

The pollinator conservation approach “Farming with Alternative Pollinators”: Success and drivers

Ahlam Sentil^{a,b,*}, Patrick Lhomme^b, Sara Reverté^a, Insafe El Abdouni^{a,b}, Laila Hamroud^{a,b}, Oumayma Ihsane^{a,b}, Youssef Bencharki^{a,b}, Orianne Rollin^c, Pierre Rasmont^a, Moulay Chrif Smaili^d, Denis Michez^a, Axel Ssymank^e, Stefanie Christmann^b

^a University of Mons, Research institute for Biosciences, Laboratory of Zoology, Place du Parc 20, Mons 7000, Belgium

^b International Center of Agricultural Research in the Dry Areas, BP 6299, Station Exp. INRA-Quich, rue Hafiane Cherkaoui, Rabat 10112, Morocco

^c Centre apicole de recherche et d'information, Louvain-la-Neuve, Belgium

^d National Institute of Agricultural Research, Regional Center of Agricultural Research of Kenitra, Laboratory of Entomology, P.O. Box 257, Kenitra 14000, Morocco

^e German Federal Agency for Nature Conservation (Bundesamt für Naturschutz, BfN), Konstantinstraße 110, Bonn 53179, Germany

ARTICLE INFO

Keywords:

Agro-ecosystem

Bee

Climate

Morocco

Phylogenetic distance

ABSTRACT

Global food security is heavily reliant on crop pollination. However, evidence on pollinator decline has been reported in all continents. Globally affordable conservation strategies need to be developed, as high-cost measures like European agri-environment schemes are not scalable in all countries. Here, we test, if a low-cost conservation approach named “Farming with Alternative Pollinators” (FAP) can benefit wild pollinator abundance and richness in agro-ecosystems and in crops, through establishment of marketable habitat enhancement plants (MHEP). The study was carried out in four Moroccan agro-climatic regions, during two years, using 6 main crops (pumpkin, zucchini, faba bean, tomato, eggplant and apple) and 201 sites. Additionally, we investigated how crop type, crop-MHEP composition (i.e. phylogenetic distances among crop and MHEP) and local climate can drive the success of the approach in comparison to monocultural fields. Based on 7097 recorded specimens, our results show that the wild pollinators of the entire FAP fields (i.e. 75% main crop and 25% MHEP) were significantly more abundant and species-rich than those of control fields (i.e. 100% main crop). Considering the main crop wild pollinators, FAP did not display any significant effect either on wild pollinator abundance or on pollinator richness. The mean phylogenetic distance between the main crop and MHEP, and climatic variables were not correlated with increase in wild pollinator abundance and richness in FAP fields. The crop type was found to influence the effect of the FAP approach. Our study provides strong evidence that FAP constitutes a relevant method for wild pollinator conservation in agro-ecosystems. Further research on additional environmental factors is necessary to outline the circumstances under which the FAP approach can positively affect wild pollinator communities.

1. Introduction

The global human population is rapidly growing and meeting the increasing food demand has raised concerns (Prosekov and Ivanova, 2018). Moreover, the area for global production of pollinator dependent crops has substantially increased (Potts et al., 2016). This trend can be attributed to the high average market values of pollinator-dependent crops and the low yield growth of most pollinator-dependent crops that requires higher expansion rates to meet the growing demands (Aizen et al., 2019). 75% of the leading food crops rely on animals for

pollination (Klein et al., 2007). Clear evidence for severe negative population trends and/or mortality increase in domesticated and wild pollinators has been reported in all continents (Dicks et al., 2021; Zattara et al., 2021). Pollinator decline has been attributed to many potentially interacting anthropogenic drivers (e.g. crop intensification, pesticides, habitat loss, invasive species and climate change) (Nieto et al., 2014; Sánchez-Bayo and Wyckhuys, 2019; Duchenne et al., 2020). Thus, managers have to tackle the double challenge of maintaining high crop production and protecting pollinators.

Several mitigation strategies have been implemented in agro-

* Corresponding author at: University of MONS, Research institute for Biosciences, Laboratory of Zoology, Place du Parc 20, Mons 7000, Belgium
E-mail address: ahlam.sentil@umons.ac.be (A. Sentil).

ecosystems to conserve, support and/or restore pollinator communities. The strategies include pesticide regulation and restriction (Gary et al., 2014; Tyrell, 2015), organic farming, management of road side vegetation (Phillips et al., 2020, 2019), set up of bee hotels (Warzecha et al., 2018), raising farmers' awareness and plantation of mass flowering crops (Holzschuh et al., 2013). Within the framework of Agri-Environmental Schemes (AES), European farmland managers are financially compensated for dedicating parts of their agricultural lands to seed wildflower strips to support pollinators (Batáry et al., 2015). Nevertheless, the generalization, the effectiveness and the cost of wildflower strips have been broadly questioned in their efficiency in supporting pollinators (Kleijn and Sutherland, 2003; Christmann et al., 2017, 2021a, 2021b).

In this context, the Farming with Alternative Pollinators (FAP) approach was developed in 2012 to serve pollinator conservation and farmers in particular in low- and middle-income countries, which cannot afford AES (Christmann and Aw-Hassan, 2012; Christmann, 2020; Christmann et al., 2017, 2021a, 2021b). The main crop in FAP small-holder fields covers 75% of the field area and 25% is occupied by pollinator-attractive crops called Marketable Habitat Enhancement Plants (MHEP). MHEP offer highly attractive floral resources to diverse pollinator species, and may therefore induce a spillover of pollinators to the main crop, and thus increase pollination service (Christmann et al., 2017, 2021a, 2021b; Sentil et al., 2022a, 2022b; Bencharki et al., 2022). Contrary to wildflower strips that reduce the field area for crop production, the FAP approach uses the entire area for production. Previous publications on FAP showed higher pollinator diversity and abundance in FAP fields (Christmann et al., 2017, 2021a, 2021b; Sentil et al., 2022a, 2022b; Bencharki et al., 2022). Nevertheless, several questions remain to be addressed, like the impact of the approach on the main crop pollinators using a large experimental set-up and the investigation of the factors governing the success or the failure of the approach in supporting pollinators.

Here we aim to evaluate the FAP approach as a conservation tool for wild pollinators and contributor to pollination delivery in 6 leading food entomophilous crops (i.e. eggplant, faba bean, pumpkin, zucchini, apple and tomato) in four different agro-climatic regions of Morocco. Using an experimental set of 201 fields, we compared the abundance and the richness of wild pollinators between control fields (100% main crop) and FAP fields (75% main crop + 25% MHEP). Moreover, we tested the potential impact of two factors that may govern the efficiency of FAP: the FAP field composition (i.e. the selected main crop and the MHEP mixture) and the climate. As shown in previous studies, the response of pollinators and pollination service to conservation measures has been demonstrated to rely on the main crop and the habitat enhancement plant (e.g. MHEP or wildflower strips) composition (Albrecht et al., 2020). The selection of habitat enhancement plants has been broadly considered to explain the success or the failure of habitat plants in supporting pollinators. Indeed, some research has shown that certain habitat enhancement plant mixtures (e.g., wildflower strips) benefit only a limited range of pollinator species, particularly the common ones (Wood et al., 2015; Venturini et al., 2017; Albrecht et al., 2020). Thus, if a wider range of pollinator species is to be sustained, the habitat enhancement plant mixtures should be thoroughly assessed, in order to select the mixture that satisfy long-term pollinator conservation goals. However, to date no research testing the impact of selection of MHEP on pollinator communities in FAP trials has been published. Climatic variables, temperature and rainfall are known to strongly affect pollinator communities (Rasmont et al., 2015; Arena et al., 2018; Martinet et al., 2021a, 2021b). Giving the fact that our study was carried out in four different Moroccan eco-climatic regions, we analyzed the climatic impacts on the FAP approach.

Specifically, in this study we aim to address the following questions: 1. Does the FAP approach increase wild pollinator abundance and richness in FAP fields? 2. Does the FAP approach promote spillover of wild pollinators from MHEP to the main crops? 3. Do climatic variables, MHEP composition and crop type explain the variation in the effect of

the FAP approach on wild pollinator abundance and richness? We hypothesize that: 1. The FAP approach will increase wild pollinator abundance and richness in the fields; 2. The FAP approach will induce a spillover of wild pollinators from MHEP into the main crops; 3. The type of crop, MHEP composition and climate will give more insight about the variation of the effect of the FAP approach on wild pollinator communities.

2. Materials and methods

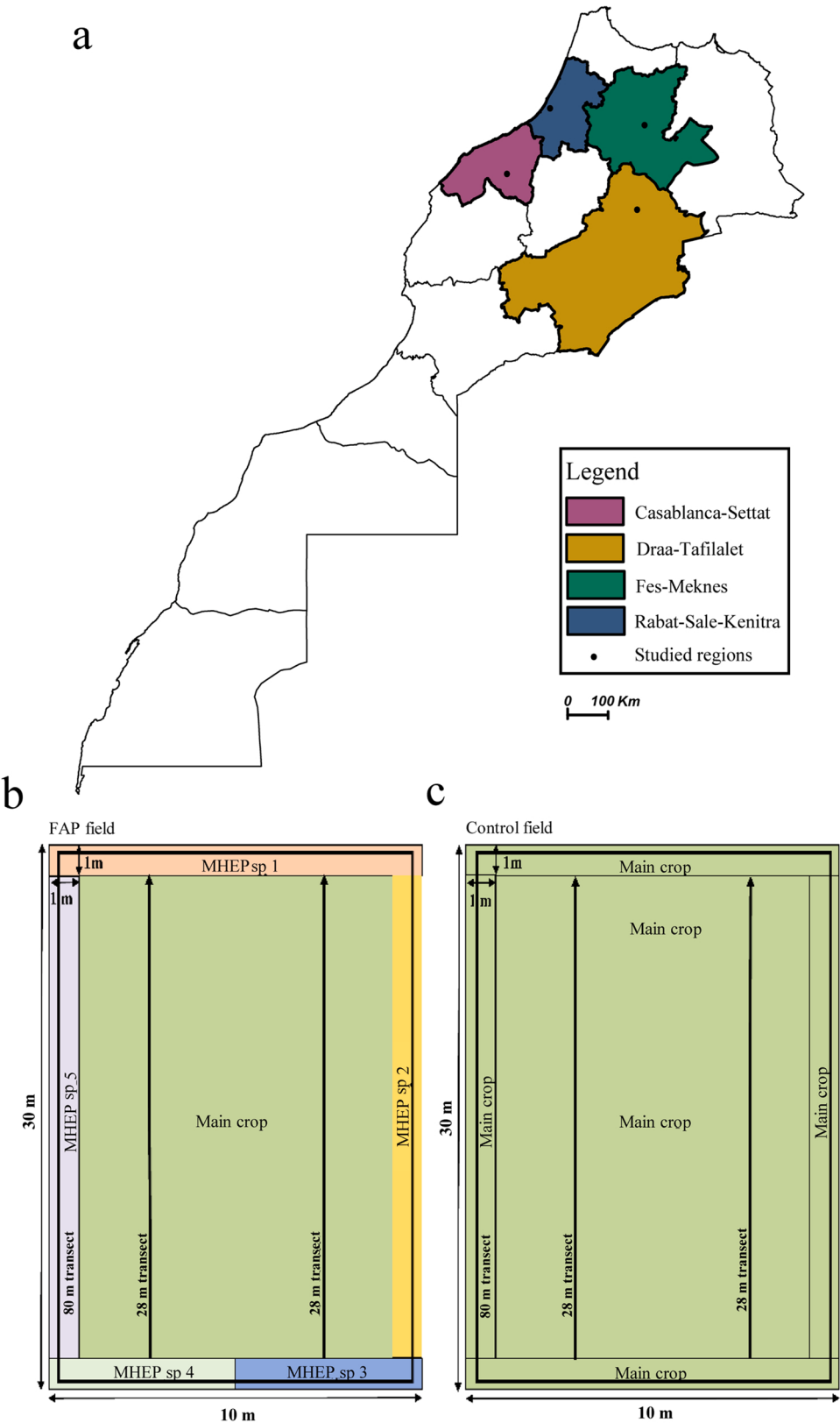
2.1. Study area

The study was carried out in four different regions in Morocco (Settat, Kenitra, Sefrou and Errachidia) (Fig. 1.a). The regions cover different aridity levels (semi-arid: Settat, humid: Kenitra, mountainous: Sefrou and arid: Errachidia) and present a high agricultural importance. The regions were distant of at least 200 km from each other. Errachidia province (latitude: 32.3876° to 32.2146°, longitude: -4.5020° to -4.7609°) belongs to Draa-Tafilalet region located at the South-Eastern Morocco. The climate in Errachidia is arid and the landscape includes oasis, Sahara and Atlas Mountains. Sefrou province (latitude: 33.9033° to 33.6191°, longitude: -4.6488° to -4.9016°) is a mountainous region in the North center of Morocco, exhibiting a continental climate with forest covering a large area. Kenitra province (latitude: 34.1508° to 34.0608°, longitude: -6.5352307 to -6.6258°) is situated in the North-West of Morocco and is surrounded by large bark oak (*Quercus suber*) forest remnants. The climate in this region is Mediterranean, with warm, dry summers and mild winters. Settat province (latitude: 32.9757° to 32.7744°, longitude: -7.4906° to -7.6835°) is located in the North-West of Morocco, its climate is semi-arid and the landscape is characterized by cultivated lands of cereals.

2.2. Selection of crops and marketable habitat enhancement plants

Among the main crops selected in collaboration with the regional departments of Ministry for Agriculture, we chose six pollinator dependent main crops: Faba bean (*Vicia faba*, Fabaceae), zucchini (*Cucurbita pepo*, Cucurbitaceae), pumpkin (*Cucurbita maxima*, Cucurbitaceae), eggplant (*Solanum melongena*, Solanaceae), apple (*Malus domestica*, Rosaceae) and tomato (*Solanum lycopersicum*, Solanaceae). These crops are staple crops in Morocco (Ministry of Agriculture, Fisheries, Rural Development, Water, and Forests, 2020). The six main crops were selected based on their good adaptation to the local climatic conditions and their high or moderate reliance to pollinators for pollination (Klein et al., 2007). Faba bean, pumpkin and zucchini were planted in the four regions, eggplant in Settat and Kenitra, tomato in Kenitra and apple in Sefrou (Table 1). The study was conducted during two consecutive years (2018 and 2019). The crops were planted in 2018 and replicated in 2019, except pumpkin, zucchini and faba bean in Errachidia, faba bean in Settat and pumpkin in Kenitra (Table 1), which resulted in 27 crop trials (Table 1).

For each single crop trial, 4–8 MHEP were chosen among the following plant families (Appendix A): Fabaceae (faba bean *Vicia faba*, cultivated and wild lupins *Lupinus albus* and *L. luteus*, grass pea *Lathyrus sativus*, alfalfa *Medicago sativa*, clover *Trifolium repens* and vetch *Vicia sativa*), Brassicaceae (canola *Brassica napus* var. *oleifera* and arugula *Eruca sativa*), Apiaceae (anise *Pimpinella anisum*, dill *Anethum graveolens*, celery *Apium graveolens*, coriander *Coriandrum sativum* and cumin *Cuminum cyminum*), Solanaceae (green pepper *Capsicum annum*, eggplant *Solanum melongena* and tomato *Solanum lycopersicum*), Cucurbitaceae (cucumber *Cucumis sativus*, armenian cucumber *Cucumis melo* var. *flexuosus*, watermelon *Citrullus lanatus*, melon *Cucumis melo*, pumpkin *Cucurbita maxima* and zucchini *Cucurbita pepo*), Lamiaceae (chia *Salvia hispanica*) and Asteraceae (sunflower *Helianthus annuus*). To attract diverse wild pollinators and provide floral resources throughout the blooming season of the main crop, we selected MHEP based on their



(caption on next page)

Fig. 1. (a) Map of Morocco showing the four administrative regions where the study was conducted: Casablanca-Settat (purple), Draa-Tafilalet (yellow), Fes-Meknes (green) and Rabat-Sale-Kenitra (blue). The dots represent the locations of the four studied regions: Settat located in Casablanca-Settat, Errachidia in Draa-Tafilalet, Sefrou in Fes-Meknes and Kenitra in Rabat-Sale-Kenitra (b) Experimental design of FAP (Farming with Alternative Pollinators) field (the main crop in 75% of the field surrounded by marketable habitat enhancement plant species) and (c) Experimental design of control field (pumpkin only). The main crops used in this study are: faba bean, zucchini, pumpkin, eggplant, tomato and apple. For each crop trial, the main crop in FAP fields was surrounded by 4–8 marketable habitat enhancement plant species, among the following species: faba bean, cultivated and wild lupins, grass pea, alfalfa, clover, vetch, canola, arugula, anise, dill, celery, coriander, cumin, green pepper, eggplant, tomato, cucumber, armenian cucumber, watermelon, melon, pumpkin, zucchini, chia and sunflower. The three black arrows in each experimental design correspond to the three transect walks. Two 28 m transect walks in the 75% zone (i.e., in the main crop in FAP and control fields) and one 80 m transect walk in the 25% zone (i.e., in MHEP in FAP fields and in the main crop in control fields).

Table 1

The crop trials carried out in 2018 and 2019 in the four regions. Each crop trial represents one crop in one year and one region (e.g. faba bean in 2018 in Settat). Number one indicates the occurrence of the crop trial (27 crop trials overall) and the hyphen indicates that the crop trial was not carried out. Four fields were selected for each of the two apple trials, while 8 fields were selected for each of the remaining crop trials (i.e. 25 trials). This resulted in 201 fields, after the exclusion of seven fields due to their low maintenance ($2 \times 4 + 8 \times 25 - 7 = 201$ fields).

	Zucchini		Pumpkin		Faba bean		Apple		Eggplant		Tomato	
	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
Settat	1	1	1	1	1	-	-	-	1	1	-	-
Kenitra	1	1	-	1	1	1	-	-	1	1	1	1
Sefrou	1	1	1	1	1	1	1	1	-	-	-	-
Errachidia	1	-	-	1	-	1	-	-	-	-	-	-

adaptation to the local climatic conditions, their attractiveness to pollinators (Williams, 1987; Delaplane and Mayer, 2000; Vaz Patto et al., 2011; Meena et al., 2015; Vastola, 2015; Thom et al., 2018; Shakeel et al., 2019; Sharma and Meena, 2019), their phenology (Appendix B), floral traits and the preferences of participating farmers. The mixture of MHEP when possible should prolong the flowering time of the entire field before and after the flowering of the main crop and it has to cover the following traits: deep and short corolla, diverse colors (white, yellow and purple), showy and hardly accessible flowers (i.e., flowers that display morphological barriers, such as curved corolla). The selected MHEP were the only plants meeting these criteria, which explains the small number of MHEP in some crop trials (i.e., less than 8 MHEP).

2.3. Experimental set up

Eight fields of 300 m² (30 m*10 m) were selected each year in each region (i.e. 5 FAP fields and 3 control fields) for each of the trials of faba bean (i.e. 6 trials), zucchini (i.e. 7 trials), pumpkin (i.e. 6 trials), tomato (i.e. 2 trials) and (eggplant i.e. 4 trials) (Table 1), while the experiments of the two apple trials took place in four orchards per trial (i.e. two FAP orchards and two control orchards). This resulted in 208 fields for all the crop trials conducted (i.e. 25 crop trials*8 fields + 2 crop trials*4 orchards= 208 fields). Seven fields (3 control fields and 4 FAP fields) were excluded from the analyses because of their low maintenance (i.e., insufficient water and nutrients, as well as damage caused by pests) (Appendix C.1), which resulted in a total of 201 fields (Appendices A and C.2). FAP and control fields within each crop trial were distant of minimum 500 m and maximum 20.3 km, which usually exceeds the average foraging distance of most main wild pollinator groups, which include bees, hoverflies and bumble bees (Wratten et al., 2003; Elliott, 2009; Bommarco et al., 2012) and insures independence of wild pollinator communities between fields. Though the landscape differed widely between the four regions, we assumed that the local landscape and the potential regional wild pollinator communities were largely similar within each region.

In FAP fields, the main crop was planted in 75% of the field area and MHEP were planted in the remaining area (i.e. 25% surrounding zone) (Fig. 1.b), whilst in control fields the main crop was planted in 100% of the field area (Fig. 1.c). The MHEP strips were all 1 m wide and their lengths varied between 5 and 30 m depending on the number of MHEP selected for each crop trial (Fig. 1.b) (details of the MHEP selected for each crop trial and field configuration in Appendices A, D.1, D.2, D.3 and D.4).

In apple trials, for each FAP and control orchard, two plots (i.e. two consecutive apple rows) were selected, with each plot comprising seven consecutive trees within the same row. In FAP orchards, MHEP strips were planted on the sides of the orchards. Control orchards were used without habitat enhancement. The trees of apple trials were of similar cultivar, age, size and farming practices.

2.4. Data collection

2.4.1. Record of pollinator communities

For each crop trial, four insect samplings were conducted (T1-T4), one before the blooming of the main crop (T1, in MHEP), two during the flowering of the main crop (T2 and T3, in the main crop and MHEP) and one after the blooming of the main crop (T4, in MHEP). When the flowering of the MHEP and the main crop occurred at the same time, the sampling number was restricted to three (two insect samplings during the blooming of the main crop and one after the flowering of the main crop). In order to provide reliable visitation data we employed direct observation methods (transect and observation) using sweep nets and vacuums (Popic et al., 2013). In each sampling, two areas of the field were evaluated, the center (the 75% zone) and the surrounding (the 25% zone). First, the main crop pollinators (pollinators of the 75% zone in control and FAP fields) were recorded by walking along two 28 m transects. Each transect was 4 m wide and pollinators were recorded by walking in the middle of the transect during 5 min. Second, the pollinators within the 25% surrounding area (i.e. main crop in control fields and MHEP strips in FAP fields) were assessed along an 80 m transect (1 m wide * 80 m long) for 10 min. The insect survey in orchards (i.e. apple) consisted of walking alongside trees of the two plots during 10 min and visits in MHEP were assessed within a 10 min transect.

With the exception of *Bombus terrestris* and *Xylocopa pubescens* that were identified visually, all insects that visited the flowers of the main crops and the MHEP were collected when possible or recorded to the lowest taxonomic level possible on the wing. Bees were identified in the laboratory to the genus level (Michez et al., 2019), then they were sent with hoverflies to expert taxonomists for identification to species level. The other non-bee pollinators, representing 28% of the collected wild pollinators, were identified to the lowest possible taxonomic level in the laboratory using entomological publications (Borror and White, 1991).

2.4.2. MHEP composition

The impact of species composition of MHEP was evaluated based on the mean phylogenetic distance between the main crop and MHEP.

Phylogenetic analyses have proved to be a potential instrument in understanding variation in species composition (Pistón et al., 2015; Ribeiro et al., 2016). Generally, related plant species tend to share and interact with largely overlapping ecological assemblages of animals (Zheng et al., 2018) including pollinators (Cirtwill et al., 2020). Thereby, we emphasize that phylogenetic distance among the main crop and MHEP could be a powerful factor influencing the community of wild pollinators recorded in FAP fields.

For each crop trial, we measured the phylogenetic distance between the main crop and MHEP. Since we have to compute the distance between one main crop and several MHEP, we measured the Mean Phylogenetic Distance (MPD), which is a value that describes the general structure of the phylogenetic community by analyzing all combinations of species pairs (de Sousa Costa et al., 2018). Phylogenetic distances between the main crop and MHEP (measured as millions of years of divergence) were obtained from TimeTree database (Hedges et al., 2006).

2.4.3. Climatic variables

We considered four climatic parameters to assess the influence of climate on the effectiveness of the FAP approach: monthly mean temperature, monthly maximum and minimum temperature and monthly precipitation (Classen et al., 2015; Lawson and Rands, 2019)(Appendix E). Since the blooming of each crop occurred in a specific period ranging from 2 to 6 weeks, we computed the climatic parameters for each month and we attributed to each crop trial the variable value of the peak bloom. For each region, we collected the climatic data covering the period from 2015 to 2019 to capture a representative climatic information, then we calculated the mean of monthly: mean temperature; maximum temperature; minimum temperature; and precipitation, for the four-year period. We obtained the climatic variables from Worldclim (Fick and Hijmans, 2017) with 1 km spatial resolution.

2.5. Statistical analyses

The honey bee (*Apis mellifera*) records were excluded from all analyses because their abundance could be biased by the presence of hives even in some kilometers distance (Kennedy et al., 2013). Though we tried to avoid any honey bee hives in and close to farmers' fields. We used the visitation data of all insect samplings (i.e. 3 or 4 insect samplings) when assessing the impact of FAP on wild pollinators in the whole field area, and we used the data of two insect samplings (T2 and T3) when testing the effect of the approach on the main crop wild pollinators. Statistical analyses were conducted with R statistical software (version 3.6.3; R Core Team, 2020).

2.5.1. Impact of the FAP approach on wild pollinator communities

We assessed the impact of the FAP approach on wild pollinators by comparing wild pollinator abundance and richness between FAP and control fields. As 28% of the wild pollinator individuals were not identified to the species level, we used the lowest taxonomic level available for these pollinators to compute the pollinator richness (i.e. genus or family for unidentified Hymenoptera, order for all Lepidoptera specimens and Diptera for unidentified flies).

Though the flowering area in FAP and control fields differed across time, due to the varying phenology of MHEP, we did not extrapolate pollinator abundance and richness in FAP fields. In fact, the MHEP were selected not to bloom simultaneously, but to bloom over prolonged period. Thus, the extrapolation of the pollinator abundance and richness depending on the flowering area, will display unrealistic results, as the FAP approach intentionally avoids simultaneous blooming of all plants.

Firstly, we tested the impact of the FAP approach on wild pollinator conservation in agro-ecosystems by comparing wild pollinator abundance and richness in the whole fields (i.e. addition of the 3 transects from the 75% central zone and the 25% zone) between FAP and control fields. We did not solely consider the 25% zone to address this question,

as both zones provision pollinators with floral resources, and thus contribute to pollinator conservation. Secondly, since insect visits to flowers are a reliable predictor of pollination service (Garibaldi et al., 2013), and considering the higher productivity of the main crop in FAP fields described in (Christmann, Bencharki, et al., 2021), we assessed the impact of FAP on pollination service by comparing wild pollinator richness and abundance between FAP and control fields in the main crops (i.e. the 75% zone). The replicates of wild pollinator abundance and richness represent the number of wild pollinator individuals and taxa, respectively per crop trial, field and sampling.

The differences in wild pollinator richness and abundance between FAP and control fields were analyzed using Generalized Linear Mixed Models (GLMM). First, wild pollinator abundance and richness were compared between treatments (i.e. FAP and control) using the entire data with region and crop as random effects and field as a nested effect within region. Then, the response variables were compared for each region separately with crop and field as random effects. We did not include the year as a random effect, but as a fixed factor, due to insufficient factor levels (Bolker et al., 2022). GLMM were fitted with a negative binomial distribution using the function `glmmTMB` from the `glmmTMB` package. Residuals of the models were inspected for homogenous variance and distributions with the function `simulateResiduals` from the package `DHARMa` (Hartig et al., 2019).

2.5.2. Effect of crop, MHEP composition and climate on wild pollinator communities

To underline the effect of the type of crop on the success of the FAP approach in increasing wild pollinator abundance and richness in the main crop and in the whole field area, we compared separately wild pollinator abundance and richness between FAP and control fields for each crop using GLMM. Treatment (i.e. FAP or control) and year were included as fixed explanatory factors. Region was incorporated as a random factor and field as a nested effect within region.

To assess whether MHEP composition (i.e., mean phylogenetic distance main crop-MHEP) and climatic variables influenced the effectiveness of the FAP approach, we employed linear mixed models. Four response variables were used in the lineal mixed models: (i) distance 1: indicates the difference in wild pollinator abundance between FAP and control in the whole field, (ii) distance 2: difference in wild pollinator abundance between FAP and control in the 75% zone, (iii) distance 3: difference in wild pollinator richness in the whole field and (iv) distance 4: difference in wild pollinator richness in the 75% zone. The differences between FAP and control fields were simply calculated for each crop trial by subtracting the value of wild pollinator abundance or richness recorded in FAP fields from the corresponding value in control fields. This procedure was performed for all combinations of pairs of FAP and control fields for each crop trial. To account for any possible variation in farming practices, field margin vegetation and surrounding habitats within each crop trial, distances were standardized to z-scores (Garibaldi et al., 2013). To calculate the z-scores we used field as a replicate instead of sampling, due to the problem of null z-score values in some samplings. Mean phylogenetic distance, climatic variables (i.e., mean of monthly: mean temperature; maximum temperature; minimum temperature; and precipitation) and year were used as fixed effects (i.e., predictors). Crop and region were entered as random effects. We ran separate models for each response variable (the four distances) to avoid collinearity between wild pollinator abundance and richness. Models were generated using `lmer` function from the `lme4` R package (Bates et al., 2020).

To prevent redundancy between predictor variables, we assessed the multicollinearity using the variance inflation factor (VIF) with the function `vif` within the package `car` (Fox et al., 2020), a threshold of 4 was set as an indicator of high collinearity (Zuur et al., 2010). Based on this threshold, mean phylogenetic distance, mean monthly temperature and monthly precipitation were included in the models, whereas monthly minimum and maximum temperature were removed from the models. As the distribution of the data did not fit any of the common

distributions, it was transformed to a Gaussian distribution with the function `orderNorm` within the package `bestNormalize` to achieve a normal distribution (Beasley et al., 2009). P values of the model residues were interpreted using Satterthwaite's approximations to determine denominator degrees of freedom within the package `lmerTest` (Alexandra et al., 2020).

3. Results

3.1. Wild pollinator communities

The overall abundance of wild pollinators from the 27 crop trials pooled a total of 7097 specimens of 257 identified wild pollinator species (Sentil et al., 2023). Of these, 2043 specimens were observed visiting the six main crops. The proportions of the wild pollinators collected in the six main crops represented: 33% in faba bean, 28% in pumpkin, 21% in zucchini, 11% in eggplant, 6% in tomato and 2% in apple. Most of the main crop wild pollinators were wild bees (61%), followed by wasps (20%), butterflies (12%), syrphids (6.7%) and other flies (0.3%). The wild pollinator community differed between the main crops (Fig. 2.a). For instance, wild bees were the main wild pollinators of faba bean (60%), pumpkin (66%) and zucchini (81%). Surprisingly, butterflies were frequent visitors of tomato (58%) and eggplant (38%), followed by wild bees (23% in tomato and 31% in eggplant). Apple was equally visited by syrphids (35%) and butterflies (38%), followed by wild bees (26%). Bee species from six families (i.e., Halictidae, Megachilidae, Apidae, Andrenidae, Colletidae and Melittidae) were observed foraging in the main crops. However, their abundance differed between the main crop species (Fig. 2.b). Apidae species, excluding honey bees were by far the most abundant visitors recorded in faba bean, eggplant and tomato, while Halictidae were the most abundant wild bees recorded in zucchini and pumpkin. Andrenidae, Apidae and Halictidae were equally abundant visitors of apple.

3.2. Impact of the FAP approach on wild pollinator communities

Using the compiled data from 201 fields, distributed in four regions, we found that the FAP approach significantly increased the overall abundance of wild pollinators in the whole field (GLMM with negative binomial distribution, $p\text{-value}=0.213 \times 10^{-14}$; Fig. 3.a). Considering the effect of the FAP approach on wild pollinators at regional level, the results showed that wild pollinator abundance was significantly higher in FAP fields in comparison to control fields in all regions (Fig. 4.a; Table 2). Regarding the effect of the FAP approach on the wild

pollinators visiting the main crop (i.e., the 75% zone), wild pollinator abundance did not show a significant difference between FAP and control fields (GLMM with negative binomial distribution, $p\text{-value}=0.285$; Fig. 3.b). When assessing the regions separately, none of the four regions displayed a significant increase in wild pollinator abundance in the main crop in response to the FAP approach (Fig. 4.b; Table 2).

Regarding wild pollinator richness, the FAP approach clearly increased the overall wild pollinator richness in the whole field (GLMM with negative binomial distribution, $p\text{-value}=0.002 \times 10^{-14}$; Fig. 3.c). When splitting the dataset between regions, the positive contribution of FAP on wild pollinator richness remained significant in all regions (Fig. 4.c; Table 2). We did not record a significant difference in the main crop wild pollinator richness between FAP and control fields (GLMM with negative binomial distribution, $p\text{-value}=0.224$; Fig. 3.d). Considering the regions separately, the FAP approach did not promote wild pollinator richness in the main crop in the four regions (Fig. 4.d; Table 2).

3.3. Impact of crop, MHEP composition and climate

Our results demonstrated that wild pollinator abundance and richness were significantly higher in the whole FAP fields compared to control fields for all crops (Table 2; Figs. 5a, 5c), except in apple where the approach did not display a significant increase either on wild pollinator abundance or on wild pollinator richness (GLMM with negative binomial distribution, $p\text{-value}=0.592$; GLMM with negative binomial distribution, $p\text{-value}=0.311$; Fig. 5.a and 5.c, respectively). Regarding the effect of the FAP approach on wild pollinator abundance and richness in the main crop, none of the crops displayed a significant positive difference in wild pollinator abundance and richness (Table 2; Fig. 5.b, 5d), except on pumpkin wild pollinator abundance (GLMM with negative binomial distribution, $p\text{-value}=0.044$; Fig. 5.b). Surprisingly, wild pollinator abundance and richness in tomato in the 75% zone were significantly higher in control fields than in FAP fields (GLMM with negative binomial distribution, $p\text{-value}=0.126 \times 10^{-4}$; GLMM with negative binomial distribution, $p\text{-value}=0.020$; Fig. 5.b and 5.d, respectively), whilst no differences between FAP and control fields were observed on wild pollinator abundance and richness in the remaining crops (Table 2).

Considering the impact of the climate and MHEP composition in driving the effect of the FAP approach, the linear models showed that the four distances (i.e. D1: difference in wild pollinator abundance between FAP and control in the whole field; D2: difference in wild

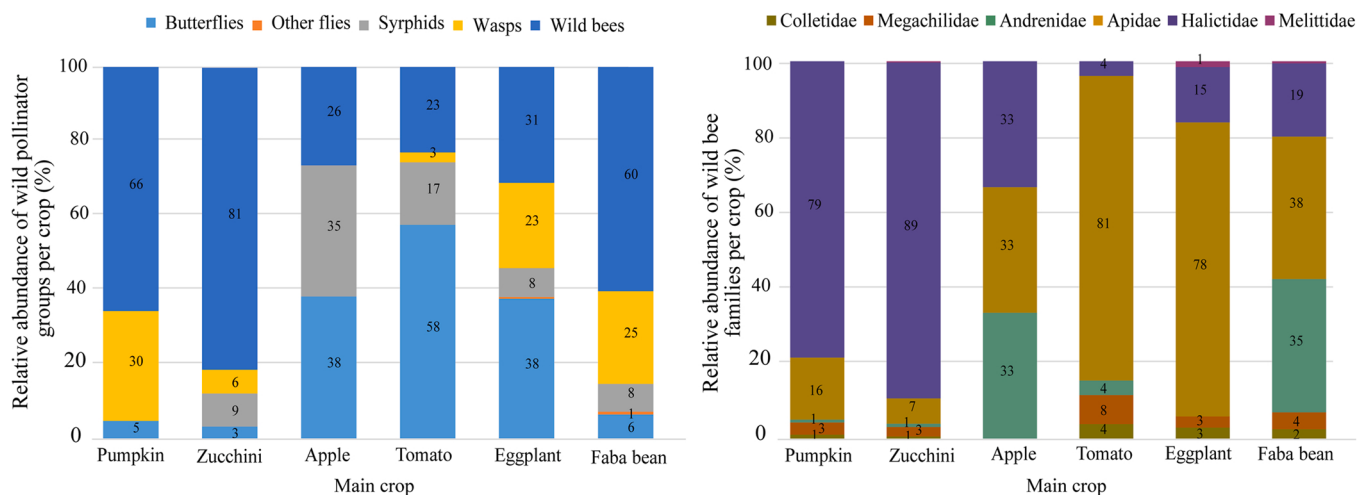


Fig. 2. The relative abundance of wild pollinator groups in each main crop and (b) the relative abundance of wild bee families in each main crop. The abundance of pollinator groups is presented as "%".

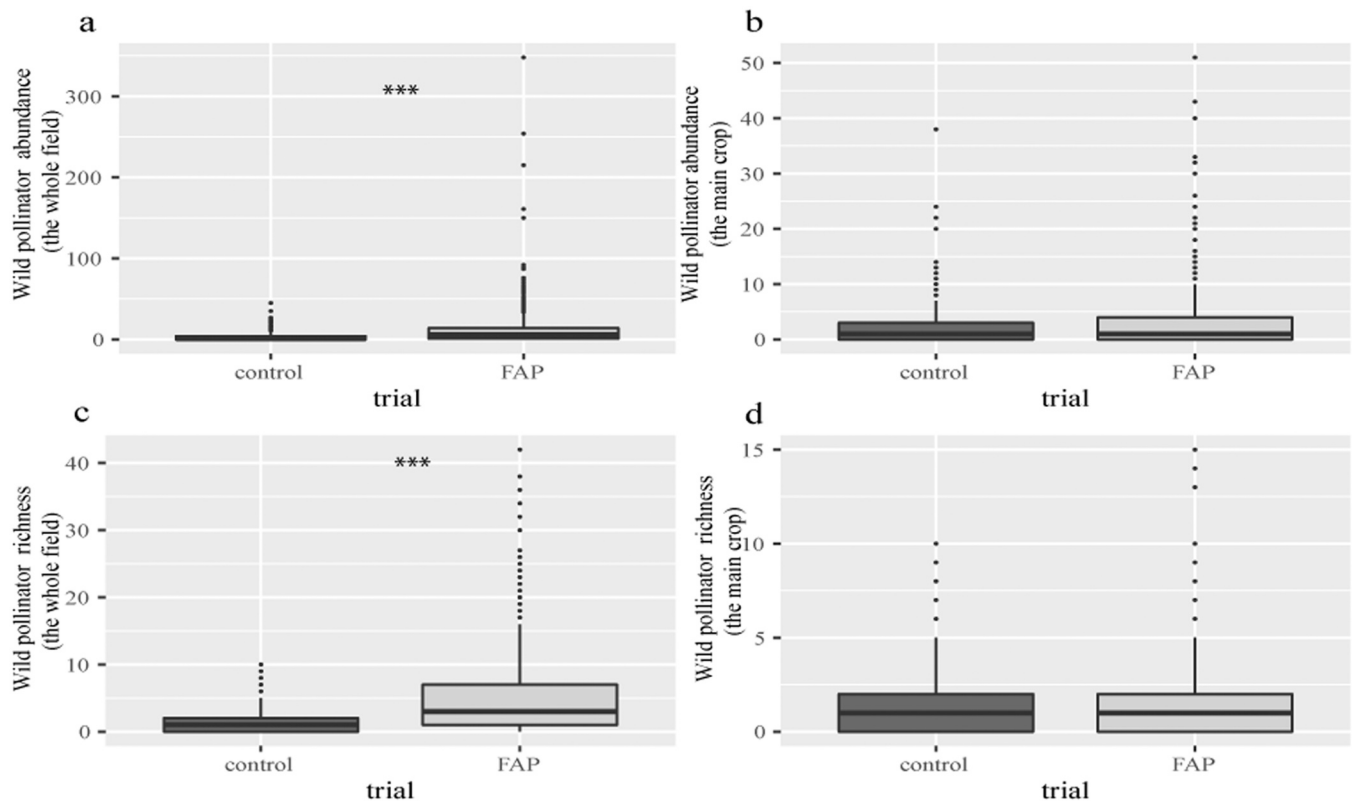


Fig. 3. Box plots comparing the overall wild pollinator abundance and richness between FAP (Farming with Alternative Pollinators) and control fields using the entire wild pollinator data. (a) Wild pollinator abundance in the whole FAP and control fields, (b) Wild pollinator abundance in the 75% zone in FAP and Control fields, (c) wild pollinator richness in the whole FAP and control fields and (d) wild pollinator richness in the 75% zone in FAP and control fields. Box plots show the median and 25–75% percentiles. Whiskers show all data excluding outliers. Outliers (circles) are values being more than 1.5 times box length from upper and lower edge of respective box. Asterisks indicate significant differences in pollinator abundance and richness between FAP and control fields (Generalized linear mixed models with negative binomial distribution; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

pollinator abundance between FAP and control in the 75% zone; D3: difference in wild pollinator richness in the whole field; D4: difference in wild pollinator richness distance in the 75% zone) were not affected by either the mean phylogenetic distance between MHEP and the main crop, the monthly mean temperature or the monthly precipitation (Table 3).

4. Discussion

4.1. Effect of the FAP approach on wild pollinator communities

In line with previous research (Christmann et al., 2017, 2021a, 2021b; Sentil et al., 2022a, 2022b; Bencharki et al., 2022), we confirmed that FAP fields show a significant increase in wild pollinator abundance and richness at the entire field level (i.e. 75% main crop + 25% MHEP) compared to control fields (i.e. 100% main crop). Our result adds to the growing literature a key finding. Small-scale flower plantings (i.e. FAP fields) can be effective tools to promote wild pollinators. The increase in wild pollinator diversity and abundance is associated with the high plant diversity provided by FAP fields. Indeed, control fields show one plant species (i.e. the main crop) while FAP fields offer from 5 to 9 plant species. Plant diversity is a key factor shaping positively wild pollinator community structure (Nicholls and Altieri, 2013; Fornoff et al., 2017; Isbell et al., 2017; Garibaldi et al., 2019; Christmann et al., 2017, 2021a, 2021b). Diverse plant communities offer various nesting materials (Campbell et al., 2017a; Ganser et al., 2021) and floral rewards (Roger et al., 2017; Ganser et al., 2021) at different times (Bartomeus et al., 2013). They can also boost pollinator health (Vaudo et al., 2015), development (Moerman et al., 2017) and reproduction (Klatt et al.,

2020).

Regarding the impact of FAP on the main crop wild pollinators (i.e. the 75% zone), we did not record a significant effect of the FAP approach. This result supports the findings of previous studies using either MHEP, hedgerows or wildflower strips (Morandin and Kremen, 2013; Albrecht et al., 2020; Zamorano et al., 2020; von Königslöw et al., 2022). Yet, this finding does not align with other studies (Blaauw and Isaacs, 2014b, 2014a; Campbell et al., 2017; Eckert et al., 2022; Fountain, 2022). To date, two hypotheses have been proposed to explain what drives the failure or the success of floral planting habitats in promoting the diversity of the main crop wild pollinators: the “exporter” hypothesis and the “concentrator” hypothesis (Morandin and Kremen, 2013; Nicholson et al., 2019). The “exporter” hypothesis (Morandin and Kremen, 2013; M’Gonigle et al., 2015) predicts an increase in pollination service due to spillover of pollinators from habitat plants to adjacent crops. The second is the “concentrator” hypothesis or “the circle principle” (Lander et al., 2011), in which habitat enhancement plants act as concentrators of pollinator populations and negatively affect insect visitation to the main crop (Nicholson et al., 2019). Our result supports the second hypothesis, suggesting that MHEP might concentrate wild pollinators away from the main crops. However, the economic assessments conducted in Morocco (Christmann et al., 2021a, 2021b) and in Uzbekistan (Christmann et al., 2017) demonstrated an increase in the main crops’ productivity due to enhanced crop pollination service, thus indirectly implying an increase of pollinators in the main crop. A possible explanation to these contrasting results (i.e. increase in the main crop yield in Christmann, Bencharki, et al. (2021) and neutral effect on crop wild pollinator abundance and richness in the present study) might be the limited sampling effort. Indeed, to acquire a general

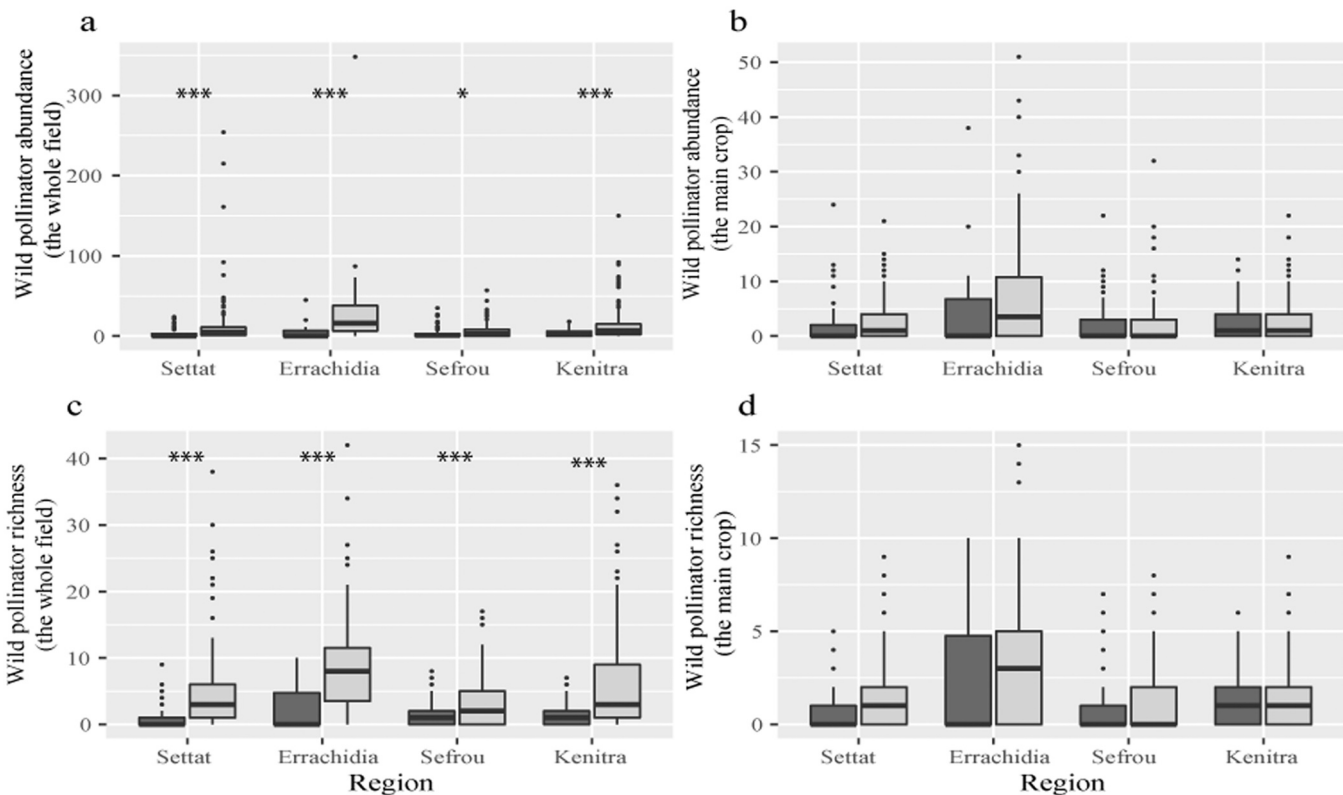


Fig. 4. Boxplots comparing wild pollinator abundance and richness between FAP (Farming with Alternative Pollinators) and control fields per region. (a) Wild pollinator abundance in the whole FAP and control fields, (b) wild pollinator abundance in the 75% zone in FAP and Control fields, (c) wild pollinator richness in the whole FAP and control fields and (d) wild pollinator richness in the 75% zone in FAP and control fields. Box plots show the median and 25–75% percentiles. Whiskers show all data excluding outliers. Outliers (circles) are values being more than 1.5 times box length from upper and lower edge of respective box. Asterisks indicate significant differences in pollinator abundance and richness between FAP and control fields for each region (Generalized linear mixed models with negative binomial distributions; *P < 0.05, ** P < 0.01, *** P < 0.001).

Table 2

p-value of comparison of wild pollinator abundance and richness between FAP and control fields in the whole field area and in the main crop (the 75% zone), analyzed with Generalized Linear Mixed Models (GLMM) with negative binomial distribution. Asterisks indicate significant differences in wild pollinator abundance and richness between FAP and control fields (*P < 0.05, ** P < 0.01, *** P < 0.001). The analyses were conducted at three levels: using the entire wild pollinator data, at the regional level and at the crop level.

		p-value of mean comparison of wild pollinator abundance		p-value of mean comparison of wild pollinator richness	
		Entire field	75% zone	Entire field	75% zone
Full dataset		0.213×10 ⁻¹⁴ ***	0.285	0.2×10 ⁻¹⁷ ***	0.224
Region	Settat	0.221×10 ⁻⁵ ***	0.860	0.213×10 ⁻⁶ ***	0.111
	Kenitra	0.583×10 ⁻⁹ ***	0.489	0.186×10 ⁻¹⁰ ***	0.718
	Errachidia	0.102×10 ⁻⁶ ***	0.089	0.265×10 ⁻⁶ ***	0.170
	Sefrou	0.022*	0.599	0.598×10 ⁻⁴ ***	0.674
Main crop	Pumpkin	0.334×10 ⁻¹⁰ ***	0.044*	0.101×10 ⁻⁷ ***	0.095
	Zucchini	0.014 *	0.478	0.266×10 ⁻⁴ **	0.727
	Faba bean	0.756×10 ⁻⁶ ***	0.245	0.384×10 ⁻⁶ ***	0.413
	Tomato	0.048*	0.126×10 ⁻⁴ **	0.35×10 ⁻⁴ **	0.020 *
	Eggplant	0.316×10 ⁻⁸ ***	0.547	0.907×10 ⁻⁹ ***	0.295
	Apple	0.592	0.628	0.311	0.622

picture that can be better extrapolated to other regions and climates, we opted for sampling more sites less intensely, rather than sampling less sites more intensely. Importantly, the sampling effort was consistent between the two treatments (i.e., FAP and control), thus preventing biases. The neutral effect of the approach on the main crop wild pollinators could also be related to the time of establishment of MHEP. Indeed, this factor was found to influence greatly the success of the flowering strips in promoting the wild pollinators of the main crop (Albrecht et al., 2020). As habitat plants need time to develop and wild pollinators take time to colonize newly established habitats (Williams et al., 2001), the build-up and the restoration of the local crop pollinator

populations may require time (Morandin and Kremen, 2013; Albrecht et al., 2020), and thus the timescale of the study was probably not long enough to detect an effect. Future studies with extended sampling duration and long term experiments are warranted to gain more insight about effect of FAP on crop wild pollinators.

The effect of the FAP approach on wild pollinator abundance and richness was significantly higher in the whole field area in the four regions. Several studies showed that the effectiveness of flower plantings in supporting pollinators depends on the landscape context (Tscharntke et al., 2005; Venturini et al., 2017; Rundlöf et al., 2018). Specifically, in highly simplified landscapes, source of forage and nesting sites are

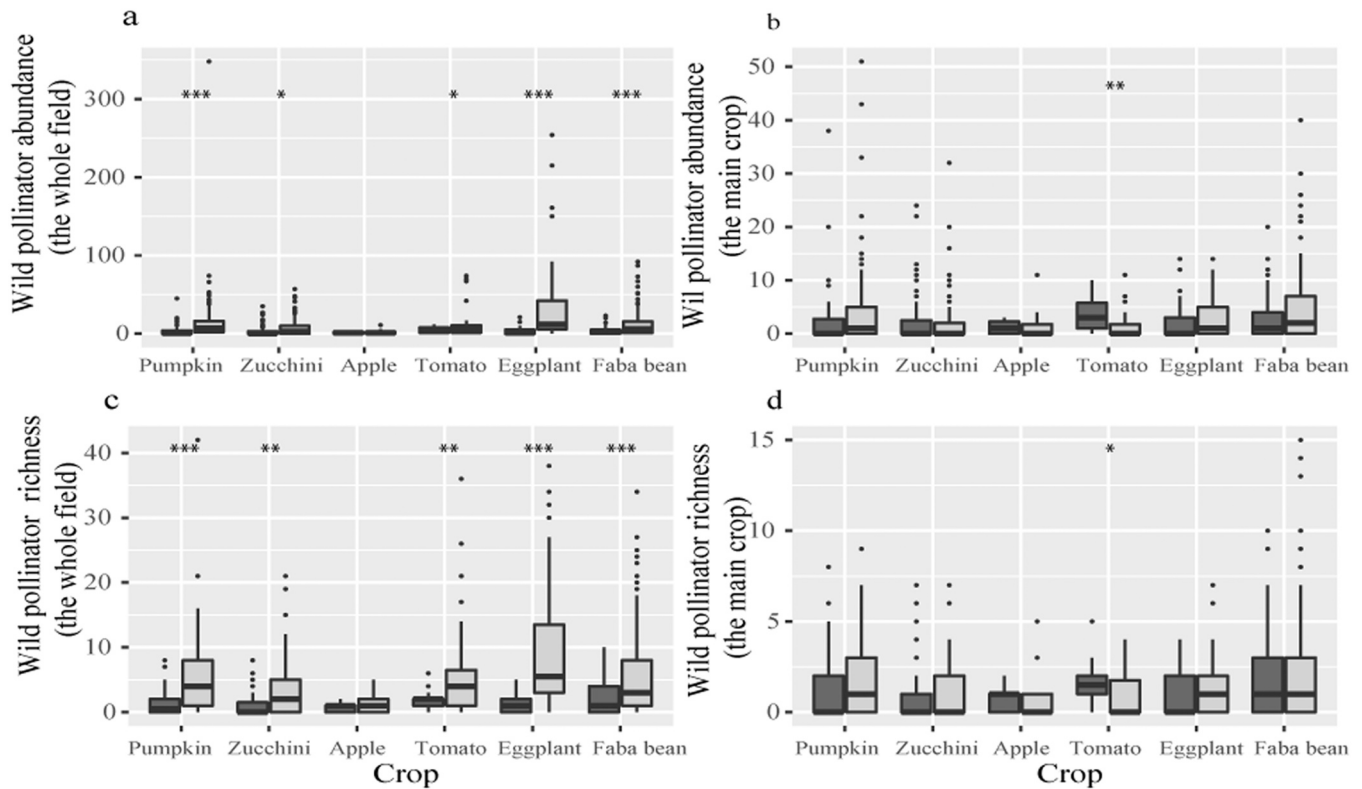


Fig. 5. Boxplots comparing wild pollinator abundance and richness between FAP (Farming with Alternative Pollinators) and control fields per crop. (a) Wild pollinator abundance in the whole FAP and control fields, (b) wild pollinator abundance in the 75% zone in FAP and control fields, (c) Wild pollinator richness in the whole FAP and control fields and (d) wild pollinator richness in the 75% zone in FAP and control fields. Box plots show the median and 25–75% percentiles. Whiskers show all data excluding outliers. Outliers (circles) are values being more than 1.5 times box length from upper and lower edge of respective box. Asterisks indicate significant differences in pollinator abundance and richness between FAP and control fields for each crop (Generalized linear mixed models with negative binomial; *P < 0.05, ** P < 0.01, *** P < 0.001).

Table 3

Relationships between wild pollinator distances (i.e. difference in wild pollinator richness and abundance between FAP and control fields) and mean phylogenetic distance, and climatic variables (i.e. monthly precipitation and mean monthly temperature), analyzed by Linear Mixed Models (LMM). MPD = Mean phylogenetic distance, MMT = Monthly Mean Temperature and MP = Monthly Precipitation.

Response variable	Explanatory variables	Estimate	Se	P-value
Distance 1: difference in wild pollinator abundance in the whole field	MPD	-0.343×10^{-05}	0.423×10^{-04}	0.081
	MMT	0.623×10^{-04}	0.2078×10^{-03}	0.300
	MP	0.914×10^{-05}	0.389×10^{-04}	0.235
Distance 2: difference in wild pollinator abundance in the 75% zone	MPD	-0.133×10^{-04}	0.423×10^{-04}	0.753
	MMT	0.493×10^{-04}	0.207×10^{-03}	0.812
	MP	0.101×10^{-04}	0.389×10^{-04}	0.795
Distance 3: difference in wild pollinator richness in the whole field	MPD	0.111×10^{-05}	0.423×10^{-04}	0.979
	MMT	0.323×10^{-04}	0.207×10^{-03}	0.876
	MP	0.664×10^{-05}	0.389×10^{-03}	0.864
Distance 4: difference in wild pollinator richness in the 75% zone	MPD	0.163×10^{-05}	0.423×10^{-04}	0.969
	MMT	0.516×10^{-04}	0.207×10^{-03}	0.804
	MP	0.992×10^{-05}	0.388×10^{-04}	0.799

scarce, consequently few pollinator communities are present to colonize the established habitat plants, whilst in complex landscapes, flower plantings may fail to create sufficient contrast to significantly foster pollinator diversity (Scheper et al., 2015, 2013). In our study, the landscape composition and configuration of the four regions were not assessed to provide conclusive interpretations. Yet, considering the increase in wild pollinator abundance and richness in FAP fields compared to control fields in the four regions, we presume that the landscape in these regions was probably intermediate. Further studies are certainly required to determine whether the landscape context modulates the effect of the FAP approach on wild pollinator communities.

Similarly, the FAP approach did not show an effect on the main crop wild pollinators in any of the four regions, which may be explained by the fact that wild pollinator abundance and richness visiting the main crop were consistently low across treatments (Fig. 5).

4.2. Factors driving the effectiveness of the FAP approach concerning wild pollinators

4.2.1. Main crop type

Given the diverse MHEP provided in all the crop trials, we hypothesized that the FAP approach would influence positively wild pollinator abundance and richness at least in the whole field area for all crops. However, contrary to our expectations we found that the crop type modulates the impact of the FAP approach on wild pollinator abundance and richness in the whole field area and in the 75% zone. The neutral effect of the FAP approach on wild pollinator abundance and richness observed in the whole field area in apple crops can be explained by two potential causes: first, the flowering season of apple occurs in early spring when the overall abundance of wild pollinators is lower than later

in the season (Weekers et al., 2022); second, our fields were immersed within large areas of mass flowering apple orchards. At such large scale of flowering apple, wild pollinator abundance and richness might be spatially diluted (Holzschuh et al., 2016). Apart from the neutral effect of the FAP approach in apple, the approach influenced positively wild pollinator abundance and richness at the FAP field level in all the remaining crop species (see discussion above for possible mechanisms). These results corroborate the findings of previous studies on the positive effect of hedgerows, wildflower strips and MHEP in a range of crops (Morandin and Kremen, 2013; Sardiñas and Kremen, 2015; Morandin et al., 2016; Sardiñas et al., 2016; Christmann et al., 2017, 2021a, 2021b).

Regarding the impact of the crop factor in the 75% zone (i.e. the main crop), none of the studied crops displayed a significant effect in the main crop wild pollinator abundance and richness in response to the FAP approach, except pumpkin (positive effect in pollinator abundance) and tomato (negative effect in abundance and richness). The unexpected negative effect of the FAP approach on tomato wild pollinator abundance and richness could be associated to the morphological constraints displayed by tomato flower. In fact, the pollen of tomato flower is trapped inside the anthers, and few pollinator species are capable to extract it (Cooley and Vallejo-Marín, 2021; Franceschinelli et al., 2013). In FAP field, wild pollinators have diverse foraging options, so they can readily switch to the accessible floral rewards provided by MHEP when the main crop flower rewards are unfavorable or hardly accessible. In contrast, wild pollinators in tomato control fields are supplied with a single foraging option, and thus though the pollen of the crop is hardly accessible, wild pollinators become less choosy and fed on the available flowering crop. Though eggplant and tomato have similar flower type, we did not observe a negative effect in eggplant. However, we did not also report a significant positive effect in this crop either. The significant positive effect of the FAP approach on pumpkin wild pollinator abundance and the negative effect on tomato wild pollinator abundance reported in this study may show that the response is crop-dependent. Future studies should focus on understanding the causes underlying the variation of effect of the FAP approach across crop species to be able to develop more tailored protocols.

4.2.2. Mean phylogenetic distance

Previous studies reported a higher insect diversity with increasing phylogenetic distance between plant species (Fontaine and Thébaud, 2015; Hutchinson et al., 2017; Cirtwill et al., 2020). Closely related animals tend to interact with identical or congeneric plants (Janz and Nylin, 1998; Vamosi et al., 2014), due to the maintenance of ancestral ecological characteristics (Fontaine and Thébaud, 2015). However, our results showed that the differences in wild pollinator abundance and richness between FAP and control fields (i.e. proxy of impact of FAP approach on wild pollinator community) were neither significantly increased by the mean phylogenetic distance between crop and MHEP at the whole field level nor in the main crop.

The MHEP in our study were mainly selected together with the farmers based on the suitability, their high specific diversity (i.e. different plant species) and their similar phenologies (i.e. the timing of blooming). However, communities that are species rich may not necessarily have equally high levels of phylogenetic diversity (Rissler et al., 2006; Forest et al., 2007; Devictor et al., 2010), whereas plant species sharing similar phenologies are more phylogenetically related (Kang and Jang, 2004; Losos, 2008; Davis et al., 2010). For instance, in faba bean trials, we selected diverse MHEP species. Yet, due to the limited number of plants flowering already in March, the majority was from the family Fabaceae that includes closely related species with similar phylogenetic traits (i.e. wild lupinus, cultivated lupinus, alfalfa, clover, grasspea and vetch). Therefore, the absence of the effect of the mean phylogenetic distance on the FAP approach could result from the low phylogenetic distance that was probably not high enough to exhibit a significant effect on wild pollinator abundance and richness in FAP

fields despite the diverse MHEP species provided.

Future studies should deepen on the understanding of the effect of plant composition on wild pollinator communities visiting FAP fields.

4.2.3. Climate

None of the climatic variables were significant predictors of the four wild pollinator distances (i.e., distance 1: difference in wild pollinator abundance between FAP and control in the whole field, distance 2: difference in wild pollinator abundance between FAP and control in the 75% zone, (iii) distance 3: difference in wild pollinator richness in the whole field and (iv) distance 4: difference in wild pollinator richness in the 75% zone). Temperature and precipitation are known to affect pollinator richness at regional level (Classen et al., 2015) and continental level (Patin et al., 2009), but we did not find an effect of the climate on the richness and abundance of pollinators between regions. The neutral effect of the climatic variables on wild pollinator distances may indicate that temperature and precipitation ranges used in our study were within the optimal climatic conditions of the wild pollinators recorded in the course of these experiments. Hence, a significant positive or negative effect of climatic variables on the effectiveness of the FAP approach might have occurred if temperature and precipitation exceeded the optimal conditions of pollinating insects.

5. Conclusion

Our study demonstrates that the FAP approach is an effective tool for promoting wild pollinators in agroecosystems, with significant implications for pollinator conservation and sustainable agricultural practices. The impact of the FAP approach on the abundance and the richness of wild pollinators on the whole field area was positive considering the global dataset, the four regions and most crops; in contrast to the general lack of differences in wild pollinator abundance and richness visiting the main crop. The mean phylogenetic distance between MHEP and the main crop and the climatic variables were not shown to affect the effectiveness of the FAP approach, whereas the crop factor appears to modulate its effectiveness. It would be interesting to conduct further research on additional factors that either promote or hinder spill-over of wild pollinators from MHEP to main crops, such as the landscape context and the time since establishment of MHEP. Our analysis demonstrated that FAP is a tool capable to support pollinators in low- and middle-income countries.

Funding sources

This study is mainly funded by The German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU), within the International Climate Initiative (IKI). AS and LH received a PhD grant from ICARDA/IKI (Rabat) and UMons. IEA has been granted by ICARDA/IKI (Rabat) and ARES (Belgium), OI has been granted by ICARDA/IKI. DM and SR were supported by the Fonds National de la Recherche Scientifique (FNRS, Belgium)/FWO joint program “EOS – Excellence of Science” under the project “CliPS: Climate change and its effects on Pollination Services” (project 30947854).

CRedit authorship contribution statement

Denis Michez: Writing – review & editing, Supervision, Resources, Funding acquisition, Data curation, Conceptualization. **Pierre Rasmont:** Supervision, Resources, Data curation. **Charif Smaili:** Investigation. **Laila Hamroud:** Investigation. **Oumayma Ihsane:** Investigation. **Orianne Rollin:** Formal analysis. **Youssef Bencharki:** Investigation. **Stefanie Christmann:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition. **Patrick Lhomme:** Writing – review & editing, Supervision, Methodology, Data curation. **Axel Ssymank:** Investigation. **Ahlam Sentil:** Writing – review & editing, Writing – original draft, Formal

analysis, Conceptualization. **Insafe El Abdouni:** Investigation. **Sara Reverte Saiz:** Writing – review & editing, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data availability

The data supporting this research will be openly accessible after the publication of this research

Acknowledgement

We would like to thank all specialists who contributed to the taxonomical expertise required for this work: Holger Dathe (Humboldt Universität zu Berlin, Germany) for the genus *Hylaeus*, Achik Dorchin (Tel Aviv University, Israel and UMons, Belgium) for Eucerini, Max Kasperek (Heidelberg, Germany) for Anthidiini, Andreas Müller (ETH Zürich, Switzerland) for Osmiini, Sébastien Patiny (Syngenta, Belgium) for Panurginae, Alain Pauly (Royal Belgian Institute of Natural History, Belgium) for Halictini, Christophe Praz (Université de Neuchâtel, Switzerland) for Megachilini, Jakub Straka (Charles University, Czech Republic) for *Sphecodes* and Nomadinae, Michael Terzo (UMons, Belgium) for Xylocopini, Thomas James Wood (UMons, Belgium) for the genus *Andrena* and Panurgini (partim) and Christian Schmid-Egger (Ökoteam Institute for Animal Ecology and Landscape Planning, Berlin, Germany) for most wasps (Crabronidae, Masaridae, Pompilidae, Scolidae, Sphecidae, Vespidae). We also received a great help from Dimitri Evrard (UMons) for collection management and digitization.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2024.109029](https://doi.org/10.1016/j.agee.2024.109029).

References

- Aizen, M.A., Aguiar, S., Biesmeijer, J.C., Garibaldi, L.A., Inouye, D.W., Jung, C., Martins, D.J., Medel, R., Morales, C.L., Ngo, H., Pauw, A., Paxton, R.J., Sáez, A., Seymour, C.L., 2019. Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Glob. Change Biol.* 25, 3516–3527. <https://doi.org/10.1111/gcb.14736>.
- Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D.A., Loebe, G.M., Marini, L., Mc Kerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlöf, M., Sardiñas, H., Scilligo, A., Thies, C., Tschamrtke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498. <https://doi.org/10.1111/ele.13576>.
- Alexandra, K., Brockhoff, P.B., Christensen, R.H.B., Pødenphant Jensen, S., 2020. Package ‘lmerTest’.
- Arena, M.V.N., Destéfani, F.C., da Silva, T.N., Mascotti, J.C., da, S., da Silva-Zacarin, E.C. M., Toppa, R.H., 2018. Challenges to the conservation of stingless bees in Atlantic Forest patches: old approaches, new applications. *J. Insect Conserv.* 22, 627–633. <https://doi.org/10.1007/s10841-018-0090-8>.
- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* 110, 4656–4660. <https://doi.org/10.1073/pnas.1218503110>.
- Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. *Conserv. Biol.* 29, 1006–1016. <https://doi.org/10.1111/cobi.12536>.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2020. lme4: linear mixed-effects models. R. Package Version 1 (1), 21.
- Beasley, T.M., Erickson, S., Allison, D.B., 2009. Rank-based inverse normal transformations are increasingly used, but are they merited? *Behav. Genet.* 39, 580–595. <https://doi.org/10.1007/s10519-009-9281-0>.
- Bencharki, Y., Christmann, S., Lhomme, P., Ihsane, O., Sentil, A., El Abdouni, I., Hamroud, L., Rasmont, P., Michez, D., 2022. Farming with Alternative Pollinators ” approach supports diverse and abundant pollinator community in melon fields in a semi-arid landscape. *Renew. Agric. Food Syst.* 1–34. <https://doi.org/10.1017/S1742170522000394> (Published).
- Blaauw, B.R., Isaacs, R., 2014b. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.12257>.
- Blaauw, B.R., Isaacs, R., 2014a. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic Appl. Ecol.* 15, 701–711. <https://doi.org/10.1016/j.baae.2014.10.001>.
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025–1032. <https://doi.org/10.1007/s00442-012-2271-6>.
- Borror, D.J., White E.R., 1991. “Les insectes de l’Amérique du Nord (au Nord du Mexique)”. Broquet.
- Campbell, A.J., Wilby, A., Sutton, P., Wäckers, F.L., 2017. Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agric. Ecosyst. Environ.* 239, 20–29. <https://doi.org/10.1016/j.agee.2017.01.005>.
- Christmann, S., 2020. Pollinator protection strategies must be feasible for all nations. *Nat. Ecol. Evol.* 4, 896–897. <https://doi.org/10.1038/s41559-020-1210-x>.
- Christmann, S., Aw-Hassan, A.A., 2012. Farming with alternative pollinators (FAP)-An overlooked win-win-strategy for climate change adaptation. *Agric. Ecosyst. Environ.* 161, 161–164. <https://doi.org/10.1016/j.agee.2012.07.030>.
- Christmann, S., Aw-Hassan, A., Rajabov, T., Khamraev, A.S., Tselivikas, A., 2017. Farming with alternative pollinators increases yields and incomes of cucumber and sour cherry. *Agron. Sustain. Dev.* 37. <https://doi.org/10.1007/s13593-017-0433-y>.
- Christmann, S., Aw-hassan, A., Güler, Y., Cumhur, H., Bernard, M., Smali, M.C., Tselivikas, A., 2021a. Two enabling factors for farmer-driven pollinator protection in low- and middle-income countries. *Int. J. Agric. Sustain.* 0, 1–14. <https://doi.org/10.1080/14735903.2021.1916254>.
- Christmann, S., Bencharki, Y., Anougmar, S., Rasmont, P., Smali, M.C., Tselivikas, A., Aw-Hassan, A., 2021b. Farming with Alternative Pollinators benefits pollinators, natural enemies, and yields, and offers transformative change to agriculture. *Sci. Rep.* 10 (1) <https://doi.org/10.1038/s41598-021-97695-5>.
- Cirtwill, A.R., Dalla Riva, G.V., Baker, N.J., Ohlsson, M., Norström, I., Wohlfarth, I.M., Thia, J.A., Stouffer, D.B., 2020. Related plants tend to share pollinators and herbivores, but strength of phylogenetic signal varies among plant families. *N. Phytol.* 226, 909–920. <https://doi.org/10.1111/nph.16420>.
- Classen, A., Peters, M.K., Kindeketa, W.J., Appelhans, T., Eardley, C.D., Gikungu, M.W., Hemp, A., Nauss, T., Steffan-Dewenter, I., 2015. Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania? *Glob. Ecol. Biogeogr.* 24, 642–652. <https://doi.org/10.1111/geb.12286>.
- Cooley, H., Vallejo-Marín, M., 2021. Buzz-Pollinated Crops: A Global Review and Meta-analysis of the Effects of Supplemental Bee Pollination in Tomato. *J. Econ. Entomol.* 114, 505–519. <https://doi.org/10.1093/jeet/toab009>.
- Davis, C.C., Willis, C.G., Primack, R.B., Miller-Rushing, A.J., 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 3202–3213. <https://doi.org/10.1098/rstb.2010.0130>.
- Delaplane, K.S., Mayer, D.F., 2000. Crop pollination by bees. CABI Publishing, London, UK.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., Mouquet, N., 2010. Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecol. Lett.* 13, 1030–1040.
- Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, J., Lattorff, G., Lungarwar, H.M., Seymour, T., Vanbergen, C.L., Potts S.G., A.J., Potts, S. G., 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* 5, 1453–1461. <https://doi.org/10.1038/s41559-021-01534-9>.
- Duchenne, F., Thébault, E., Michez, D., Gérard, M., Devaux, C., Rasmont, P., Vereecken, N.J., Fontaine, C., 2020. Long-term effects of global change on occupancy and flight period of wild bees in Belgium. *Glob. Chang. Biol.* 26, 6753–6766. <https://doi.org/10.1111/gcb.15379>.
- Eckerter, P.W., Albrecht, M., Bertrand, C., Gobet, E., Herzog, F., Pfister, S.C., Tinner, W., Entling, M.H., 2022. Effects of temporal floral resource availability and non-crop habitats on broad bean pollination. *Landsc. Ecol.* 37 (6), 1573–1586. <https://doi.org/10.1007/s10980-022-01448-2>.
- Elliott, S.E., 2009. Subalpine Bumble Bee Foraging Distances and Densities in Relation to Flower Availability. *Environ. Entomol.* 38, 748–756. <https://doi.org/10.1603/022.038.0327>.
- Fick, E.S., Hijmans, J.R., 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Fontaine, C., Thébault, E., 2015. Comparing the conservatism of ecological interactions in plant–pollinator and plant–herbivore networks. *Popul. Ecol.* 57, 29–36. <https://doi.org/10.1007/s10144-014-0473-y>.
- Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Procheş, Ş., Van Der Bank, M., Reeves, G., Hedderson, T.A.J., Savolainen, V., 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757–760. <https://doi.org/10.1038/nature05587>.

- Fornoff, F., Klein, A.M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. *Oikos* 126, 1020–1030. <https://doi.org/10.1111/oik.03869>.
- Fountain, M., T., 2022. Impacts of Wildflower Interventions on Beneficial Insects in Fruit Crops: A Review. *Insects* 13. <https://doi.org/10.3390/insects13030304>.
- Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-ovy, G., Bolker, B., Ellison, S., Graves, S., Krivitsky, P., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Ogle, D., Ripley, B., Venables, W., Walker, S., Winsemius, D., 2020. Package 'car'. Franceschinelli, E.V., Silva Neto, C.M., Lima, F.G., Gonçalves, B.B., Bergamini, L.L., Bergamini, B.A.R., Elias, M.A., 2013. Native bees pollinate tomato flowers and increase fruit production. *J. Pollinat. Ecol.* 11, 41–45. [https://doi.org/10.26786/1920-7603\(2013\)4](https://doi.org/10.26786/1920-7603(2013)4).
- Ganser, D., Albrecht, M., Knop, E., 2021. Wildflower strips enhance wild bee reproductive success. *J. Appl. Ecol.* 58, 486–495. <https://doi.org/10.1111/1365-2664.13778>.
- Garibaldi, L.A., Steffan-dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 80- (339), 1608–1611.
- Garibaldi, L.A., Pérez-Méndez, N., Garratt, M.P.D., Gemmill-Herren, B., Miguez, F.E., Dicks, L.V., 2019. Policies for Ecological Intensification of Crop Production. *Trends Ecol. Evol.* 34, 282–286. <https://doi.org/10.1016/j.tree.2019.01.003>.
- Gary, C., Jolain, N.M., Fanny, P., Laurence, C., Ariane, G., 2014. Mise en place d'une politique publique de réduction des usages de pesticides: le plan Ecophyto Contexte.
- Hartig, F., 2019. DHARMA: residual diagnostics for hierarchical (multi level/mixed) regression models. R package version 0.2.4. (<https://CRAN.R-project.org/package=DHARMA>) (accessed 20 November 2023).
- Hedges, S.B., Dudley, J., Kumar, S., 2006. TimeTree: A public knowledge-base of divergence times among organisms. *Bioinformatics* 22, 2971–2972. <https://doi.org/10.1093/bioinformatics/bti505>.
- Holzschuh, A., Dormann, C.F., 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* 477–484. <https://doi.org/10.1007/s00442-012-2515-5>.
- Holzschuh, A., Dainese, M., Gonzalez-Varo, P., Mudri-Stojnic, J., Riedinger, S., Rundlöf, V., Scheper, M., B. J., Wickens, J., Bommarco, V., Kleijn, R., Potts, D., P. M., S.G., Roberts, S., Smith, G., Vilà, H., Vujic, M., Steffan-Dewenter, I., A., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* 19, 1228–1236. <https://doi.org/10.1111/ele.12657>.
- Hutchinson, M.C., Cagua, E.F., Stouffer, D.B., 2017. Cophylogenetic signal is detectable in pollination interactions across ecological scales. *Ecology* 98, 2640–2652. <https://doi.org/10.1002/ecy.1955>.
- Isbell, F., Adler, P.R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D. K., Liebman, M., Polley, H.W., Quijas, S., Scherer-Lorenzen, M., 2017. Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.* 105, 871–879. <https://doi.org/10.1111/1365-2745.12789>.
- Janz, N., Nylin, S., 1998. Butterflies and plants: A phylogenetic study. *Evol. (N. Y.)* 52, 486–502. <https://doi.org/10.1111/j.1558-5646.1998.tb01648.x>.
- Kang, H., Jang, J., 2004. Flowering patterns among angiosperm species in Korea: Diversity and constraints. *J. Plant Biol.* 47, 348–355. <https://doi.org/10.1007/BF03030550>.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A. M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599. <https://doi.org/10.1111/ele.12082>.
- Klatt, B.K., Nilsson, L., Smith, H.G., 2020. Annual flowers strips benefit bumble bee colony growth and reproduction. *Biol. Conserv.* 252. <https://doi.org/10.1016/j.biocon.2020.108814>.
- Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* 40, 947–969. <https://doi.org/10.1111/j.1365-2664.2003.00868.x>.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Lander, T.A., Bebbler, D.P., Choy, C.T.L., Harris, S.A., Boshier, D.H., 2011. The circe principle explains how resource-rich land can waylay pollinators in fragmented landscapes. *Curr. Biol.* 21, 1302–1307. <https://doi.org/10.1016/j.cub.2011.06.045>.
- Lawson, D.A., Rands, S.A., 2019. The effects of rainfall on plant–pollinator interactions. *Arthropod Plant. Interact.* 13, 561–569. <https://doi.org/10.1007/s11829-019-09686-z>.
- Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11, 995–1003. <https://doi.org/10.1111/j.1461-0248.2008.01229.x>.
- Martinet, B., Dellicour, S., Ghisbain, G., Przybyla, K., Zambra, E., Lecocq, T., Boustani, M., Baghirov, R., Miché, D., Rasmont, P., 2021a. Global effects of extreme temperatures on wild bumblebees. *Conserv. Biol.* 0, 1–12. <https://doi.org/10.1111/cobi.13685>.
- Martinet, B., Zambra, E., Przybyla, K., Lecocq, T., Anselmo, A., Nonclercq, D., Rasmont, P., Miché, D., Hennebert, E., 2021b. Mating under climate change: Impact of simulated heatwaves on the reproduction of model pollinators. *Funct. Ecol.* 1–14. <https://doi.org/10.1111/1365-2435.13738>.
- Meena, N.K., Singh, B., Kant, K., Meena, R.D., Solanki, R.K., 2015. Role of insect pollinators in pollination of seed spices-A review. *Int. J. Seed Spices* 5, 1–17.
- Michez, D., Rasmont, P., Terzo, M., Vereecken, N.J., 2019. Bees of Europe. NAP Editions.
- Moerman, R., Vanderplanck, M., Fournier, D., Jacquemart, A.L., Michez, D., 2017. Pollen nutrients better explain bumblebee colony development than pollen diversity. *Insect Conserv. Divers.* 10, 171–179. <https://doi.org/10.1111/icad.12213>.
- Morandin, L.A., Kremen, C., 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl.* 23, 829–839. <https://doi.org/10.1890/12-1051.1>.
- Morandin, L.A., Long, R.F., Kremen, C., 2016. Pest control and pollination cost-benefit analysis of hedgerow restoration in a simplified agricultural landscape. *J. Econ. Entomol.* 109, 1020–1027. <https://doi.org/10.1093/jeet/tow086>.
- Nicholls, C.I., Altieri, M.A., 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agron. Sustain. Dev.* 33, 257–274. <https://doi.org/10.1007/s13593-012-0092-y>.
- Nicholson, C.C., Ricketts, T.H., Koh, I., Smith, H.G., Lonsdorf, E.V., Olsson, O., 2019. Flowering resources distract pollinators from crops: Model predictions from landscape simulations. *J. Appl. Ecol.* 56, 618–628. <https://doi.org/10.1111/1365-2664.13333>.
- Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Window, Q., Michez, D., J., 2014. Eur. Red. List Bees, IUCN Glob. Species Program. <https://doi.org/10.2779/77003>.
- Patiny, S., Rasmont, P., Michez, D., 2009. A survey and review of the status of wild bees in the West-Palaeartic region. *Apidologie* 40, 313–331. <https://doi.org/10.1051/apido/2009028>.
- Phillips, B.B., Gaston, K.J., Bullock, J.M., Osborne, J.L., 2019. Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. *J. Appl. Ecol.* 56, 2316–2327. <https://doi.org/10.1111/1365-2664.13470>.
- Phillips, B.B., Wallace, C., Roberts, B.R., Whitehouse, A.T., Gaston, K.J., Bullock, J.M., Dicks, L.V., Osborne, J.L., 2020. Enhancing road verges to aid pollinator conservation: A review. *Biol. Conserv.* 250, 108687. <https://doi.org/10.1016/j.biocon.2020.108687>.
- Pistón, N., Armas, C., Schöb, C., Macek, P., Pugnaire, F.I., 2015. Phylogenetic distance among beneficiary species in a cushion plant species explains interaction outcome. *Oikos* 124, 1354–1359. <https://doi.org/10.1111/oik.01979>.
- Popic, T.J., Davila, Y.C., Wardle, G.M., 2013. Evaluation of Common Methods for Sampling Invertebrate Pollinator Assemblages: Net Sampling Out-Perform Pan Traps. *PLoS One* 8. <https://doi.org/10.1371/journal.pone.0066665>.
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229. <https://doi.org/10.1038/nature20588>.
- Prosekov, A.Y., Ivanova, S.A., 2018. Food security: The challenge of the present. *Geoforum* 91, 73–77. <https://doi.org/10.1016/j.geoforum.2018.02.030>.
- Rasmont, P., Franzén, M., Lecocq, T., Harpke, A., Roberts, S.P.M., Biesmeijer, K., Castro, L., Cederberg, B., Dvorák, L., Fitzpatrick, Ú., Gonseth, Y., Haubruge, E., Mahé, G., Manino, A., Michez, D., Neumayer, J., Ødegaard, F., Paukkunen, J., Pawlikowski, T., Potts, S.G., Reemer, M., Settele, J., Straka, J., Schweiger, O., 2015. Climatic Risk and Distribution Atlas of European Bumblebees. *Biorisk*, 10: 1–236.
- Ribeiro, E.M.S., Santos, B.A., Arroyo-Rodríguez, V., Tabarelli, M., Souza, G., Leal, I.R., 2016. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology* 97, 1583–1592. <https://doi.org/10.1890/15-1122.1>.
- Rissler, L.J., Hijmans, R.J., Graham, C.H., Moritz, C., Wake, D.B., 2006. Phylogeographic lineages and species comparisons in conservation analyses: A case study of California herpetofauna. *Am. Nat.* 167, 655–666. <https://doi.org/10.1086/503332>.
- Roger, N., Moerman, R., Carvalheiro, L.G., Aguirre-Gutiérrez, J., Jacquemart, A.L., Kleijn, D., Lognay, G., Moquet, L., Quinet, M., Rasmont, P., Richel, A., Vanderplanck, M., Michez, D., 2017. Impact of pollen resources drift on common bumblebees in NW Europe. *Glob. Chang. Biol.* 23, 68–76. <https://doi.org/10.1111/gcb.13373>.
- Rundlöf, M., Lundin, O., Bommarco, R., 2018. Annual flower strips support pollinators and potentially enhance red clover seed yield. *Ecol. Evol.* 8, 7974–7985. <https://doi.org/10.1002/ecs3.4330>.
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>.
- Sardiñas, H.S., Kremen, C., 2015. Pollination services from field-scale agricultural diversification may be context-dependent. *Agric. Ecosyst. Environ.* 207, 17–25. <https://doi.org/10.1016/j.agee.2015.03.020>.
- Sardiñas, H.S., Tom, K., Ponisio, L.C., Rominger, A., Kremen, C., 2016. Sunflower (*Helianthus annuus*) pollination in California's Central Valley is limited by native bee nest site location. *Ecol. Appl.* 26, 438–447. <https://doi.org/10.1890/15-0033>.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecol. Lett.* 16, 912–920. <https://doi.org/10.1111/ele.12128>.
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and landscape-level floral resources explain effects of

- wildflower strips on wild bees across four European countries. *J. Appl. Ecol.* 52, 1165–1175. <https://doi.org/10.1111/1365-2664.12479>.
- Sentil, A., Lhomme, P., Michez, D., Reverté, S., Rasmont, P., Christmann, S., 2022a. Farming with Alternative Pollinators" approach increases pollinator abundance and diversity in faba bean fields. *J. Insect Conserv.* 26, 401–414. <https://doi.org/10.1007/s10841-021-00351-6>.
- Sentil, A., Reverté, S., Lhomme, P., Bencharki, Y., Rasmont, P., Christmann, S., Michez, D., 2022b. Wild vegetation and 'farming with alternative pollinators' approach support pollinator diversity in farmland. *J. Appl. Entomol.* 146, 1155–1168. <https://doi.org/10.1111/jen.13060>.
- Sentil, A., Lhomme, P., El Abdouni, I., Hamroud, L., Ihsane, O., Bencharki, Y., Rasmont, P., Michez, D., Christmann, S., (2023). Pollinator data [Data set]. Zenodo. (<https://doi.org/10.5281/zenodo.7769167>).
- Shakeel, M., Ali, Hussain, Ahmad, S., Said, F., Ali, K., Amjad, M., Ishtiaq, S., Islam, W., Ghramh, H.A., Javed, M., Ali, Habib, 2019. Saudi Journal of Biological Sciences Insect pollinators diversity and abundance in *Eruca sativa* Mill. (*Arugula*) and *Brassica rapa* L. (*Field mustard*) crops. *Saudi J. Biol. Sci.* 26, 1704–1709. <https://doi.org/10.1016/j.sjbs.2018.08.012>.
- Sharma, K., Meena, N.K., 2019. Diversity of insect pollinators in coriander (*Coriandrum sativum* Linn.) VAR. ACR-1 under Semi-Arid region of Rajasthan. *J. Pharmacogn. Phytochem.* 8, 198–201.
- de Sousa Costa, R.W., da Silva, G.L.F., de Carvalho Filho, A.O., Silva, A.C., de Paiva, A.C., Gattass, M., 2018. Classification of malignant and benign lung nodules using taxonomic diversity index and phylogenetic distance. *Med. Biol. Eng. Comput.* 56, 2125–2136. <https://doi.org/10.1007/s11517-018-1841-0>.
- Thom, M.D., Eberle, C.A., Forcella, F., Gesch, R., Weyers, S., 2018. Specialty oilseed crops provide an abundant source of pollen for pollinators and beneficial insects. *J. Appl. Entomol.* 142, 211–222. <https://doi.org/10.1111/jen.12401>.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecol. Lett.* 8, 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.
- Vamosi, J.C., Moray, C.M., Garcha, N.K., Chamberlain, S.A., Mooers, A., 2014. Pollinators visit related plant species across 29 plant-pollinator networks. *Ecol. Evol.* 4, 2303–2315. <https://doi.org/10.1002/ece3.1051>.
- Vastola, A., 2015. The Sustainability of Agro-Food and Natural Resource Systems in the Mediterranean Basin. <https://doi.org/DOI 10.1007/978-3-319-16357-4>.
- Vaudo, A.D., Tooker, J.F., Grozinger, C.M., Patch, H.M., 2015. Bee nutrition and floral resource restoration. *Curr. Opin. Insect Sci.* 10, 133–141. <https://doi.org/10.1016/j.cois.2015.05.008>.
- Venturini, E.M., Drummond, F.A., Hoshide, A.K., Dibble, A.C., Stack, L.B., 2017. Pollination reservoirs for wild bee habitat enhancement in cropping systems: a review. *Agroecol. Sustain. Food Syst.* 41, 101–142. <https://doi.org/10.1080/21683565.2016.1258377>.
- Warzecha, D., Diekötter, T., Wolters, V., Jauker, F., 2018. Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conserv. Divers.* 11, 32–41. <https://doi.org/10.1111/icad.12264>.
- Weekers, T., Marshall, L., Leclercq, N., Wood, T.J., Cejas, D., Drepper, B., Garratt, M., Hutchinson, L., Roberts, S., Bosch, J., Roquer-Beni, L., Lhomme, P., Michez, D., Molenberg, J.M., Smaghe, G., Vandamme, P., Vereecken, N.J., 2022. Ecological, environmental, and management data indicate apple production is driven by wild bee diversity and management practices. *Ecol. Indic.* 139, 108880 <https://doi.org/10.1016/j.ecolind.2022.108880>.
- Williams, I.H., 1987. The pollination of lupins. *Bee World* 68, 10–16. <https://doi.org/10.1080/0005772X.1987.11098904>.
- Williams, N.M., Minckley, R.L., Silveira, F.A., 2001. Variation in native bee faunas and its implications for detecting community changes. *Ecol. Soc.* 5 <https://doi.org/10.5751/es-00259-050107>.
- Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R., Tylianakis, J.M., 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia* 134, 605–611. <https://doi.org/10.1007/s00442-002-1128-9>.
- Zamorano, J., Bartomeus, I., Grez, A.A., Garibaldi, L.A., 2020. Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conserv. Divers.*, *icad.12454* <https://doi.org/10.1111/icad.12454>.
- Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123. <https://doi.org/10.1016/j.oneear.2020.12.005>.
- Zheng, Y.L., Burns, J.H., Liao, Z.Y., Li, Y. ping, Yang, J., Chen, Y. jun, Zhang, J. lin, Zheng, Y. guo, 2018. Species composition, functional and phylogenetic distances correlate with success of invasive *Chromolaena odorata* in an experimental test. *Ecol. Lett.* 21, 1211–1220. <https://doi.org/10.1111/ele.13090>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210x.2009.00001>.