 m) scale, testing for variation of drivers within WFS. Explanatory variables selection was based on ecological and biological prediction (Zuur *et al.* 2009). Moreover, strongly correlating explanatory variables ($r \geq 0.6$) were excluded from the models to avoid potential co-linearity issues (Zuur *et al.* 2009).

To analyse effects of vegetation characteristics on nesting incidence at the site (WFS) scale, the mean proportion of grass and bare ground, flowering species diversity, and floral abundance of the control plots per sampling round were included as fixed explanatory variables and site ID as a random factor. To test for effects of soil characteristics at the site scale, mean scaled bulk density, sand proportion, and humus of the control samples were used as fixed effects and site ID as a random factor. Explorative analyses revealed no significant effects of area, age, or slope, and they were therefore not included in any of the models to avoid overfitting of models. Moreover, including sampling round as a fixed explanatory variable did not improve the models (log-likelihood ratio test), and sampling round showed no significant effect in any of the models. It was therefore not included in these models.

A further soil model was conducted to compare soil samples (i.e. nest vs. control) of nest presence sites by including bulk density and sand content as fixed effects. Humus strongly correlated with both bulk density and sand content and was therefore not incorporated in the model. Bin plots (the average versus the fitted residual) were used to test the assumption of the model. However, the bin plot does not support the assumption of the soil model. This suggests that soil properties do not differ considerably near a nest entrance and the rest of the WFS.

Data deriving from WFS where at least once a nest was found ("presence" sites) were used to analyse the potential influences on nest presence at a 1 x 1 m plot scale. Therefore "control" and "nest" 1 x 1 m plots were compared in a generalized linear model. To analyse the effects of vegetation properties the model was simplified by excluding floral abundance and flower diversity since no effect on the plot level was expected. Instead, the sampling round was added as a further fixed effect, since at this scale including sampling round improved the model based on log-likelihood ratio tests. The model assumption was again tested with a bin plot.

Influence on the number of nests (i.e. abundance) at site scale was first analysed with two simple linear models. Therefore, the total numbers of nests at "presence" sites were tested with the mean flowering species diversity respectively mean floral abundance over all sampling rounds as explanatory variables. Since the assumptions of linear models (analysed with diagnostic plots) did not fit the data the analysis was repeated with general linear models and a Poisson error distribution. Again, model assumptions were tested with diagnostic plots, but violated by the data. This indicates that no statistical analysis of the number of nests was possible due to the lack of power from the data.

All statistical analyses were performed with R version 3.6.3 (R Core Team 2020). Due to the low number of captured and identified nesting bees, no bee species-specific statistical analyses were performed.

Results

A total of 86 nests in five of the twelve studied wildflower strips were found (Fig. 6). From 44 of those nests, a total of 67 bees were collected. Hence, the catching rate was 51%. Overall, 14 species of four different genera were found (Table 1). Most species belonged to the genera of *Lasioglossum* (n = 59). Furthermore, nesting bees of *Halictus* (n = 4), *Andrena* (n = 1), and three parasitic bees of the genus *Sphecodes* were found.

At the WFS scale, nesting incidence tended to increase with flowering plant species diversity (Fig. 7). However, no other vegetation (Table 2) or soil explanatory variables (Table 3) had any significant effects on the nesting incidence of ground-nesting wild bees.

At the 1x1 m plot scale nesting incidence was negatively influenced by the proportion of grass cover (Fig. 8a, $P = 0.002$) but positively by the bare ground proportion (Fig. 8b, $P = 0.007$). Furthermore, nesting incidence differs between sampling rounds (Table 4, $P = 0.006$). According Fig. 9 nesting incidence seems to be highest during the second sampling round.

Discussion

Wild bees belong to the most important pollinators of wild plants and crops (Garibaldi *et al.* 2013, Kleijn *et al.* 2015, IPBES 2016). Providing good foraging as well as a suitable nesting habitat is crucial for the efficient protection and promotion of ground-nesting wild bee communities. With this study, we aimed to assess the potential of WFS as a nesting habitat for ground-nesting wild bees and to reveal the major habitat (vegetation and soil) characteristics, which drive the nesting incidence of ground-nesting wild bees. Our results suggest that across WFS the availability of diverse floral food resources is the best predictor for nesting incidence, even though the importance of nesting resources was hypothesized in previous studies (Gathmann & Tscharntke 2002, Potts *et al.* 2003, Potts *et al.* 2005). We could also show that not every WFS provides a suitable habitat for nesting wild bees since we only found on five of our twelve study sites nests of ground-nesting wild bees. Even the landscape effect was not considered in this study, we assume that the WFS properties itself influences the nest presence of wild bee in this region.

Nesting incidence of ground-nesting bees across wildflower strips (site scale)

We found no significant influence of any of the investigated soil or vegetation variables on ground-nesting bees nest presence at the site scale. But the nesting incidences tend to increase with a more diverse flowering plant species community. On average two more flowering plant species were present on colonized WFS, which indicates that increasing the flowering of only a few more plant species might be sufficient to promote the nesting incidence of wild bees. The importance of flower abundance and diversity for wild bee communities has been shown previously in WFS (Scheper *et al.* 2015) as well as in other habitats (e.g. Steffan-Dwenter & Tscharntke 2001, Potts *et al.* 2003, Ebeling *et al.* 2008, Grundel *et al.* 2010, Papanikolaou *et al.* 2017*b,* Bartual *et al.* 2019). Short foraging distance between nest location and foraging places seems to be beneficial (Greenleaf *et al.* 2007). In general, the maximal foraging distance range between 150 – 1200 m (Gathmann & Tscharntke 2002) and the body size of the bees correlates with their foraging range (Greenleaf *et al.* 2007), thus especially small wild bees will benefit from small foraging distances (Ganser *et al.* 2021). Beyond previous studies, our findings indicate that the habitat colonization of ground-nesting wild bees as a nesting habitat is more limited by the available floral feeding resources than other vegetation or soil factors associated with their nesting requirements. Hence, ground-nesting wild bees are more likely attracted and supported by suitable foraging resources than a good nesting habitat in the studied agro-ecosystems. To maintain and provide wild bee communities it is therefore essential to provide enough feeding habitats within the ordinary foraging range of most species (Greenleaf *et al.* 2007).

Besides the number of flowering plant species, we found no significant difference in the vegetation properties between WFS with and without nest presences. In consequence it was not possible to expect wild bee nesting incidence from the overall field characteristics of a specific WFS. Even though the vegetation composition on such sites is supposed to be similar, considering that all WFS have been sown with a standardized recommended seed mixture, and the management of the WFS is regulated by the Swiss agri-environmental scheme.

We could not find any evidence that the bulk density, sand, or humus content of the soil influences ground-nesting bees' presence. Some previous studies detected preferences of several ground-nesting bees for sandy soils (Cane 1991, Potts & Willmer 1997, Polidori *et al.* 2010, Bossart 2020) and a negative influence of a high amount of silt or clay (Potts & Willmer 1997, Julier & Roulston 2009, Sardiñas *et al.* 2016). This preference for sandier soil in a variety of different habitat types and from several ground-nesting wild bee species might indicate that we did not find an effect due to the low sample size. Sand content in the mentioned studies ranged between 34% and 99% at nesting places (Cane 1991, Potts & Willmer 1997). Similarly, we measured sand contents between 36% and 62.6% at study sites with nest presences. Further, the soil composition influences, among other soil properties, the bulk density and thus the hardness of a soil. The preference for sandier and therefore often less compact soil might be explained by the lower energy cost during nest construction (Potts & Willmer 1997). On the other hand, the soil should not be too soft, otherwise, the risk of nest collapsing is too high, especially in aggregations with high nest density (Potts & Willmer 1997). No effect was detected of soil organic matter content (i.e. humus) on wild bee nesting incidences. Humus was proven in the study of Osgood Jr. (1972) to negatively influence the nesting of *Andrena* in low-bush blueberries (8.5% in nesting vs. 15.8% organic-Cs in control areas). Avoidance of soil with high humus amount was explained by the higher risk of nest collapsing during nest construction or the high moisture that the organic matter keeps in the soil, which in turn can retarding the development of immature bees (Osgood Jr. 1972). Soil moisture was shown in several studies to influence wild bee nesting behavior (Greenberg 1982, Wuellner 1999, Julier & Roulston 2009). Still, it remains ambiguous if females choose nesting sites according to moisture or soil texture (Potts & Willmer 1997) and the preferences are likely species-specific. However, soil moisture was not analysed in this study, but might be an important factor to consider in future studies.

The fact that in only five of the total twelve wildflower strips nests were found, and without a significant difference in vegetation and soil characteristics, leads to the assumption that landscape composition and large-scale environmental factor (e.g. pesticide application, habitat connectivity and heterogeneity, foraging resources) may influence the presence of wild bee nests stronger than the WFS properties itself. The effect of the landscape composition on local wild bee abundance, diversity and populations have previously demonstrated (Steffan-Dewenter *et al.* 2002, Kim *et al.* 2006, Williams & Kremen 2007, Kremen & M'Gonigle 2015, Carrié *et al.* 2018, Eeraerts *et al.* 2019). In general, the amount of semi-natural habitat within the agricultural landscape had a positive influence on wild bees in these studies, but also high habitat diversity at a 500 m scale was found to increase bee diversity in agricultural landscapes (Földesi *et al.* 2016). Landscapes, which provide on a broad scale favorable habitats with good connectivity should facilitate the spreading of ground-nesting bees, thus increase also their colonization rate in WFS. Additionally, exposition and slope were as well associated with good nesting habitats (Potts & Willmer 1997, Carrié *et al.* 2018). However, this aspect cannot be the reason for different nesting incidences across studied WFS in this study, since most study sites were flat, thus didn't have an exposition at all. Bossart (2020), who studied in the same region the nesting incidence of ground nesting wild bees in differently managed meadows, found in all nine investigated extensively and in six of nine intensively managed meadows nests of ground-nesting wild bees. As the study of Bossart (2020) shows, are ground nesting wild bee commonly found in this study region. This indicates that in our study region the landscape context is not necessarily the reason for the absence of wild bee nests in a particular WFS. It seems rather that the local condition at the WFS limits the colonization. Regardless of the former argumentation, analysing the landscape-level effects is still recommended in future research to better understand why no nests of ground-nesting wild bees were found in the majority of the investigated WFS.

Nesting incidence within wildflower strips (1 x 1 m plot scale)

Within a wildflower strip, higher grass cover significantly decreased the probability of wild bee nest presence, whereas it was increased by the amount of bare ground. Interestingly bare ground and grass cover were not negatively correlated, even this can intuitively be assumed. Our results are supported by previous studies, which show that ground-nesting wild bees prefer a higher amount of bare ground in different habitat contexts (Potts & Willmer 1997, Potts *et al.* 2005, Sardiñas *et al.* 2016, Carrié *et al.* 2018). Moreover, Bossart (2020) found in the same study region, but in extensively managed meadows, higher nest abundance with decreasing grass cover and increasing bare ground amount. Sites comprised of a high amount of bare ground experience more insolation and reduced shadowing, which leads to a warmer soil surface. Higher soil temperature influence larvae development (Forrest *et al.* 2019) and increase activity and nest construction rates (Forrest *et al.* 2017). Open ground might also facilitate the nest relocation due to easier perceivable visual cues (Wuellner 1999). Further, it implicates generally fewer plant roots in the soil, which could make nest construction easier (Wuellner 1999). Wild bees' avoidance of places with high coverage of grass can be explained by difficulty to find a suitable and open surface to build a nest between dense grass growths. Nevertheless, we found no significant correlation between grass and herb respectively grass and bare ground coverage. Since nesting requirements vary among species (Carrié *et al.* 2018), different nesting preferences from different species might have canceled out each other and thus masked general findings. It is therefore even more important to provide a wide range of different habitat characteristics within a WFS, but also within the whole agricultural landscape in order to support a variety of different nesting requirements.

Effect of the sampling round

At the two sites with the most found nest, the nest abundance was low at the beginning of the season, peaked in April, and then slowly decreased until the end of the sampling period in June (Fig. 9). But statistical analysis of the data does not suggest that nest presence at site scale differs significantly across the sampling season. The main breeding season of most sampled wild bee species was in April, which would lay mainly in the second sampling round (14.04 - 24.04.2020). On the other side nest presence at 1 x 1 m plot level was influenced by the second (14.04 - 24.04.2020) and third (07.05 - 20.05.2020) round. The plot-level model only included data from "presence" sites, which probably explains the difference to the site level models. Increasing the number of investigated WFS with actual nest presence might reveal the same pattern at the site scale.

Nest searching and trapping method

In contrary to our sampling method, pan traps or sweep netting do not allow a direct association of the sampling site with the nesting habitat. Instead, our method allows quantifying nesting incidence and can be used to directly link it with potential drivers. However, a potential constraint of this method could be the detection probability. To address this issue, we tested the detection probability of nests by multiple observers. These tests indicate that the probability of missing nests was relatively low, although it cannot be completely ruled out that not every present nest in a WFS was detected, or that a nest was wrongly identified as a wild bee nest while it was built by another organism. A further constraint of the method is the limitation to detect only nests with clear tumuli and nest entrances. Nests of ground-nesting bees that are not associated with any visible tumulus or old, damaged nests are not considered by this method. This may bias the discoverable nesting species composition to tumuli constructing species with more obvious nests. Further, dense or high vegetation may impede the recognition of nests and can therefore affect detection probability.

In the present study, we only found bees in 51% of all traps. Catching ground-nesting wild bee with an individual emergence trap should be possible since they return to the same nest in the evening as well as after foraging (Lonsdorf et al. 2009, Zurbuchen & Müller 2012). The low catching rate can be related to the possibility that the nest was already abandoned, i.e. that nesting bees were no longer active, thus the next generation will earliest emerge in the coming spring. To the best of my knowledge no other study used (emergence)-traps for individual nests. Allowing a direct link between a wild bee and her nest offers a high potential of this trapping method to investigate ground-nesting wild bees nesting habitats and resources. Especially when considering the difficulty to sample insects with other methods due to their small size and the high rate of spatial and temporal turnover and abundance (e.g. Minckley et al. 1999). To increase the trapping rate, we suggest figuring out the optimal time during the day for the trap installation, rather than change the construction, respectively, principal of the traps themselves.

Bee species composition

All sampled species are listed as least concern according to the European Red List of Bees (Nieto *et al*. 2014) except for *Andrena humilis* for which the data is deficient. Besides *Halictus subauratus* and *Lasioglossum glabriusculum* none of the other species are listed on the Swiss Red List (Amiet 1994).It has to be kept in mind that the Swiss Red list is from the early 90s, hence it is likely that the state of endangerment has changed. Moreover, it is important to note that the list of sampled species should not be considered as a complete list of all ground-nesting species present in WFS but rather gives some first insights into the wild bee species, which can potentially be found in the WFS of the study region. The low sample size reduces the chance to catch rare species. However, the main goal of this study was not the identification of the existing ground-nesting wild bees in the study region. In order to reveal the species composition in Swiss WFS, a higher sampling effort is needed maybe by adding other sampling methods (i.e. pan traps or sweep nets; Rhoades *et al*. 2017). From the detected and sampled wild bees *Lasioglossum malachurum, L. pauxillum*. *H. subauratus* and *L. glabriusculum* are social species. *Lasioglossum calceatum* produce first a generation of female workers, which then fosters the second generation later in the season. Hence, they are classified as semi-social (Amiet *et al.* 2010). This social lifestyle explains that in some of the nests from *L. malachurum, L. calceatum, L. glabriusculum*, and *L pauxillum* more than one individual per trap was sampled, in the case of *L. malachurum* even up to 11 individuals. On some occasions, a parasitic wild bee was sampled together with its host (*Sphecodes gibbus* - *L. leucozonium* and *S. ephippius* - *L. lucidulum*). Both *S. gibbus* and *S. ephippius* are known to parasitize species from the genera *Halictus* and *Lassioglossum*. However, the specific host-parasite interaction was not found to be reported until now (Amiet *et al.* 2010, Westrich 2019).

Conclusions and conservation implications

Understanding the nesting requirements of ground-nesting wild bees is essential for the successful protection and promotion of this important pollinator group. . Providing only good foraging habitat is not enough. Our results suggest that across sites the flowering plant species diversity attract ground-nesting wild bees to nest in a WFS and the existing nesting resources at the site remains less important. Where on the other hand within a colonized WFS, the high amount of bare ground and low grass cover positively influence nesting of ground-nesting bees. This finding suggests that diverse food resources attract wild bees and heterogeneous vegetation that is not too dense or dominated by grasses with patches of bare soil promotes nesting within WFS. We only found ground-nesting bee nests on five of the twelve study sites. This further indicates that many ground-nesting bees will use WFS only as foraging, but not as nesting habitat. Since in other studies in the same region wild bees nests were frequently found on extensively as well as on intensively managed meadows we rather rule out a limitation of the colonization due to the regional agricultural landscape framework

In order to promote the potential of WFS as nesting habitat for ground-nesting wild bees in agricultural landscapes is it important to provide a high diversity of flowering plants. Increasing the actual flowering plant species diversity assures diverse foraging resources for the whole activity phase of the bees. Even though the recommended seed mixtures for WFS contains theoretically sufficient plant species (at minimal 24 species) is it unlikely that all species will establish. Only increasing the number of plant species in the seed mixture is therefore not enough, it must be ensured that also sufficient species actually germinate. At nest presence sites of our study on average 5.5 flowering plant species per 1 x 1 m plots (deriving from a total of 10 m^2 sampling area) were found. This are considerably less species than the applied seed mixtures contained. To ensure the germination and establishment of sufficient and locally adapted flowering plant species, the seed mixture might ideally be assembled site-specific. Moreover, it is important to maintain this plant diversity over the years maybe by controlling the number of flowering plants. Reseeding of WFS with poor quality, which is dominated by grasses and harbor low flower diversity could be considered too. Further, a heterogeneous structured wildflower strip with patches of bare ground will attract ground-nesting wild bee not only to forage, but also to use as nesting habitat. In conclusion, WFS should be prevented from high grass pressure and dense vegetation cover. It remains unclear if this can be attained by regular disturbance for example by manual weeding or mowing. Harrowing a small part of the wildflower strip during the winter might be another possibility to maintain some open ground. We recommend testing in further studies the effect of occasional disturbances and reseeding on WFS properties on ground-nesting wild bee nesting incidence.

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Tables & Figures

Table 1. List of sampled bee species (n = 67) and their abundance (i.e. number of individuals) at the corresponding sampling site. Bees were collected across all four sampling rounds at five sampling sites. At the installed traps in Bellikon south was never a ground-nesting wild bee sampled.

Sites	*Lasioglossum calceatum (Scopoli 1763)*	*Lasioglossum glabriusculum* (Morawitz, 1872)	*Lasioglossum leucozonium* (Schrank 1781)	*Lasioglossum lucidulum (Schenck 1861)*	*Lasioglossum malachurum* (Kirby 1802)	*Lasioglossum pauxillum* (Fabricius 1793)	*Lasioglossum zonulum* (Schrank 1781)	*Halictus subauratus* (Rossi 1792)	*Halictus simplex agg.* (Blüthgen 1923)	*Halictus tumulorum* (Linnaeus 1758)	*Andrena humilis* (Imhoff 1832)	*Sphecodes ephippius* (Linnaeus 1767)	*Sphecodes gibbus* (Linnaeus 1758)	*Sphecodes monilicornis (Kirby 1802)*
Buch am Irchel			3			4								
Lengnau nord		3	2	2	24			2	1			1	1	1
Niederglatt	8	3	1			1	3			1	1			
Niederrohrdorf			1			4								
Bellikon south														
total	8	6	7	2	24	9	3	2	1	1	1	1	1	1

Table 2. Effect of the percentage of grass and bare ground cover, number of flowering species (flower diversity), and the cover of flowers (floral resources) on nest presence at wildflower strip scale. The marginal R^2 describes the proportion of variance explained by the fixed factors, whereas the conditional R^2 describes the proportion of variance, which is explained by the fixed and random factor (Nakagawa & Shielzeth 2012). Marginally significant results ($P > 0.05 \leq 0.1$) are presented in bold italics.

Response variable	**Predictors**	**Estimate**	**SE**	**z value**	**P**
Nest presence	(Intercept)	0.1	0.22	- 1.05	0.293
	Grass cover	0.93	0.07	- 0.99	0.323
	Bare ground	0.98	0.07	- 0.34	0.731
	Flower diversity	1.59	0.41	1.79	***0.074***
	Floral resources	0.83	0.17	- 0.93	0.354
Marginal R^2 / Conditional R^2		0.254 / 0.693			
log-Likelihood		-19.066			

Table 3. Effect of bulk density (cm^3/g) and sand proportion on nest presence at the wildflower strip scale. The marginal R^2 describes the proportion of variance explained by the fixed factors, whereas the conditional R^2 describes the proportion of variance, which is explained by the fixed and random factor (Nakagawa & Shielzeth 2012).

Response variable	**Predictors**	**Estimate**	**SE**	**z value**	**P**
Nest presence	(Intercept)	0.07	0.12	- 1.63	0.103
	Bulk density	3.88	7.65	0.69	0.492
	Sand	15.62	36.46	1.18	0.239
	Humus	4.10	10.75	0.54	0.591
Marginal R^2 / Conditional R^2		0.310 / 0.794			
log-Likelihood		-19.631			

Table 4. The effect of grass and bare ground cover proportion and the sampling round on nest presence at 1x1 m plot scale (i.e. within a wildflower strip). The marginal R^2 describes the proportion of variance explained by the fixed factors, whereas the conditional R^2 describes the proportion of variance, which is explained by the fixed and random factor (Nakagawa & Shielzeth 2012).

Response variable	**Predictors**	**Estimate**	**SE**	**z value**	**P**
Nest presence	(Intercept)	0.15	0.10	- 2.70	***0.007***
	Grass cover	0.93	0.02	- 3.05	***0.002***
	Bare ground	1.05	0.02	2.70	***0.007***
	Second sampling round	5.95	3.88	2.73	***0.006***
	third sampling round	3.25	2.12	1.80	0.072
	fourth sampling round	2.04	1.35	1.07	0.284
Marginal R^2 / Conditional R^2		0.288 / 0.384			
log-Likelihood		-113.855			

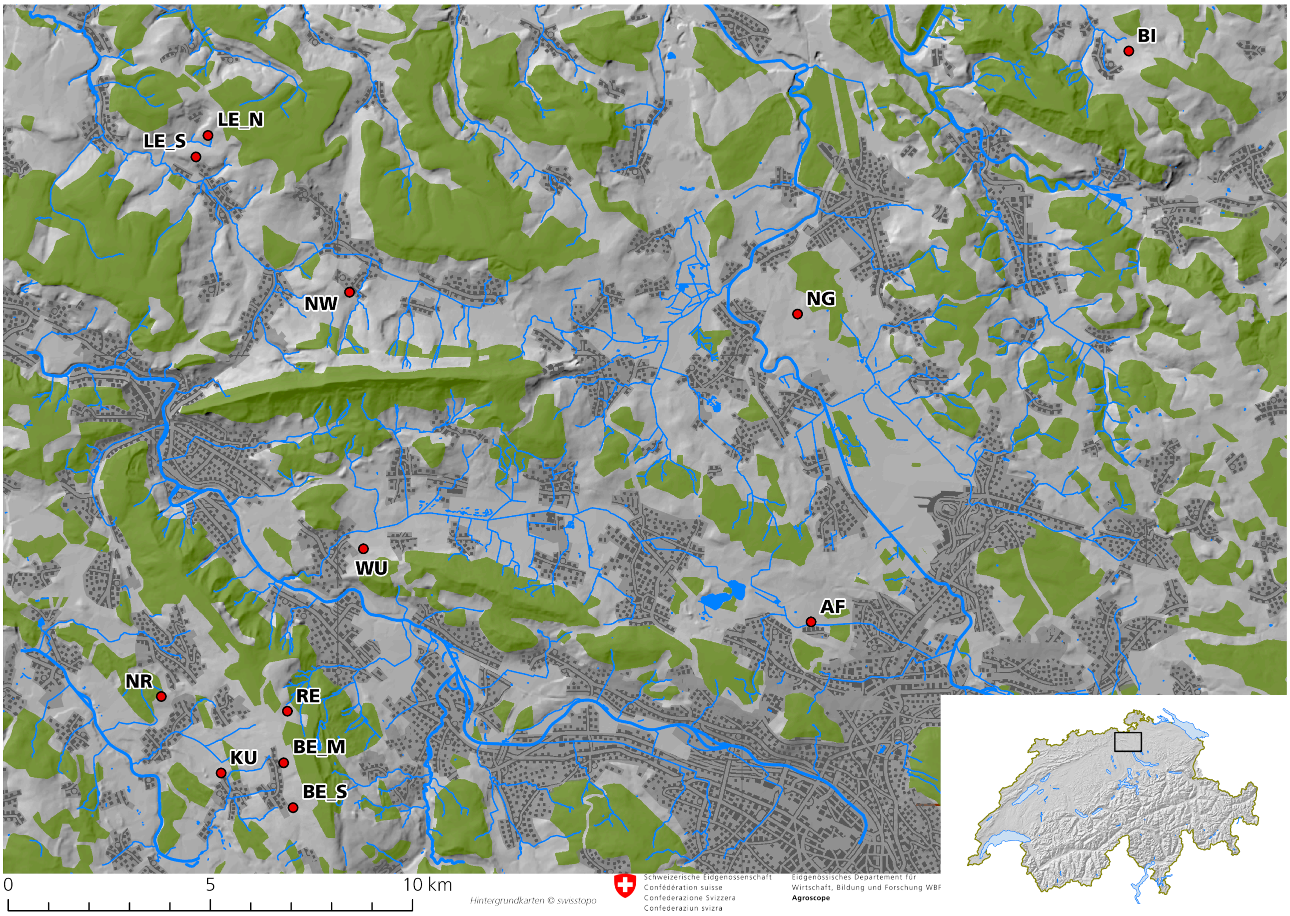

Figure 1. Map of all twelve study sites (red dots) in the canton of Aargau and Zurich. The sites are labeled with the corresponding ID. Wild bee nests were found in Bellikon south (BE_S), Buch am Irchel (BI), Lengnau nord (LE_N), Niederglatt (NG) and Niederrohrdorf (NR).

Figure 2. Nest entrance with visible tumulus of the species *Lasioglossum leucozonium*.

Figure 3. Emergence trap placed over a single nest entrance. The bee can climb along a wooden stick into the plastic container on the top, where it is preserved in propylene glycol (60%) until the trap was remove.

Figure 4. 1 x 1 m frame plot to estimate the vegetation cover of the wildflower strip. The yellow cord divided the plot into four quarters.

Figure 5. Soil cutter with the 100 ml sampling cylinder next to a taken soil sample.

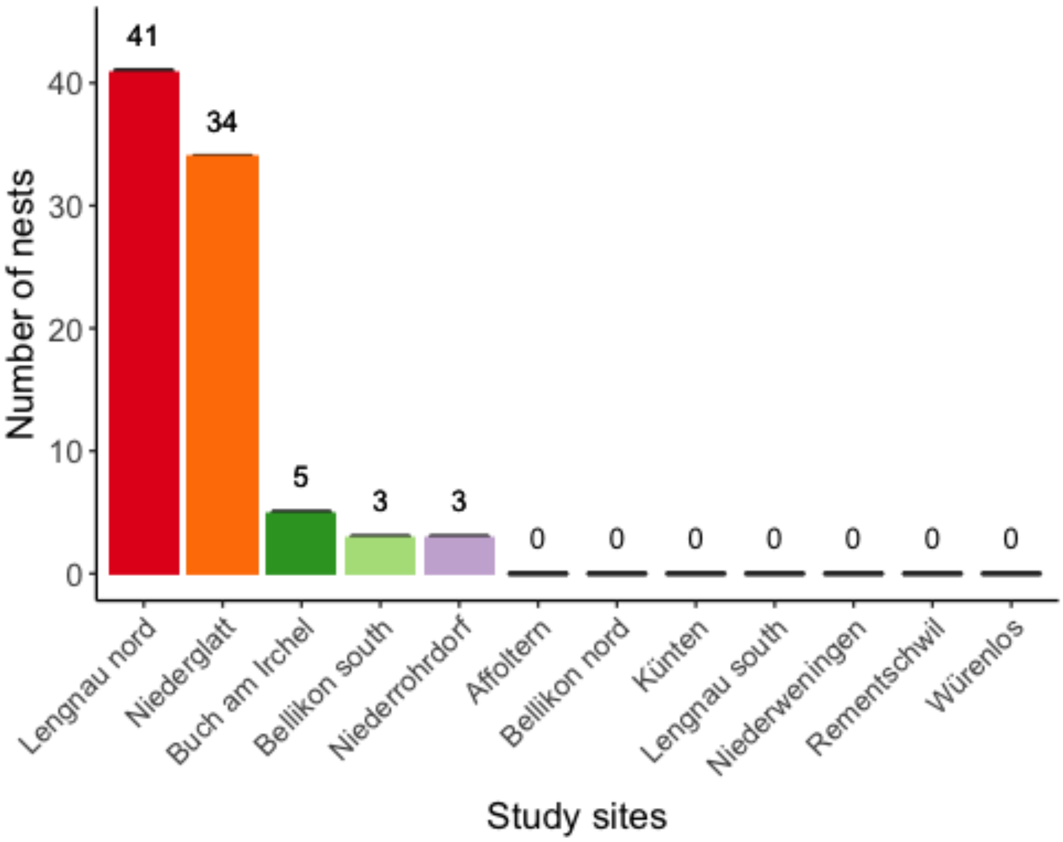

Figure 6. The total number of nests of ground-nesting wild bees found on 500 m² within each study site over the four sapling rounds.

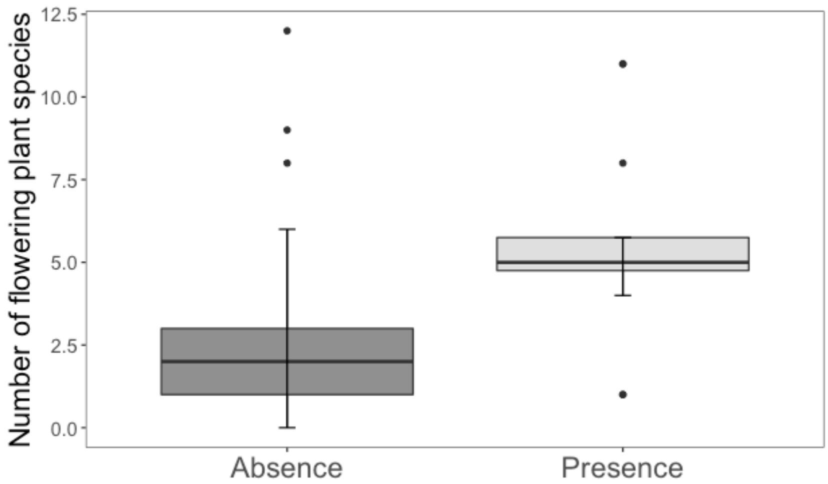

Figure 7. The mean number of flowering plant species in control plots (ten 1 x 1 m) across all sampling round in wildflower strips (WFS) where nests were present (presence, n = 20, mean = 5.5) or in WFS where no nest were found (absence, n = 28, mean = 2.8). The boxes represent the 75% and 25% quartiles from the median (thick black line), whiskers represent the minimum and maximum values. Outliers are represented as open dots. See table 2 for test statistics.

(a) (b)

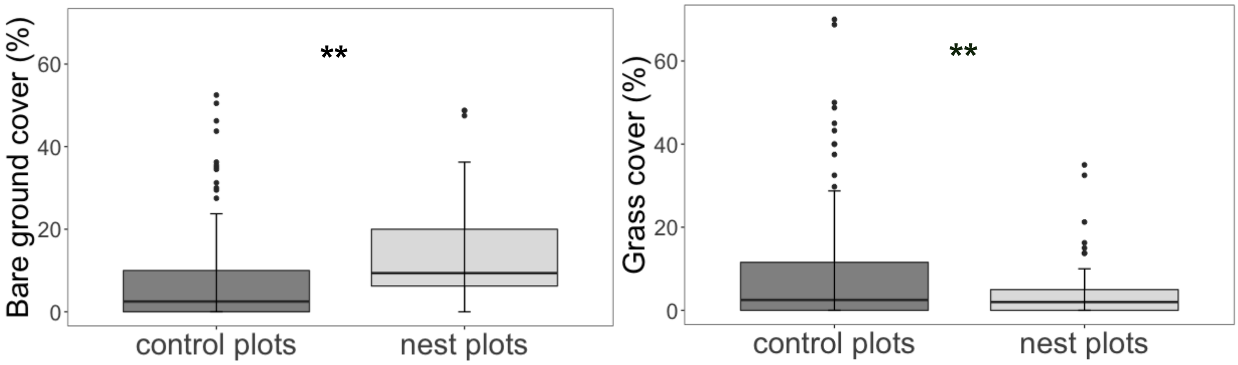

Figure 8. Comparison of the (a) mean grass proportion (%) and (b) mean bare ground proportion (%) in the 1 x 1 mcontrol plots (n = 120) and nest plots (n = 86). Only data from sites with nest presence (n= 5) were used. See table 4 for test statistics.

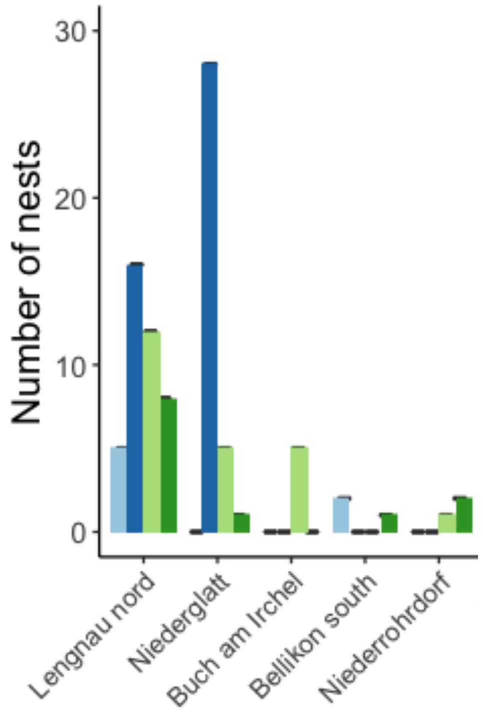

Figure 9. Number of nests at nest presence sites depending on sampling round: light blue = first sampling round (24.03. – 09.04.2020), blue = second sampling round (14.04 - 24.04.2020), light green = third sampling round (07.05 - 20.05.2020), green = fourth sampling round (26.05 - 24.06.2020).

Appendix

Table A1. Study sites with site ID, year of establishment, area (size in ha), applied seed mixture and the coordinates (Swiss coordinate system).

Site	Site ID	Seeding year	area (ha)	seed mixture	GPS E	GPS N
Affoltern	AF	2018	0.36	UFA Grundversion	681708	253409
Bellikon	BE_S	2017	0.2	Labiola Buntbrache mit Wildbienenzu-satz	668892	248820
Bellikon	B_M	2017	0.33	Labiola Buntbrache mit Wildbienenzu-satz	668661	249930
Buch am Irchel	BI	2018	0.6	UFA Vollversion	689562	267522
Künten	KU	2017	0.24	Labiola Buntbrache CH-2017 (UFA)	667114	249679
Lengnau	L_S	2017	0.45	UFA-Salvia	666484	264902
Lengnau	L_N	2018	0.25	Labiola Buntbrache mit Wildbienenzu-satz	666788	265437
Niederglatt	NG	2016	1.12	UFA Grundversion	681370	261021
Niederrohrdorf	NR	2018	0.65	unknown	665631	251566
Niederwenigen	NW	2013	0.41	UFA Grundversion	2670285	1261564
Rementschwil	RE	2018	0.12	Labiola Buntbrache CH-2016 (UFA)	668749	251201
Würenlos	WU	2018	0.54	Labiola Buntbrache mit Wildbienenzu-satz	670636	255213

Table A2. Lists of the applied seed mixtures. Both UFA-Grundversion and -Vollversion are available at the Swiss scale for perennial wildflower strips. The “Buntbrache Grundversion mit Wildbienenzusatz” is a special seed mixture used in the special biodiversity program „Labiola“ of the canton Aargau. The “UFA Salvia CH-G” is normally used for species-rich hay meadows and was only applied at Lenganu south, but see appendix A1 for the site with the corresponding used seed mixture.

UFA-Grundversion

Latin name	German name
Achillea millefolium	Wiesen-Schafgarbe
Agrostemma githago	Kornrade
Anthemis tinctoria	Färber-Hundskamille
Centaurea cyanus	Kornblume
Centaurea jacea	Wiesen-Flockenblume
Cichorium intybus	Wegwarte
Daucus carota	Wilde Möhre
Dipsacus fullonum	Wilde Karde
Echium vulgare	Gemeiner Natterkopf
Fagopyrum esculentum	Echter Buchweizen
Hypericum perforatum	Echtes Johanniskraut
Legousia speculum-veneris	Venus-Frauenspiegel
Leucanthemum vulgare	Wiesen-Margerite
Malva moschata	Bisam-Malve
Malva sylvestris	Wilde Malve
Melilotus albus	Weisser Honigklee
Onobrychis viciifolia	Saat-Esparsette
Origanum vulgare	Echter Dost
Papaver rhoeas	Klatsch-Mohn
Pastinaca sativa	Gewöhnlicher Pastinake
Silene pratensis	Weisse Waldnelke
Tanacetum vulgare	Rainfarn
Verbascum densiflorum	Grossblütige Königskerze
Verbascum lychnitis	Lampen-Königskerze gelb

UFA-Vollversion

Latin name	German name
Achillea millefolium	Wiesen-Schafgarbe
Agrostemma githago	Kornrade
Anthemis tinctoria	Färber-Hundskamille
Buglossoides arvensis	Acker-Steinsame
Camelina sativa	Saat-Leindotter
Centaurea cyanus	Kornblume
Centaurea jacea	Wiesen-Flockenblume
Cichorium intybus	Wegwarte
Daucus carota	Wilde Möhre
Dipsacus fullonum	Wilde Karde
Echium vulgare	Gemeiner Natterkopf
Fagopyrum esculentum	Echter Buchweizen
Hypericum perforatum	Echtes Johanniskraut
Legousia speculum-veneris	Venus-Frauenspiegel
Leucanthemum vulgare	Wiesen-Margerite
Malva moschata	Bisam-Malve
Malva sylvestris	Wilde Malve
Melilotus albus	Weisser Honigklee
Onobrychis viciifolia	Saat-Esparsette
Origanum vulgare	Echter Dost
Papaver dubium	Saat-Mohn
Papaver rhoeas	Klatsch-Mohn
Pastinaca sativa	Gewöhnlicher Pastinak
Silene notiflora	Acker-Waldnelke
Silene pratensis	Weisse Waldnelke
Stachys annua	Einjähriger Ziest
Tanacetum vulgare	Rainfarn
Tanacetum vulgare	Rainfarn
Tragopogon orientalis	Habermarch
Verbascum densiflorum	Grossblütige Königskerze
Verbascum lychnitis	Lampen-Königskerze Gelb

Buntbrache Grundversion mit Wildbienenzusatz

Latin name	**German name**
Achillea millefolium	Wiesen-Schafgarbe
Agrostemma githago	Kornrade
Anthemis tinctoria	Färber-Hundskamille
Centaurea cyanus	Kornblume
Centaurea jacea	Wiesen-Flockenblume
Cichorium intybus	Wegwarte
Daucus carota	Wilde Möhre
Dipsacus fullonum	Wilde Karde
Echium vulgare	Gemeiner Natterkopf
Fagopyrum esculentum	Echter Buchweizen
Hypericum perforatum	Echtes Johanniskraut
Legousia speculum-veneris	Venus-Frauenspiegel
Leucanthemum vulgare	Wiesen-Margerite
Malva alcea	Sigmarswurz
Malva sylvestris	Wilde Malve
Melilotus albus	Weisser Honigklee
Onobrychis viciifolia	Saat-Esparsette
Origanum vulgare	Echter Dost
Papaver rhoeas	Klatsch-Mohn
Pastinaca sativa	Gewöhnlicher Pastinak
Silene pratensis	Weisse Waldnelke
Tanacetum vulgare	Rainfarn
Verbascum densiflorum	Grossblütige Königskerze
Verbascum lychnitis Gelb	Lampen-Königskerze Gelb
Sinapis arvensis	Acker-Senf
Camelina sativa	Saat-Leindotter
Campanula rapunculoides	Acker-Glockenblume
Linaria vulgaris	Gemeines Leinkraut
Potentilla argentea	Silber-Fingerkraut

UFA Salvia CH-G

Latin name	German name
Anthoxanthum odoratum	Duftendes Ruchgras
Arrhenatherum elatius	Französisches Raygras
Briza media	Mittleres Zittergras
Bromus erectus	Aufrechte Trespe
Dactylis glomerata	Wiesen-Knäuelgras
Festuca pratensis	Wiesen-Schwingel
Festuca rubra rubra	Rot-Schwingel
Helictotrichon pubescens	Flaum-Wiesenhafer
Poa pratensis	Wiesen-Rispengras
Anthyllis carpatica	Karpaten-Wundklee
Campanula patula	Wiesen-Glockenblume
Campanula rotundifolia	Rundblättrige Glockenblume
Carum carvi	Kümmel
Centaurea jacea	Wiesen-Flockenblume
Centaurea scabiosa	Skabiosen-Flockenblume
Clinopodium vulgare	Wirbeldost
Crepis biennis	Wiesen-Pippau
Daucus carota	Wilde Möhre
Knautia arvensis	Feld-Witwenblume
Lathyrus pratensis	Wiesen-Platterbse
Leontodon hispidus	Raues-Milchkraut
Leucanthemum vulgare	Wiesen-Margerite
Lotus corniculatus	Gewöhnlicher Hornklee
Medicago lupulina	Gelbklee
Onobrychis viciifolia	Saat-Esparsette
Picris hieracioides	Gewöhnliches Bitterkraut
Pimpinella major	Grosse Bibernelle
Plantago lanceolata	Spitz-Wegerich
Primula veris	Frühlings-Schlüsselblume
Salvia pratensis	Wiesen-Salbei
Sanguisorba minor	Kleiner Wiesenknopf
Scabiosa columbaria	Tauben-Skabiose
Silene vulgaris	Klatschnelke
Stachys officinalis	Echte Betonie
Tragopogon orientalis	Habermarch
Trifolium pratense	Rot-Klee
Vicia sepium	Zaun-Wicke

Declaration of consent

on the basis of Article 30 of the RSL Phil.-nat. 18

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Bachelor ☐ Master ☒ Dissertation ☐

Title of the thesis: Nesting incidence of ground-nesting bees in Swiss lowland perennial wildflower strips

Supervisor: Dr. Matthias Albrecht, Agroscope Reckenholz, Zürich
Dr. Jean-Yves Humbert, Institute of Ecology & Evolution, University of Berne

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