



Impact of the “Farming With Alternative Pollinators” Approach on Crop Pollinator Pollen Diet

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Pollinators are facing declines at a global level. One of the main factors driving this decline is insufficient access to floral resources due to habitat loss and degradation that can affect both diet generalist species as well as those with more restricted floral preferences. Here we evaluated the effect of a novel mitigation strategy in agricultural ecosystems, Farming with Alternative Pollinators (FAP) on the pollen diet of crop pollinators. The approach dedicates 25% of the cropped area to Marketable Habitat Enhancement Plants (MHEP) that attract pollinators, natural enemies of the crops, and provide farmers with income. We assessed the effect of the approach on pollen diet of faba bean (*Vicia faba*) and pumpkin (*Cucurbita maxima*) flower visitors in four different regions in Morocco during 2018 and 2019 by comparing control fields (monoculture) and FAP fields in 13 trials and 101 sites. Results from 25 wild bee species show that almost two-thirds of the species carrying or collecting pollen when visiting pumpkin flowers and half of the species carrying or collecting pollen when visiting faba bean flowers gathered this pollen from two or more host plants (i.e., MHEP, main crop, and/or wild plants) and displayed a wide dietary breadth. Pollen grains from the main crops were poorly represented on the female scopae, indicating that crops were mainly visited for nectar. Hence, crop flower visitors may require alternative pollen sources to meet their nutritional needs. The number of pollen genera collected by flower visitors and the dietary breadth of crop flower visitors did not show a significant increase in response to FAP management. Among the selected MHEP, sunflower (*Helianthus annuus*) was the pollen resource for pumpkin flower visitors. In faba bean, flower visitors collected pollen from coriander (*Coriandrum sativum*) and canola (*Brassica napus*). Our study sheds light on the importance of characterizing the pollen diet and the foraging behavior of crop pollinators to identify appropriate plant species that complement their food, maintain and conserve their populations.

Keywords: nectar, pumpkin, faba bean, wild bees, foraging behavior

Abbreviations: BDI, Berger–Parker’s dominance index; FAP, Farming with Alternative Pollinators; MHEP, Marketable Habitat Enhancement Plants.

INTRODUCTION

Pollinators provide vital and free ecosystem services that benefit human well-being, including the pollination of 75% of the most important global food crops (Klein et al., 2007). However, both wild and domesticated pollinators are showing global declines (Goulson, 2019). Several anthropogenic and environmental stressors are driving pollinator decline, including agricultural intensification, invasive species (Aizen et al., 2009, 2019; Gill et al., 2016; Duchenne et al., 2020), climate change (Gérard et al., 2020; Martinet et al., 2020) and habitat loss and fragmentation (Potts et al., 2010).

Scarcity in floral resources due to habitat loss and agricultural intensification is negatively affecting generalist and specialist pollinators, but to varying extents (Scheper et al., 2014). Some pollinator groups with narrow dietary breadth have shown a greater relative decline (Kleijn and Raemakers, 2008; Wood et al., 2019), as they might struggle to switch to other alternative plants when their main host plants are scarce. In contrast, pollinators with wide dietary breadth display a higher stability in response to these external pressures (Chacoff et al., 2018), as they interact potentially with a greater number of species of the local plant community and can shift on the expanding ones (Martín González et al., 2010; Roger et al., 2017). However, lack of diversity in floral resources may restrict their dietary breadth, and thus induce nutritional shortage in quality and quantity (Carvell et al., 2006; Goulson et al., 2015; Vaudo et al., 2020).

Managed flower-rich habitats have been one of the most commonly suggested mitigation strategies applied to curb pollinator decline in intensively managed agro-ecosystems (Grass et al., 2016; IPBES, 2016; Albrecht et al., 2020). Flower strips support diverse pollinating species (Haaland et al., 2011; Albrecht et al., 2020) and have been found to provide a majority of the pollen and nectar collected by visiting species in experimental studies (Ouvrard et al., 2018). Furthermore, several studies have demonstrated an increase in pollinator abundance and species richness in crops adjacent to nearby flower strips (Blaauw and Isaacs, 2014; Feltham et al., 2015). However, wild-flower strips are not self-sustaining and farmers dislike WFS even if they gain financial compensation (Kleijn et al., 2019), and their effectiveness at supporting sustainably pollinator diversity has been reconsidered (Klein et al., 2003; Kleijn et al., 2019) due to the high implementation costs (Batáry et al., 2015). Indeed, pollinator-protection schemes should be economically self-sustaining and feasible for all nations (Christmann, 2020).

Farming with Alternative Pollinators (FAP) (Christmann and Aw-Hassan, 2012) is an economically self-sustaining agricultural approach (Christmann et al., 2017, 2021a,b) that aims to increase income per surface through pollinator-friendly habitat enhancement as an incentive for farmers to contribute to pollinator protection. Within this framework, farmers dedicate 25% of their field area to seed Marketable Habitat Enhancement Plants (MHEP) that provide pollinators with floral rewards and farmers with additional income.

Farming with Alternative Pollinators fields provides, in addition to MHEP, nesting and water support made out of local materials. The approach demonstrated its effectiveness in

increasing crop yield and reducing pest abundance (Christmann et al., 2017, 2021a,b), and significantly boosting pollinator abundance and diversity in agro-ecosystems (Christmann et al., 2021a,b; Sentil et al., 2021).

One mechanistic explanation of the population boost could be the inclusion of additional pollen sources in the diet. However, to date, no study has assessed the contribution of the FAP approach on crop pollinator dietary breadth using pollen analyses, and no detailed research investigating the effect of flowering strips on crop pollinator dietary breadth has been conducted either. Most previous studies have assessed the effect of flower strips on crop pollinator abundance and species richness using floral visits (Blaauw and Isaacs, 2014; Garibaldi et al., 2014; Feltham et al., 2015). Floral visitation records do not provide comprehensive information regarding the dietary pollen niches of crop flower visitors, and thus lack information about the co-flowering plants that crop flower visitors use to complement and balance their diets. Floral visitation alone is therefore not sufficient for assessing the effect of marketable habitat enhancement plants on the diet or the health of crop pollinators.

In this study, we aim to describe the pollen diet and the foraging behavior of pumpkin and faba bean flower visitors and investigate whether the FAP approach is effective in supporting the flower visitors of the two crops by extending their pollen diet. More specifically, we ask the following questions: 1. Do crop flower visitor species collect or carry pollen from a single or from multiple host plants (i.e., MHEP, main crop, and/or wild plants)? 2. Do crop flower visitors visit crops for pollen or nectar? 3. Does the FAP approach increase the dietary breadth and the number of pollen genera of crop flower visitors?

We expect that: (1) crop flower visitors collect pollen from either single or multiple host plants, depending on the flower visitor species; (2) given the physical and the chemical defenses of pumpkin pollen (Lundgren, 2009) and the high-quality faba bean pollen (Goulson and Darvill, 2004), we expect that pumpkin and faba bean will be visited for nectar and pollen, respectively; and (3) the FAP approach increases the dietary breadth and the number of pollen genera collected by crop flower visitors.

MATERIALS AND METHODS

Study Sites

The experiments were carried out in four regions in Morocco (Errachidia, Settata, Sefrou, and Kenitra), representing different climate and landscape characteristics. The landscape in Settata is homogenous and dominated by intensive agriculture (90% of the arable land). The major agricultural activity in this region is cereal production. Unlike Settata, the landscape in Kenitra is characterized by diversified agricultural crop production (33%), forest plains, and several other semi-natural habitat types. In Sefrou, arable land does not exceed 34%, the remaining landscape is covered by forest and other semi-natural areas (e.g., grasslands and pastures). In contrast to the other regions, 37% of the land surface of Errachidia is covered by Hamadas, consisting of high, largely barren, hard, and rocky plateaus. The major agricultural activities in these oases are date palm, cereal, and

legume production (Ministry of Agriculture, Fisheries, Rural Development, Water, and Forests, 2020).

Field Trials

Two crops were selected: faba bean (*Vicia faba*, Fabaceae) and pumpkin (*Cucurbita maxima*, Cucurbitaceae). These crops are two of the leading food crops in Morocco and they are broadly cultivated in the four studied regions. Besides that, they show contrasting phenologies and floral traits (Ali et al., 2014; Murphy-Bokern et al., 2017) and rely on insect pollination to a differing extent, with pumpkin being essentially dependent on insect pollinators and faba bean being a moderately pollinator-dependent crop (Klein et al., 2007). Crops were planted in the four regions within two years (2018 and 2019). Faba bean and pumpkin were not planted in Errachidia in 2018 and pumpkin was not planted in Kenitra in 2018, resulting in 13 trials (i.e., three faba bean trials and two pumpkin trials in 2018 and four faba bean trials and four pumpkin trials in 2019). For each trial, eight fields of 300 m² were selected (i.e., five FAP fields and three control fields), totaling 104 FAP and control fields (Supplementary Table 1). Three fields were excluded because of their low maintenance, resulting in 101 fields. For each trial, eight MHEP were chosen among the following plants: Fabaceae (cultivated lupines *Lupinus albus*, wild lupins *Lupinus luteus*, grass pea *Lathyrus sativus*, alfalfa *Medicago sativa*, white clover *Trifolium repens*), Apiaceae (anise *Pimpinella anisum*, celery *Apium graveolens*, coriander *Coriandrum sativum*, and cumin *Cuminum cyminum*), Cucurbitaceae (melon *Cucumis melo* and zucchini *Cucurbita pepo*), Asteraceae (sunflower *Helianthus annuus*), Brassicaceae (canola *Brassica napus* and arugula *Eruca sativa*), Lamiaceae (chia *Salvia hispanica*), and Malvaceae (okra *Abelmoschus esculentus*). The number of MHEP was restricted to 4, 5, or 6 MHEP in some trials depending on the crop phenology and the MHEP that can be sown during the blooming of the main crop. Within each trial, the same 4–8 MHEP were used for all FAP fields.

Farming with Alternative Pollinators and control fields were separated from each other by a minimum distance of 200 m, which corresponds to the average or the maximum foraging distance of the main wild pollinator groups (Gathmann and Tschardt, 2002; Wratten et al., 2003; Elliott, 2009). Within FAP fields, the main crop was sown in 75% of the field area surrounded by four to eight MHEP strips in 25% of the field area. In contrast, the main crop in control fields occupied the entire field area (Figure 1). MHEP strips were all one meter wide and five to 30 m long depending on the number of selected MHEP (Figure 1 and all experimental designs in Supplementary Figures 1–4). MHEP were chosen depending on soil and climatic conditions of the regions and based on their attractiveness to insect pollinators (i.e., diverse floral traits, including color, morphology, bloom phenology, and flower rewards) and farmers. Crops were managed in a similar way under the supervision of the research team. Fields were irrigated by drip irrigation. Farmers applied manure as an organic fertilizer to improve the soil fertility and pulled out weeds manually by hand.

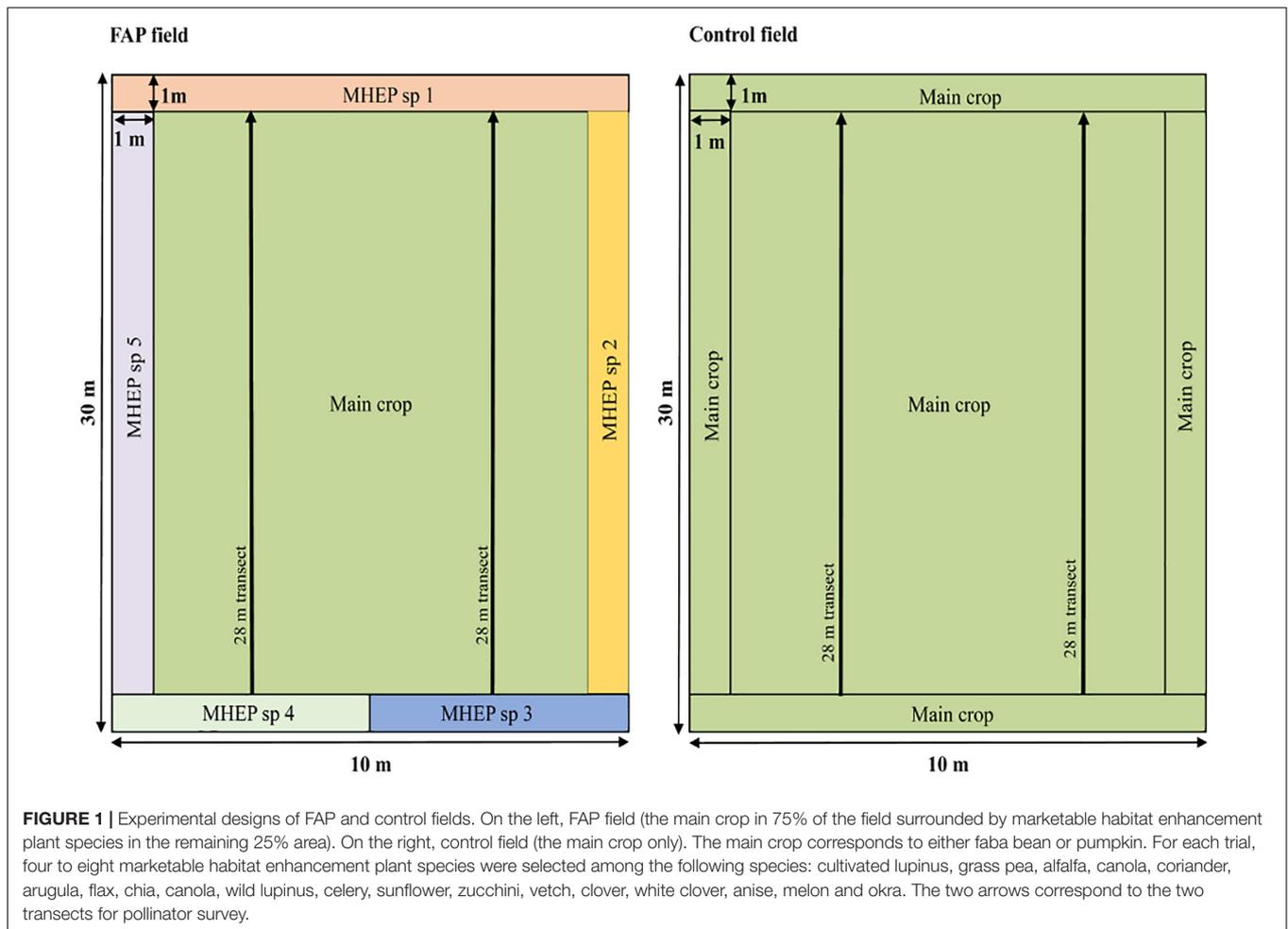
Pollinator Survey

Flower visitors of each trial were surveyed two times when the main crops and MHEP were in bloom and when climatic conditions were favorable for insect activity (i.e., sunny days). In each insect sampling, we surveyed the 75% zone (i.e., the main crop in FAP and in control fields). We observed the main crop in FAP and control fields for 10 min within two transect corridors (i.e., 5 min per transect corridor) that were 4 m wide (i.e., 2 m from each side of the transect) and 28 m long (Figure 1). The insects that were observed visiting flowers were caught using a net or hand vacuum, anesthetized with ethyl acetate and transferred into cyanide vials. They were then pinned and sent to specialists for identification to the species level using either comparative collections or identification keys (Priesner, 1957; Brooks, 1988; Osten, 2000; Michez et al., 2004; Bogusch and Straka, 2012). The remaining flower visitors were identified by the authors to the lowest taxonomic level feasible using entomological publications (Borror and White, 1991).

Pollen Preparation and Identification

All flower visitors recorded on faba bean and pumpkin flowers (322 and 499 flower visitors, respectively) were examined under a microscope. Pollen grains were also removed under a microscope. Flies, wasps, butterflies, and wild bee males were excluded, because they do not collect pollen and they were not carrying pollen on their bodies, resulting in 118 bee individuals carrying or collecting pollen grains after this exclusion (76 in pumpkin and 42 in faba bean). *Apis mellifera*, *Xylocopa pubescens*, and *Bombus terrestris* were not examined, because they were identified during insect surveys and not captured.

Before removing pollen, bees were classified as nectar collectors (those carrying pollen in a disorderly manner on their bodies, but not on their scopae) or pollen foragers (those collecting pollen on their scopae). We extracted pollen from both categories: pollen foragers and nectar collectors. For the pollen foragers, we removed pollen from the bee scopae, and for the nectar collectors, we used an entomological pin to brush the pollen off of their bodies (e.g., head and thorax) onto a microscope slide. Pollen preparation and identification were conducted using the protocol described by Wood and Roberts (2017). The size of pollen loads was visually estimated relative to the size of the bee, ranging from a full load (4/4) to a one-fourth load (1/4). After the relaxation of the pinned specimens in a sealed container filled with boiling water, we removed pollen from the scopa or the body of captured insects using an entomological pin. The pollen grains were placed in a drop of water on a glass slide to allow rehydration. After gentle heating to allow evaporation, a 2 mm³ cube of fuchsin jelly was added. The cube was then melted and covered with a microscope cover slip to create a layer of stained pollen. Pollen was identified to morphological groups, largely corresponding to genera, using an own unpublished reference collection of Mediterranean plant species. The proportion of each pollen genus in the load was estimated along three randomly selected lines across the cover slip at a ×400 magnification. The proportion of the load by volume was estimated by the relative area of the slide occupied



by each pollen genera, rather than the absolute number of grains, in order to better reflect the total volume of pollen collected. This is an important correction in mixed loads where pollen grains of different plant species often differ widely in size (Cane and Sipes, 2006). Species representing <2% of the load were excluded.

Moreover, we took into account the level of filling of the scopa with pollen. Pollen genera percentages were weighted based on the overall estimated size of each scopal load. For instance, a full load (4/4) comprised 40% of *Brassica* sp. and 60% of *Sinapis* sp. would give a final weight of 40 for *Brassica* sp. and a final *Sinapis* sp. weight of 60, while a quarter load (1/4) comprised of 40% *Brassica* sp. and 60% *Sinapis* sp. would receive a final *Brassica* sp. weight of 10 and a final *Sinapis* sp. weight of 15.

As we do not have a sufficiently large sample size to calculate dietary breadth using more established techniques (e.g., Wood and Roberts, 2017; Wood et al., 2019), a novel method was taken to calculate comparative dietary breadth. The method is based on the Berger–Parker’s dominance index (BPI). For each species, the weighted percentage of each collected pollen genus was calculated, and the highest percentage was taken as the measure of dietary breadth. For example, a species collecting pollen from a single pollen genus only (100%) would receive a score of 100, indicating a narrow dietary breadth. A species

collecting five different pollen genera at 20% each would receive a score of 20, indicating a comparatively wider dietary breadth (see **Supplementary Tables 2, 3**). We calculated the inverse of BPI (i.e., 100-BPI) to render the values of Berger–Parker’s dominance index, much more intuitive (smaller value = narrower diet). To consider the number of pollen genera, as well as the abundance of each pollen genus we computed another index for each bee species: the Shannon’s diversity index (H'), using the following formula: $H' = -\sum [p_i \times \log(p_i)]$, in which p_i is the proportion of a pollen of a specific plant genus compared to all pollen grains collected by that species.

Statistical Analyses

As test assumptions of normality and homogeneity were not met, statistical analyses using generalized linear models (GLM) (stats package) with a Quasi-Poisson error structure were performed to compare both indices of dietary breadth: Shannon’s diversity index (H') and Berger–Parker’s dominance index between the main crop in FAP and control fields. It was not possible to conduct Generalized Linear Mixed Models (GLMM) with the region as a random affect for dietary breadth, because the variable was computed at the species level, and the individuals of some flower visitor species were collected in more than one

region. The number of pollen genera of the characterized flower visitor individuals were compared between crops, and between FAP and control fields using GLMM with a negative binomial error distribution (lme4 package). The equality of variances for dietary breadth and number of pollen genera were assessed using Levene's test (Car package; Fox and Weisberg, 2020) and the normality was tested numerically using a Shapiro test (Mvnorm test package; Jarek, 2012). The statistical tests were conducted in R software (version 3.6.3; R Development Core Team, 2020). To verify whether the number of pollen genera was modulated by the number of MHEP species used in each trial, Spearman's correlation (r) test was performed using a significance levels of 5%. The result of this correlation shows that there is no significant correlation between the two variables. Contrary to the number of pollen genera, it was not possible to test this correlation for dietary breadth, because this variable was computed at the species level, and some species included individuals from different trials.

RESULTS

Dietary Breadth and Number of Pollen Genera of Crop Flower Visitors

Overall, 821 flower visitors were collected during surveys, 322 and 499 in pumpkin and faba bean, respectively. Wild bees were by far the main flower visitors of pumpkin and faba bean with 93 and 76% of the total flower visitors recorded in each crop, respectively (Figure 2A). Regarding wild bees, most of pumpkin flower visitors were Halictidae (89%), followed by Apidae (6%), while Andrenidae, Apidae, and Halictidae represented 37, 36, and 21% of the flower visitors recorded in faba bean, respectively (Figure 2B).

Among all the insect individuals caught foraging on faba bean and pumpkin (i.e., 821 flower visitors), 86% failed to carry or collect pollen, whereas only 14% (i.e., 76 and 42 flower visitors recorded on pumpkin and faba bean flowers, respectively) carried or collected pollen of crops, MHEP and/or wild plants on their bodies or on their scopae. The 118 flower visitors carrying or collecting pollen, belong to 25 bee species. In total, 20 pollen genera belonging to 10 families were identified (Supplementary Tables 2, 3).

Among the bee species that were carrying or collecting pollen in pumpkin and faba bean, 33 and 43%, respectively, carried or collected the pollen of a single plant genera, whilst the remaining bee species (67 and 57% in pumpkin and faba bean, respectively) had pollen of two or more host plants (i.e., crop, MHEP, and/or wild plants).

For dietary breadth, a similar trend was seen. A total of 67 and 44% of bee species with pollen recorded in pumpkin and faba bean, respectively, had dietary breadth with (100-BPI) values higher than 10%, and 56 and 38% of species with pollen recorded in pumpkin and faba bean, respectively, had dietary breadth with H' values higher than 0.2, indicating that these species had a comparatively wide dietary breadth.

Although species visiting pumpkin carried or collected more pollen taxa and showed a broader dietary breadth in comparison to faba bean, there were no significant differences between crops,

neither in number of pollen genera carried or collected (GLM, $p = 0.321$) nor in flower visitor species dietary breadth (Shannon's diversity index; GLM, $p = 0.19$) (Berger-Parker's dominance index; GLM, $p = 0.352$).

Foraging Behavior of Crop Flower Visitors

Among the pumpkin and faba bean flower visitors that were carrying or collecting pollen of crops, MHEP and/or wild plants either on their bodies or on their scopae, 95 and 10%, respectively, were carrying or collecting conspecific pollen. These results imply that only 22 and 1% of all flower visitors caught foraging on pumpkin and faba bean, respectively, were carrying or collecting the pollen of these crops.

Considerable variation in wild bee foraging behavior between pumpkin and faba bean was observed. Indeed, only 8% of the pollinators with conspecific pumpkin pollen, were collecting the pollen of this crop on their scopae, whereas the high proportion (92%) were carrying the pumpkin pollen in a disorderly manner on their bodies. In contrast to pumpkin, all the pollinators with conspecific pollen of faba bean were collecting the crop pollen on their scopae. These results imply that among the 76 and 42 flower visitors with pollen, recorded in pumpkin and faba bean, respectively, just 8 and 10% (i.e., 2 and 1% of all the flower visitors collected) were using the crops as pollen host plants (i.e., pollen foragers) and the remaining individuals were seeking nectar.

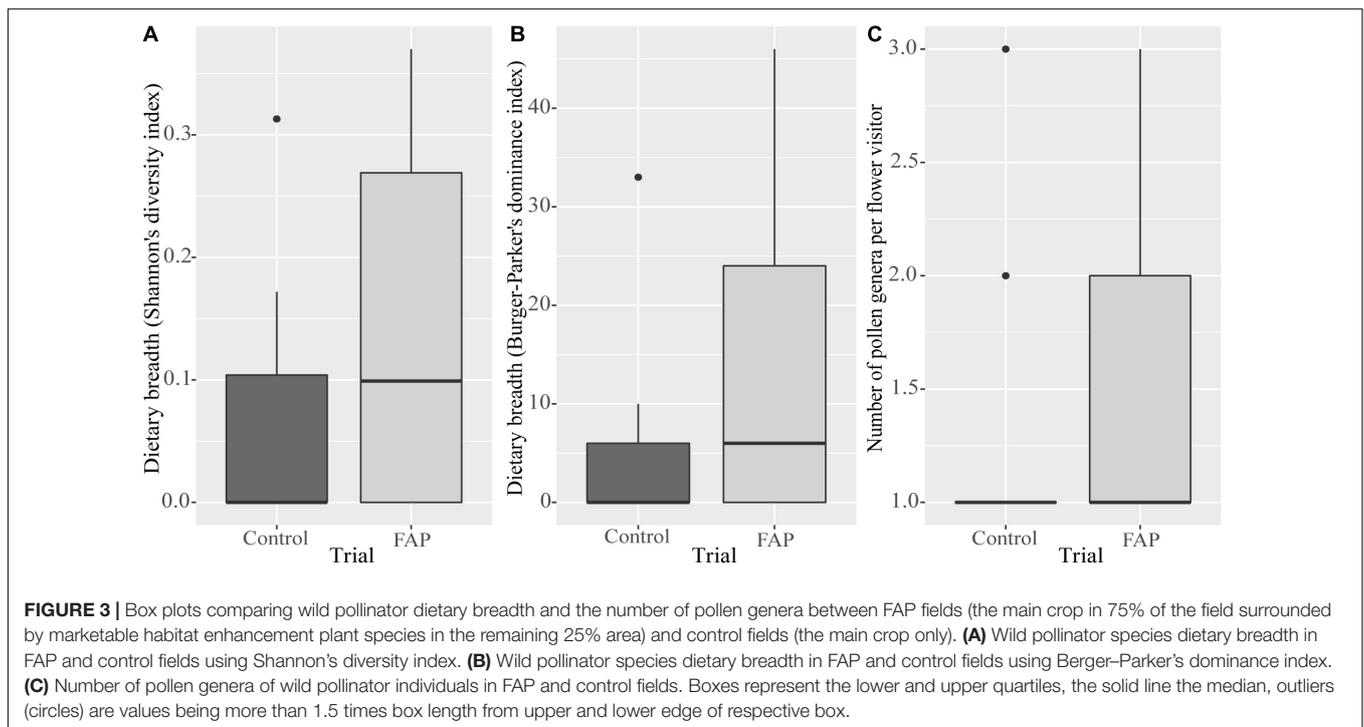
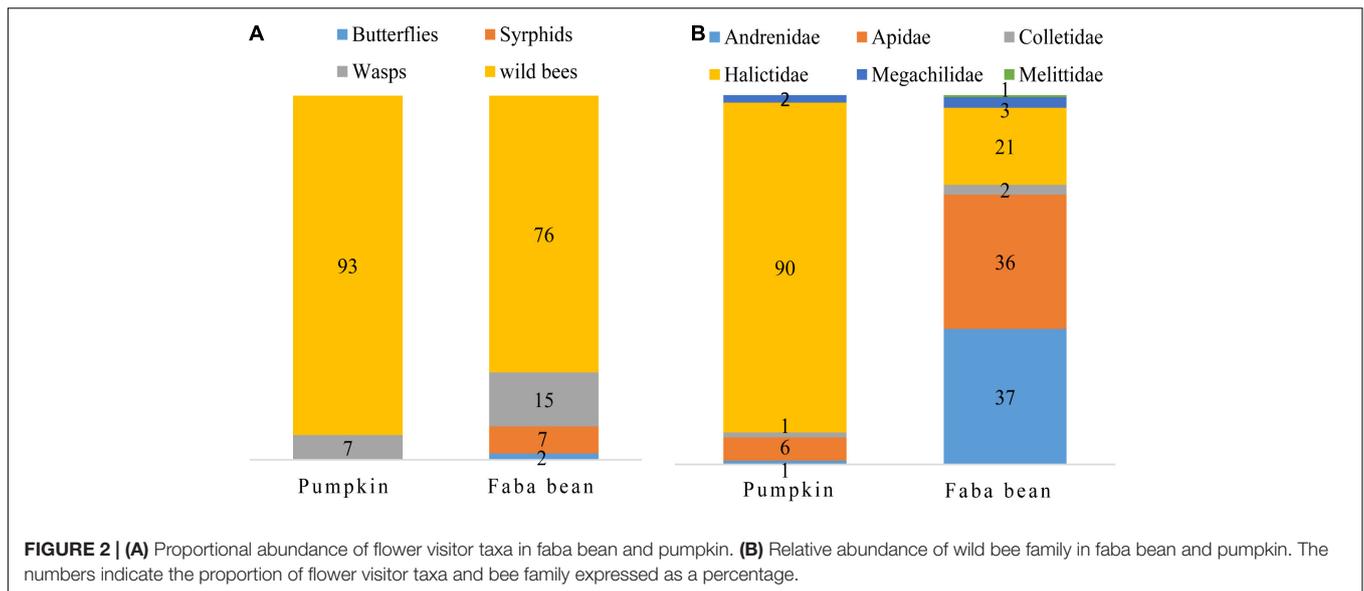
Effect of the Farming With Alternative Pollinators Approach on Crop Flower Visitor Pollen Diet

The FAP approach did neither impact the overall dietary breadth of bee species (Shannon's diversity index; GLM, $p = 0.089$; Figure 3A) (Berger-Parker's dominance index; GLM, $p = 0.107$; Figure 3B) nor the number of pollen carried or collected by bee individuals (GLMM, $p = 0.238$; Figure 3C).

The MHEP (i.e., coriander, canola, and sunflower) were substantial pollen sources for bees visiting the main crops in FAP fields (Figures 4, 5). The pollen of MHEP was recorded in the pollen loads of 35% of pumpkin flower visitors and 36% of faba bean visitors recorded in FAP fields. Wild bees recorded in pumpkin carried or collected pollen exclusively from sunflower. In faba bean, bees carried or collected pollen from coriander (27%) and canola (9%).

DISCUSSION

Our study shows that almost two-thirds of the species carrying or collecting pollen when visiting pumpkin flowers and half of the species carrying or collecting pollen when visiting faba bean flowers gathered this pollen from two or more host plants and a great proportion of the characterized bee species displayed a wide dietary breadth. Among all visitors recorded in pumpkin and faba bean (322 and 499, respectively), 22 and 1%, respectively were carrying or collecting the crop pollen, and only 2 and 1%, respectively were using crops as pollen host plants, with by far



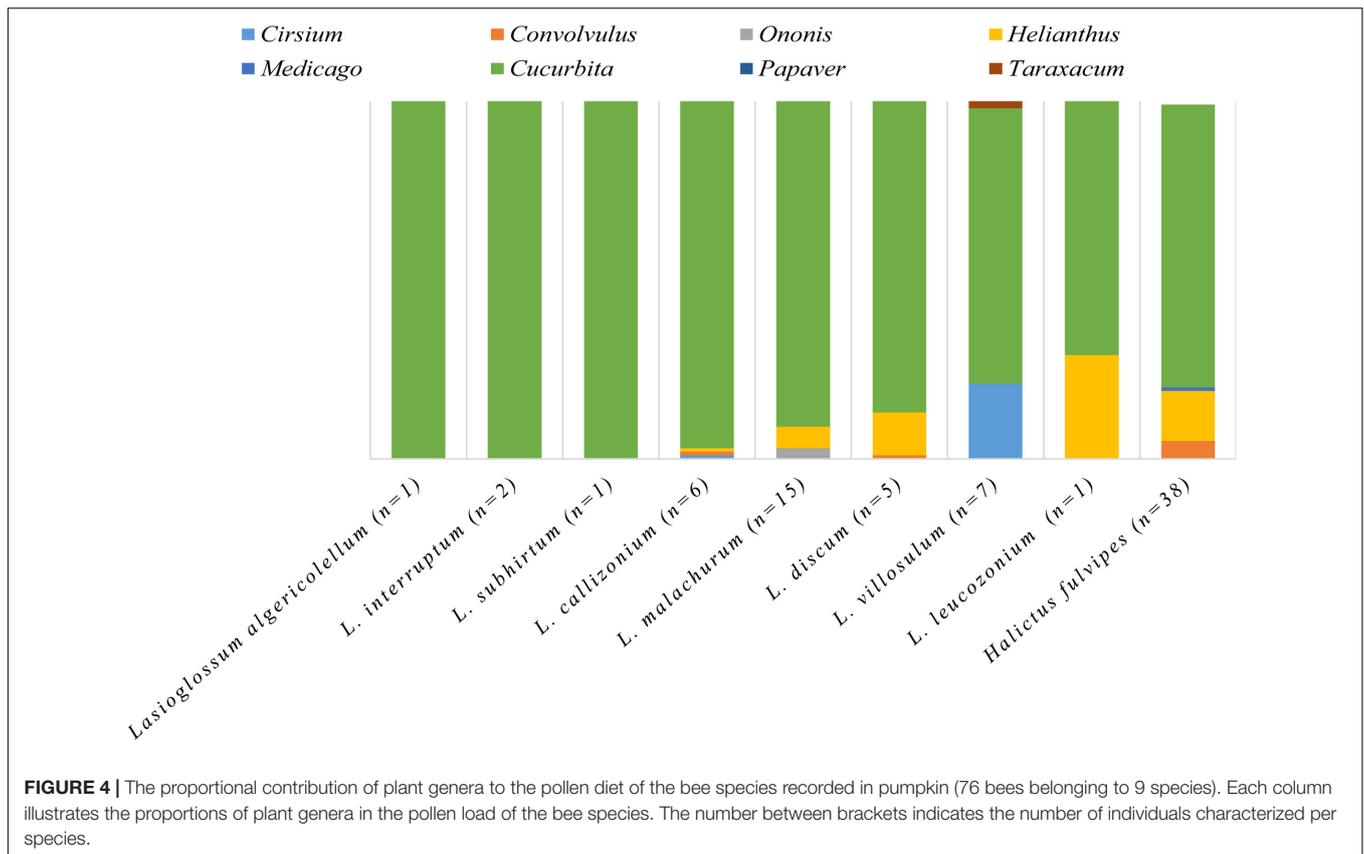
the greatest proportion seeking nectar. The FAP approach did not show an effect on the overall dietary breadth and the number of pollen genera carried or collected by flower visitors.

Dietary Breadth and Number of Pollen Genera of Crop Flower Visitors

In line with previous findings, pumpkin attracts more generalist than specialist bee species (Brochu, 2018), whereas faba bean is mainly visited by bees specialized on Fabaceae (Marzinzig et al., 2018). The deep and curved nectar tube of faba bean

corolla (Stoddard and Bond, 1987) restricts pollinator species and allows only pollinators with long tongues to really reach floral resources (Goulson and Darvill, 2004). Thus, bee species with long tongues such as *Eucera* can be more specialized in their choices of host plants than short-tongued species (Michez et al., 2019). Though we recorded a high proportion of faba bean flower visitor species with narrow dietary breadths, the proportion of visitor species with wide dietary breadth is not negligible (44% of the studied species).

Pumpkin provides abundant nectar rewards and displays accessible flowers (Vidal et al., 2006). Through the showy open



flowers and the large amount of nectar, pumpkin attracts a wide array of flower visitors (Burgett, 2000), including pollinators with wide dietary breadth (Nicodemo et al., 2009; Artz and Nault, 2011; Ali et al., 2014; Pande and Verma, 2016). The important proportion of species with wide dietary breadth visiting pumpkin and faba bean underline the importance of providing diverse flowering plants to conserve healthy crop pollinators and other pollinators living in this area or farm. Pollinator-dependent crops provide a time-limited floral resource (Guzman et al., 2019). Outside this short crop blooming period, pollinators can experience a deficiency in nutritional resources in intensified agricultural landscapes (Rundlöf et al., 2014). The direct consequences of nutritional deficiency or unbalanced intakes may result in a decrease in offspring production and fitness (Di Pasquale et al., 2013; Vanderplanck et al., 2018). Indeed, access to diverse pollen diets was found to enhance resistance to diseases, tolerance to pesticides, and immunity to parasites and pathogens in polylectic bee species (Wilson-Rich et al., 2008; Alaux et al., 2010; Colwell et al., 2017; Zhang et al., 2020). For example, Di Pasquale et al. (2013) demonstrated that when parasitized, bees fed with a poly-floral blend lived longer than bees fed with mono-floral pollen.

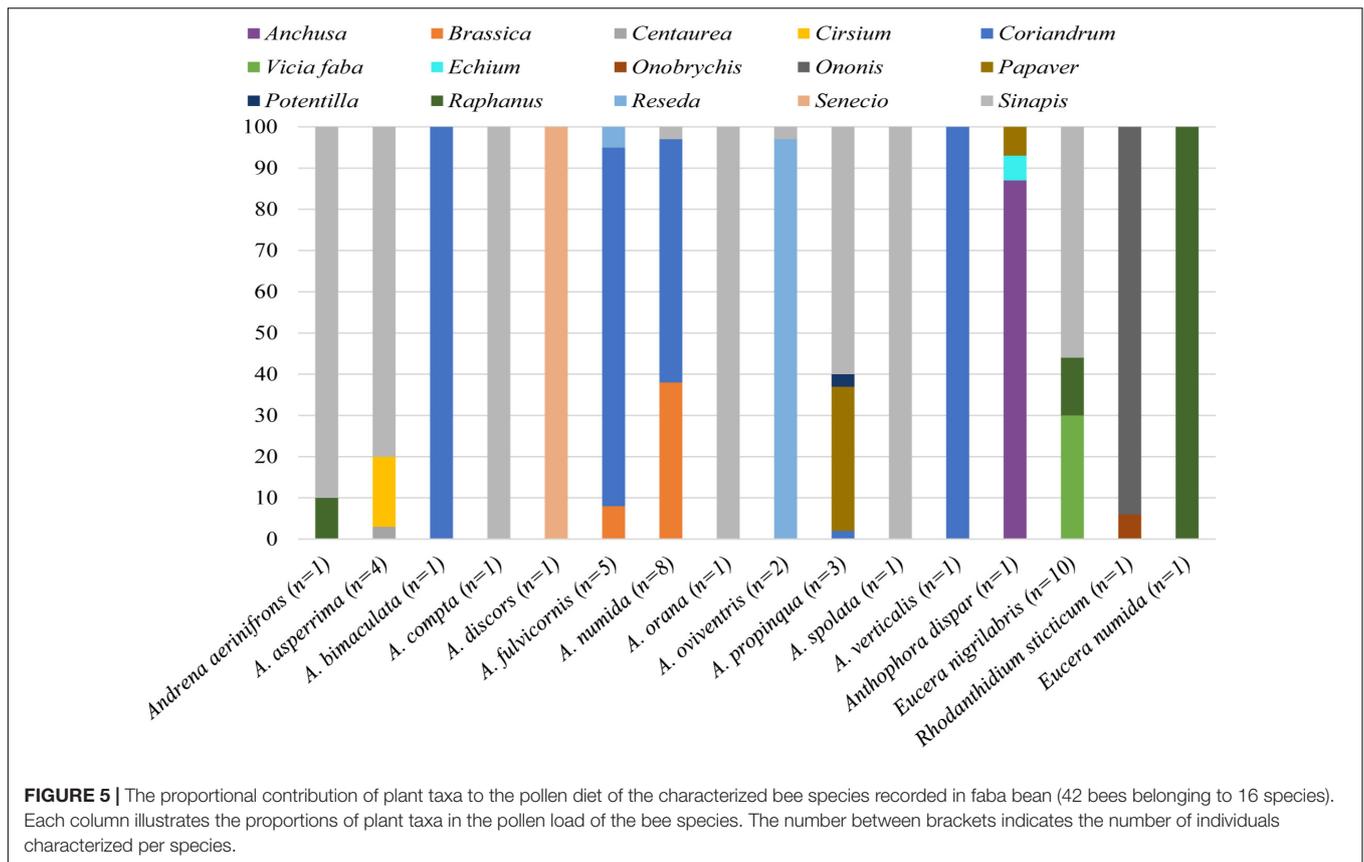
We acknowledge that our sample size was small (e.g., *Lasioglossum subhirtum* was represented by a single specimen). As the sample size affects directly the number of pollen taxa collected or carried by flower visitor species, we assume that some bee species would be regarded as more generalized if

a larger and more representative sample size of species with pollen was available.

Foraging Behavior of Crop Flower Visitors

Growing evidence suggests that insects recorded in visitation data do not necessarily carry pollen. Generally, in most bee collections, only a minority of specimens have pollen. Also, pollen grains could be lost from specimens while capturing and handling the flower visitors. For example, in the study of Popic et al. (2013), the proportion of bees not carrying pollen was high (72%). Therefore, the small percentage of specimens having pollen (i.e., 14%) among the examined flower visitors (i.e., 821 individuals) was expected. Additionally, the abundant species: *A. mellifera* and *B. terrestris* were not assessed for pollen grains, as they were identified visually during the surveys and not captured. This might shape the findings of the foraging behavior of crop flower visitors and also their dietary breadth, as these species are large-bodied, polylectic, and forage from a wide range of flowering plant species.

The low proportion of bees with crop pollen (in our case, 22 and 1% in pumpkin and faba bean, respectively) may result from differences in insect behaviors interacting with plant morphology and chemistry. For instance, faba bean visitors display three types of feeding behaviors; those visiting the front of the flowers (honest visitors), species visiting the base of the flowers (nectar robbers)



and those using extrafloral nectaries (i.e., positioned underneath the stipules) (Tasei, 1976). Based on these categories, only bees visiting the front of flowers are exhibiting legitimate flower visits and could potentially pick up pollen (Vaudo et al., 2015).

In contrast to faba bean, pumpkin does not display any morphological adaptations to limit flower visitors (Vidal et al., 2006). Consequently, visitors of male flowers that are either seeking nectar or pollen may potentially pick up pollen grains, which explains the greater proportion of individuals carrying or collecting pumpkin pollen (22%). However, the proportion of individuals using pumpkin as a pollen host plant (i.e., collecting pumpkin pollen on their scopae) was still low (2%). The open shallow flowers of pumpkin and the high amount of nectar it produces attract a wide array of flower visitor species, but to protect pollen from over collection, pumpkin uses mechanical and chemical pollen defenses (Brochu, 2018). Cucurbit pollen is large, heavy, spiky, difficult to handle, has a sticky pollenkitt, and contains many compounds that may act as defenses to discourage generalist pollinators (Lundgren, 2009). For instance, reduced pollen consumption and reproduction leading to increased mortality were observed in *Bombus impatiens* colonies fed exclusively on cucurbit pollen (Brochu et al., 2020). Therefore, most studied bees in this experiment had pumpkin pollen on their bodies but were not intentionally collecting it.

These results emphasize the importance of considering pollen analyses and foraging behavior as important factors for developing appropriate marketable habitat enhancement plants

that complement the floral resources provided by agricultural crops (Vaudo et al., 2015), rather than simply using floral visits that only partially predict pollinator pollen host plants (Bosch et al., 2009; Popic et al., 2013).

Effect of the Farming With Alternative Pollinators Approach on Crop Flower Visitor Pollen Diet

Our results show that the FAP approach displayed a neutral effect on crop flower visitor dietary breadth and the number of pollen genera carried or collected by crop flower visitors. These findings are in agreement with previous research that has found that wildflower strips, hedgerows, and MHEP do not support crop flower visitor abundance, richness, and pollen diet (Sardiñas and Kremen, 2015; Sardiñas et al., 2016; Wood et al., 2017; Zamorano et al., 2020; Sentil et al., 2021). In contrast, flower strips are also known to benefit the pollen diet of common bees (e.g., honeybees and bumblebees), but not necessarily of wild solitary bees (Carvell et al., 2007; Wood et al., 2017). In the case of our research, the common bees (i.e., honeybees and bumblebees) were not included in the study, which could have changed the results in favor of the FAP approach, especially that the *p*-value of flower visitor dietary breadth (Shannon's diversity index) was close to significance ($p = 0.08$). Adding to this, pollen load compositions of faba bean and pumpkin flower visitors show that wild flowering plants (e.g., *Centaurea* sp., *Sinapis* sp., and *Papaver*

sp.) were clearly offering supplementary pollen resources. Indeed, 87 and 55% of the flower visitor species of faba bean and pumpkin with pollen, respectively carried or collected pollen from wild plants (**Supplementary Tables 1, 2**). These results are in line with the study conducted by Wood et al. (2017) that demonstrated that the majority of solitary bee species collect most of their pollen from the existing native wild flowering plant species and not necessarily from the provided floral resources, even in areas where sown flowering plants represent the highest proportion of available floral resources.

We acknowledge that the four studied regions have contrasting landscape context (e.g., Sefrou has more semi-natural areas compared to Settat), which could potentially affect the results of the impact of the FAP approach on flower visitor dietary breadth; however, it was not possible to include the region as a random effect in our models.

In our trials, wild bees recorded in pumpkin gathered pollen exclusively from sunflower, whereas in faba bean, bees carried or collected pollen from coriander and canola. Mass-flowering crops such as sunflower, canola, and coriander are known to attract abundant and diverse wild bees (Nderitu et al., 2008; Ali et al., 2011; Sharma and Meena, 2019), as they produce abundant pollen and nectar resources (Nicolson and Human, 2013; Adamchuk et al., 2017; Thom et al., 2018), which may explain the occurrence of their pollen grains on bees visiting the crops. The occurrence of the pollen of specific MHEP (i.e., sunflower, coriander, and canola) on the pollen loads of crop flower visitors is associated with the MHEP species planted surrounding faba bean and pumpkin. Thus, if other MHEP mixtures were provided, we would record the pollen of MHEP species from the new provided mixture. Pollen genera of the other provided MHEP were not recorded in pollen loads of the studied species. The possible explanations of this result may be that these MHEP have been visited for their nectar that was not assessed in this study and/or that they were not attractive to crop flower visitors. For instance, pollen of Cucurbitaceae (e.g., zucchini and melon) is sticky, large, heavy, and contains many chemical compounds that discourage bees from its consumption (Lundgren, 2009; Rodrigo Gómez et al., 2016; Brochu et al., 2020). However, the high amount of nectar they produce attracts a wide array of flower visitor species (Ali et al., 2014; Pande and Verma, 2016). Cultivated and wild lupinus are nectarless and are mainly visited for pollen (McGregor, 1976). In addition to that, grass pea, white clover, and spices (e.g., anise, coriander, and cumin) produce abundant pollen and nectar (Laxmikant and Devendra, 2014; Meena et al., 2015; Sharma and Meena, 2019). Nevertheless, their pollen grains were not recorded on crop flower visitors. Hence, further investigations on the foraging behavior of flower visitors on MHEP can contribute to better understanding of the foraging behavior of crop flower visitors.

Agricultural intensification at the expense of natural flowering vegetation is potentially affecting pollinator health (Naug, 2009), and bees using pollen from a smaller range of plants, or non-favorite host plants, are exposed to a higher risk of stress leading to decline (Rasmont, 1988; Kleijn and Raemakers, 2008; Vanderplanck et al., 2018; Wood et al., 2019). Plant diversification in farmlands may play an important role in curbing pollinator

loss and maintaining healthy crop pollinators, in particular in countries unable to provide financial compensation for seeding wildflower strips.

Our results demonstrate that a great proportion of pumpkin and faba bean flower visitors had a wide dietary breadth and that the crop flowers were mainly visited for nectar. These results suggest that flower visitors of pumpkin and faba bean would benefit from more diverse pollen resources nearby. The FAP approach was not significantly effective in supporting the dietary breadth of crop flower visitors nor in increasing the number of pollen genera carried or collected by these visitors. Further studies on the impact of the FAP approach on the dietary breadth of other crops and using the common pollinators (i.e., honeybees and bumblebees) are needed. Additional investigations to characterize pollinator health in relation to dietary breadth (using pollen and nectar analyses) and their foraging behavior on other crops are required, in order to effectively tailor the MHEP that meet the food requirements of crop pollinators in farmlands.

We identified the contribution of MHEP to crop flower visitors' diet. Nevertheless, from the pollinator conservation viewpoint, additional investigations on the contribution of the FAP approach to the diet of pollinators present in the agroecosystems rather than pollinators visiting the crops are needed. In fact, selecting only MHEP flowering at the same time as the main crop and benefiting only the pollinators of the main crop, would drive FAP into agricultural intensification, whereas it was developed to support a wide range of different pollinators by different types of MHEP flowers and by prolonging the flowering period beyond the period of the main crop (Christmann and Aw-Hassan, 2012; Christmann et al., 2021b; Sentil et al., 2021).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AS, TW, and DM conceived the structure of the manuscript. AS performed the statistical analyses and prepared the pollen. AS, PL, LH, IE, OI, and YB made the fieldwork. TW identified the pollen. PR made the data management. SC took charge of the project management. All authors have read the manuscript, participated in the revisions, and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.824474/full#supplementary-material>

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