



## Landscape effects on pollinator communities and pollination services in small-holder agroecosystems



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### ARTICLE INFO

#### Keywords:

Arable land  
Biodiversity  
Canola  
Ecosystem service  
Yield  
Wild bee

### ABSTRACT

Pollination by insects is key for the productivity of many fruit and non-grain seed crops, but little is known about the response of pollinators to landscapes dominated by small-holder agriculture. Here we assess the relationships between landscape context, pollinator communities (density and diversity) and pollination of oilseed rape in 18 landscapes with proportions of small-holder farming ranging from 10% to 70% in southern China. To quantify the contribution of pollinators to oilseed rape yield, we manipulated pollinator access in a focal oilseed rape field in each landscape using open and closed cages. The pollinator communities in the focal fields were sampled using pan traps. The abundance of wild pollinators increased significantly with the proportion of cultivated land, but the diversity of the wild pollinator communities declined. The responses of pollinator abundance and diversity to cultivated land were best explained at scales of around 1000 m. The abundance of the unmanaged honey bee *Apis cerana* was positively associated with the proportion of cultivated land, whereas the abundance of the managed *A. mellifera* was not. A pollination services index (PSI) was calculated by comparing the reproductive investment in seeds between plants with or without pollinator access. PSI was positively correlated with wild pollinator abundance, but not with the abundance of honeybee species. PSI was also not significantly correlated with the area proportion of cultivated land. Our results indicate that crop dominated landscapes with numerous small fields supported an abundant, but relatively species poor bee community that delivered pollination services to oilseed rape. Conservation of (semi-)natural habitats, however, is important for maintaining the diversity of wild pollinators.

### 1. Introduction

Pollination by insects is an important ecosystem service for a variety of crops (Klein et al., 2007; Ollerton et al., 2011) and is associated with landscape factors that benefit pollinators (Kremen et al., 2007; Potts et al., 2010; Batary et al., 2011; Bommarco et al., 2012; Hadley and Betts, 2012; Kennedy et al., 2013; Scheper et al., 2015; Baude et al., 2016). Semi-natural habitat has been positively associated with wild bee abundance (Steffan-Dewenter et al., 2002; Öckinger and Smith, 2007) and diversity (Öckinger and Smith, 2007; Le Féon et al., 2010; Diekötter et al., 2014; Martins et al., 2015). The diversity of wild

pollinators may also be influenced by the distance between forest and crops (Klein et al., 2003, 2003b), and their abundance may be boosted by the presence of mass-flowering crops (Westphal et al., 2003; Holzschuh et al., 2013; Diekötter et al., 2014; Riedinger et al., 2014). The relationships between (i) landscape context and pollinator community structure (abundance and diversity) (Steffan-Dewenter et al., 2002; Carré et al., 2009; Tscheulin et al., 2011; Bartomeus et al., 2014; Martins et al., 2015; Holzschuh et al., 2016), and (ii) the relationship between pollinator community structure and pollination service have been well established (Sabbahi et al., 2005; Jauker and Wolters, 2008; Bommarco et al., 2012; Garibaldi et al., 2013). However, we are not

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aware of studies that report the full cascade from landscape context to pollinator community structure and yield. There is an urgent need to identify landscapes settings that support ecologically intensive production systems that are both productive and conserve biodiversity-based ecosystems services (Bommarco et al., 2013). This is not only true for intensive farming landscapes with large fields in developed countries, but it is equally relevant for farming landscapes dominated by small-holder agriculture in developing countries.

In contrast to North America and Europe, where intensive farming systems are characterized by large field sizes and monocultures of a limited number of crops, Chinese agroecosystems (especially in south China) have relatively small fields that may support a high diversity of crops and cultivars. These small-holder fields are often surrounded by small strips of non-crop habitats, potentially providing nesting habitats and floral resources for wild pollinators (Klein et al., 2003a; Kremen et al., 2007; Holzschuh et al., 2012), and are intricately interlaced in the landscape. A recent global study found that crop yield of small farms benefit more from pollination than large farms (Garibaldi et al., 2016). Managed honey bees have historically been considered a key crop pollinator, but recent studies showed that wild pollinators are also important for crop production (Winfrey et al., 2008; Garibaldi et al., 2013; Lowenstein et al., 2015; Rader et al., 2016). Little is known about the relationship between landscape context and the diversity and abundance of pollinators in small-holder farming systems.

Here we studied pollination in oilseed rape (*Brassica napus* L.), which is a globally important crop for feed, cooking oil and biofuel. China is one of the largest producers of oilseed rape in the world (FAO, 2013), but pollination services in China are under pressure as exemplified by the need for hand-pollination of apples in the Sichuan province (Partap and Ya, 2012). Ironically, in highland regions of Sichuan and Chongqing, more than 20% of the world's approximately 250 bumblebee species have been recorded (Williams et al., 2009). Although oilseed rape is a self-pollinating plant species (Williams et al., 1986), it is also pollinated by insects and attracts a wide community of insect pollinators (Sabbahi et al., 2005; Jauker and Wolters, 2008; Bommarco et al., 2012; Stanley et al., 2013), which makes this crop suitable for studying generalist pollinators. Numerous studies on pollination have been conducted (e.g. Chifflet et al., 2011; Bommarco et al., 2012; Holzschuh et al., 2013; Lindström et al., 2016; Sutter and Albrecht, 2016), but none in small-holder landscapes.

The aim of this study is fourfold. First, we assess the relevant spatial scale for associations between the landscape context and pollinator abundance and diversity in small-holder farming landscapes. Second, we identify land-use types that influence pollinator abundance and diversity in oilseed rape fields. Third, we assess how pollinator abundance and diversity influence oilseed rape yield in these fields. Fourth, we establish whether pollination services can be directly linked to landscape context without considering pollinator abundance and diversity. As a null hypothesis, we expected the abundance and diversity of wild pollinators to decrease with the proportion of cultivated land and increase with the proportion of semi-natural habitat, while the abundance of managed honey bees was expected to be independent from landscape context because it is governed by the behaviour of bee keepers. We further expected that landscapes with more abundant and more diverse pollinator communities would receive more pollination services and therefore obtain higher oilseed rape yield.

## 2. Methods

### 2.1. Study area and land use survey

We selected a total of 18 focal oilseed rape fields in the broader region around the city of Nanchang, Jiangxi Province, China (N28.35°–N28.99°, E115.26°–E115.82°). The minimum distance between two focal fields was at least 5.8 km (Fig. 1), which exceeds the maximum foraging range for most bee species (Steffan-Dewenter et al.,

2002; Chifflet et al., 2011). Fields had a mean size of  $845 \pm 86 \text{ m}^2$  (range 400–1400  $\text{m}^2$ ) and they were all sown with a single traditional oilseed rape bred cultivar (Yangguang 2009, semi-winter cabbage type oilseed rape) because pollination effects may differ among cultivars (Hudewenz et al., 2014; Lindström et al., 2016). During the study period, no pesticides were applied in the oilseed rape fields. Land use in the landscape surrounding the focal fields was quantified at a spatial scale of 2000 m radius and ground-truthed in July 2014 (2.5 m resolution). We assume the land-use data of 2014 to be representative for 2015 when measurements on pollinator community and oilseed rape yield were conducted. A total of 42 land-use types (Appendix A) were classified into seven categories: cultivated land ( $41.3 \pm 4.8\%$  (mean  $\pm$  SEM throughout text), range 10.4%–69.8% at 2000 m radius), forest ( $38.2\% \pm 5.8\%$ , range 10.4%–77.3%), grassland ( $7.2\% \pm 1.5\%$ , range 0.5%–23.5%), orchards ( $1.1\% \pm 0.5\%$ ; range 0–7.6%), and three categories that were not used in the analysis (water, built-up areas and unused land, Fig. 1). There was a mismatch between the period of cultivation of oilseed rape (October–May) and ground-truthing (July). Therefore, oil seed rape was not represented in the ground-truthing analysis, and most likely overlapped with the land-use type ‘middle rice’ (Appendix A). Visual assessment of the crops around focal fields in February 2015 indicated that approximately one third of cultivated land contained oilseed rape ( $35\% \pm 5.6\%$ , range 7%–81% at 100 m radius).

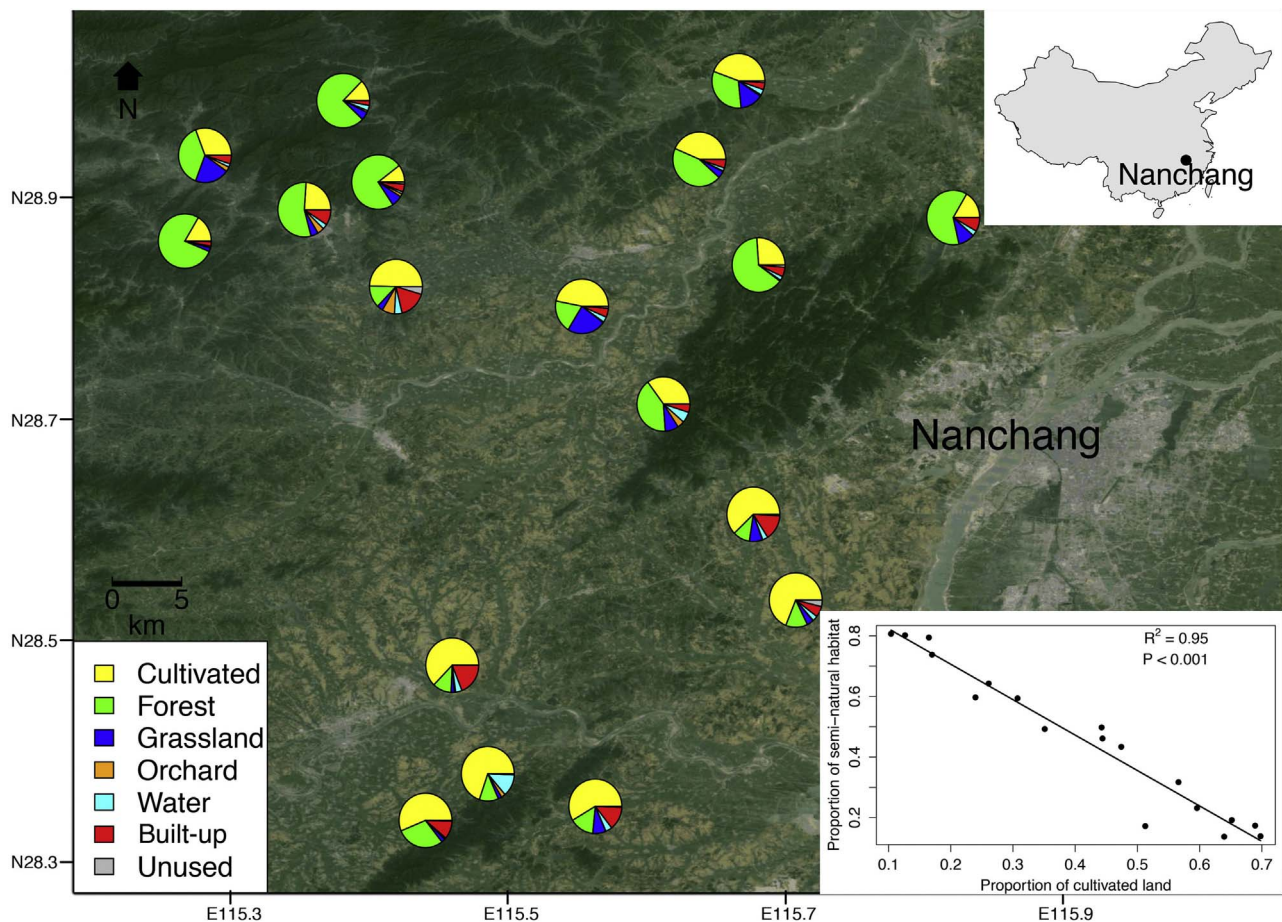
For the analysis, forest and grassland were pooled as semi-natural habitat. The proportion semi-natural habitat was not used in analysis because of a strong negative association with cultivated land (Pearson  $R^2 = 0.95$ ,  $P < 0.001$ , Fig. 1). Because of this strong correlation, results for cultivated land would also apply (but with opposite sign) for semi-natural habitat. In order to still include the potential effect of forest, we added the distance from focal field to the nearest forest as an additional explanatory variable.

### 2.2. Pollinator sampling

Pollinator communities in the field were sampled with pan traps. In the centre of each focal field, four pan trap stations were set up at the corners of a  $20 \times 20 \text{ m}^2$  square. Each station consisted of a stake with three cups (8.3 cm diameter, 13.5 cm height and a volume of 450 ml) that were painted ultraviolet (UV) yellow, UV blue and UV white from the inside. Two 3 mm-diameter holes were drilled at 3 cm from the brim of the cup in order to drain excess rainwater. Cups were established at a height of 1.5 m. We used salt (NaCl)-saturated water with a few drops of detergent as killing agent. Sufficient liquid was added in the cup to avoid drying out. Traps were installed at the end of February 2015, before the onset of blooming, and removed after 49–52 days of exposure in the field, at harvest in mid-April 2015. The slight variation in sampling period was caused by differences between sites in the date of trap placement. No influence on the sampling is likely since traps were established before the activity period of most pollinators. We therefore consider that sampling effort among sites was practically identical. Cups were emptied and refilled five times, at approximately 10-day intervals. Pollinator samples of each site and sampling period were pooled, sorted, pinned and identified to species level when possible. No cup was lost, flooded or dried out.

### 2.3. Flower cover estimation

Oilseed rape flower cover was assessed by placing four quadrats of  $0.5 \text{ m}^2$  randomly in the field and taking photos from above the canopy. Flower cover was estimated by exposing a 200 grid on top of the photo and counting the number of grids that contained oilseed rape flowers. Flower cover assessments were conducted at approximately 10-day intervals. The maximum flower cover for each focal field is referred to as ‘peak flower cover’, which was used as a proxy of the flower cover in the field. This ‘peak flower cover’ was highly correlated with



**Fig. 1.** Location of focal oilseed rape fields in the region of Nanchang City, Jiangxi province, China. Pies show the composition of the landscape at 2 km radius around focal fields. The regression shows the relationship between the proportions of cultivated land and semi-natural habitat (forest and grassland) at 2 km radius (image obtained from Google satellite map <https://maps.google.com/>).

accumulated flower cover over the whole sampling period (Pearson  $r = 0.95$ ,  $P < 0.001$ ), and was therefore representative for the flower density of the field over the blooming period.

#### 2.4. Oilseed rape yield

To measure yield with and without pollination, eight oilseed rape plants, spaced 4 m apart in a 2 by 4 grid, were selected in the centre of each focal field. Alternate plants were covered by closed or open cages (base 0.6 m  $\times$  0.6 m, 2 m height and mesh size of 1 mm<sup>2</sup>). Closed cages completely excluded pollinators, whereas open cages contained mesh only at the top 0.3 m, allowing pollinator access. All cages were set up approximately one week before oilseed rape flowering and removed at harvest. After harvest, seeds were removed from pods, dried at 60 °C for 24 h and weighed. Total seed weight reflects the yield for each plant. Plants were dried in a greenhouse for 30 days and the aboveground dry biomass (i.e. aboveground vegetative biomass excluding seeds and pods) was measured.

#### 2.5. Data analysis

We conducted four analyses. In the first analysis we assessed the spatial scale that best explained the response of the abundance and diversity of pollinators to landscape context (i.e. functional spatial scale). We used the proportion of cultivated land as a proxy for landscape context because this was a good predictor of pollinator abundance and diversity in initial exploratory analyses. Associations between cultivated land and wild pollinator abundance, wild pollinator diversity and honey bee abundance were then explored by calculating

Pearson correlation coefficients at spatial scales ranging from 200 to 2000 m radius. Wild pollinator diversity was characterized by the back-transformed Shannon entropy index (from here on: diversity) (Jost, 2006), which has been recommended as a robust indicator for the diversity of mobile insects (Jost, 2007; Beck and Schwanghart, 2010; Fiedler and Truxa, 2012). This back-transformed index was highly correlated with rarefied number of species ( $n = 54$ ) (Pearson  $r = 0.94$ ,  $P < 0.001$ ) and Fisher's alpha index ( $r = 0.91$ ,  $P < 0.001$ ) and it was therefore used as the sole indicator of diversity. Functional spatial scales were also assessed for the abundance of the seven most abundant pollinator species.

Second, the relationship between landscape context and pollinator abundance and diversity was analysed in further detail using model selection with generalized linear models (GLMs; Zuur et al., 2009). Model selection was conducted using landscape data at a scale of 1000 m radius because the strongest relationships were found at this scale. Response variables included (i) wild pollinator abundance (negative binomial error distribution with log-link function), (ii) wild pollinator diversity (Gaussian error distribution with identity-link function), and (iii) honey bee abundance (i.e. *A. mellifera* and *A. cerana*; negative binomial error distribution with log-link function). Explanatory variables were the proportion of (i) cultivated land, (ii) orchard land, (iii) distance to the nearest forest, and (iv) flower cover in the focal oilseed rape field. These variables were selected as they may potentially influence pollinator abundance and diversity and have ecological relevance. We did not include additional land use variables that were highly correlated with selected variables (e.g. semi-natural habitat which was highly correlated with cultivated land), or which were unlikely to influence pollinators (e.g. water, built-up areas and

unused land).

The third analysis focused on the relationship between the pollinator community and pollination services, while the fourth analysis focused on establishing whether pollination services were directly related to the proportion of cultivated land at a scale of 1000 m (i.e. without considering the pollinator community). Pollination services were defined as the relative yield gain attributable to insect pollinators. By using relative yield, i.e. the ratio between total dry seed weight and dry weight of the above-ground vegetative biomass, we controlled for site specific variation in local management, climate and soil conditions across the large geographical gradient (see also Zou et al., 2017). By subtracting relative yield in closed cages (pollinator exclusion) from relative yield in open cages (pollinator access), the resulting difference can be attributed to pollination services (see e.g. Woodcock et al., 2016), and then the response variable “Pollination Service Index” (PSI) was obtained, which is a measure of pollination services:

$$PSI_i = \frac{S_{Oi}}{B_{Oi} - S_{Oi}} - \frac{S_{Ci}}{B_{Ci} - S_{Ci}}$$

where  $S_{Oi}$  and  $S_{Ci}$  are the average total seed weight in open and closed cages, and  $B_{Oi}$  and  $B_{Ci}$  are the average aboveground plant total biomass in open and closed cages, respectively, at a site  $i$ . PSI thus reflects the plant's investment in seeds per unit vegetative biomass as affected by pollination, and was more robust than direct yield estimates, such as total seed weight or number of seeds per pod. To exclude bias due to unequal sample sizes, sites with damaged cages or dead plants were excluded, which resulted in a total of 12 sites for this analysis.

All calculations and analyses were conducted in R (R Core Team, 2014). GLMs were fitted using the “MASS” package (Venables and Ripley, 2002). Model selection was conducted using the “ dredge” function in the “MuMIn” package (Bartoń, 2015), based on Akaike's information criterion (AIC). Model residuals were checked for spatial autocorrelation using Moran's I (Gittleman and Kot, 1990) using the “ape” package (Paradis et al., 2004).

### 3. Results

We collected a total of 5148 individuals representing a total of 60 pollinator species. The dominant orders were Hymenoptera (44 species), Lepidoptera (9 species) and Diptera (7 species). Bees (Apoidea) were an important group with 3900 individuals and 38 species. The seven most abundant species included four wild bee species (*Eucera chinensis*, *Lasioglossum proximatium*, *L. scitulum* and *L. subopatum*), two honey bee species (*Apis mellifera* and *A. cerana*), and one butterfly species (*Pieris rapae*). Together, these seven species accounted for 87.5% of the catch (Appendix B).

#### 3.1. Functional spatial scale of landscape effects on pollinators

There was a significant positive association between the proportion cultivated land and the abundance of wild pollinators at spatial scales of 600 m and higher (Fig. 2a), with the highest correlation at a scale of 1000 m (Pearson  $R^2 = 0.62$ ;  $P < 0.001$ ; Fig. 2b). In contrast, the diversity of wild pollinators decreased with the proportion of cultivated land (Fig. 2c), with the most significant relationships at scales of 1000–1200 m ( $R^2 = 0.33$  and  $P = 0.012$  at 1000 m, Fig. 2d). A significant positive relationship between honey bee abundance (*A. mellifera* + *A. cerana*) and cultivated land was found at 800 m and 1000 m ( $R^2 = 0.23$  and  $P = 0.045$  at 1000 m; Fig. 2e and f).

The abundance of the most common wild pollinator species, *E. chinensis*, was positively associated with the area of cultivated land at all scales, and the association was most significant at 1000 m ( $R^2 = 0.61$  and  $P < 0.001$  at 1000 m, Fig. 3). A significant positive correlation between the abundance of *L. subopatum* and *L. scitulum* and the area of cultivated land was found at 400 and 600 m, respectively, while no significant trend was observed for *L. proximatium* and *Pieris*

*rapae*. Regarding the abundance of the two honey bee species, only *A. cerana* showed a significant positive relationship with land use at scales between 800 and 1800 m, with the correlation peaking at around 1000 m ( $R^2 = 0.29$  and  $P = 0.022$ ), whereas no significant relationship was observed at any scale for the managed bee species *A. mellifera* (Fig. 3).

#### 3.2. Landscape context and pollinator abundance and diversity

Model selection with landscape variables and flower cover as explanatory variables confirmed the positive effect of the proportion of cultivated land on the abundance of wild pollinators at a scale of 1000 m (Table 1). The second and third ranked models also contained the variables flower cover and distance to forest, but these variables were not significant ( $P < 0.05$ ). The three most parsimonious models for diversity of wild pollinators all contained the proportion of cultivated land (Table 1), as well as flower cover and distance to forest, but these latter two variables were again not significant. The most parsimonious model for the abundance of honey bees (*A. mellifera* + *A. cerana*) contained the proportion of cultivated land and orchards, as well as flower cover (Table 1), all with positive estimates. No significant spatial autocorrelation was found using Moran's I ( $P > 0.05$  in all models).

#### 3.3. Pollination services, pollinator community and landscape context

The yield/vegetative biomass ratio of oilseed rape in open cages ( $0.27 \pm 0.021$ ) was significantly higher than in closed cages ( $0.11 \pm 0.016$ ) (paired  $t$ -test,  $P = 0.004$ ). Pollination service index (PSI) was positively correlated with wild pollinator abundance ( $R^2 = 0.36$ ,  $P = 0.04$ ; Fig. 4b), but not significantly with the abundance of the two honey bee species ( $P > 0.05$ ). There was no significant relationship between the proportion of cultivated land and PSI ( $R^2 = 0.21$ ,  $P = 0.14$ , Fig. 4b).

### 4. Discussion

Our study has four key findings: (i) the responses of pollinator abundance and diversity to landscape context in small-holder landscapes were best explained at scales of around 1000 m; (ii) the abundance of wild pollinator species increased with the proportion of cultivated land, whereas the diversity of the wild pollinator fauna decreased with the proportion of cultivated land; (iii) the pollination service index (PSI) was positively associated with wild pollinator abundance; and (iv), PSI was not significantly correlated with the area of cultivated land.

Our study shows a strong link between agricultural land use, pollinator abundance and pollination services in small-holder farming landscapes of southern China. Pollination services in oilseed rape provided by the wild pollinator fauna were the highest in landscapes with a high proportion of cultivated land, which is in contrast to studies from Europe (e.g. Holzschuh et al., 2012; Foldesi et al., 2016) and North America (e.g. Kremen et al., 2004; Phillips and Gardiner, 2015), which report a positive association between (semi-)natural habitat and pollination services. There are several possible explanation for this finding. First, a large proportion of cultivated land in south China is left fallow in winter and early spring, providing suitable habitat for wild flowers. For instance, Chinese Milk Vetch (*Astragalus sinicus*) is a common weed in fallow agricultural land, providing nectar and pollen resources for bees (Murakami and Itino, 1990; Zheng et al., 2011). Second, the small field sizes support a dense network of field margins that provide refuges, habitat and corridors for pollinator dispersal (Jauker et al., 2009). Third, oilseed rape, which was one of the dominant crops in the study area, provides a relatively short, but massive supply of nectar and pollen resources for pollinators (Westphal et al., 2003; Holzschuh et al., 2013). Apparently, Chinese small-holder farming systems with oilseed

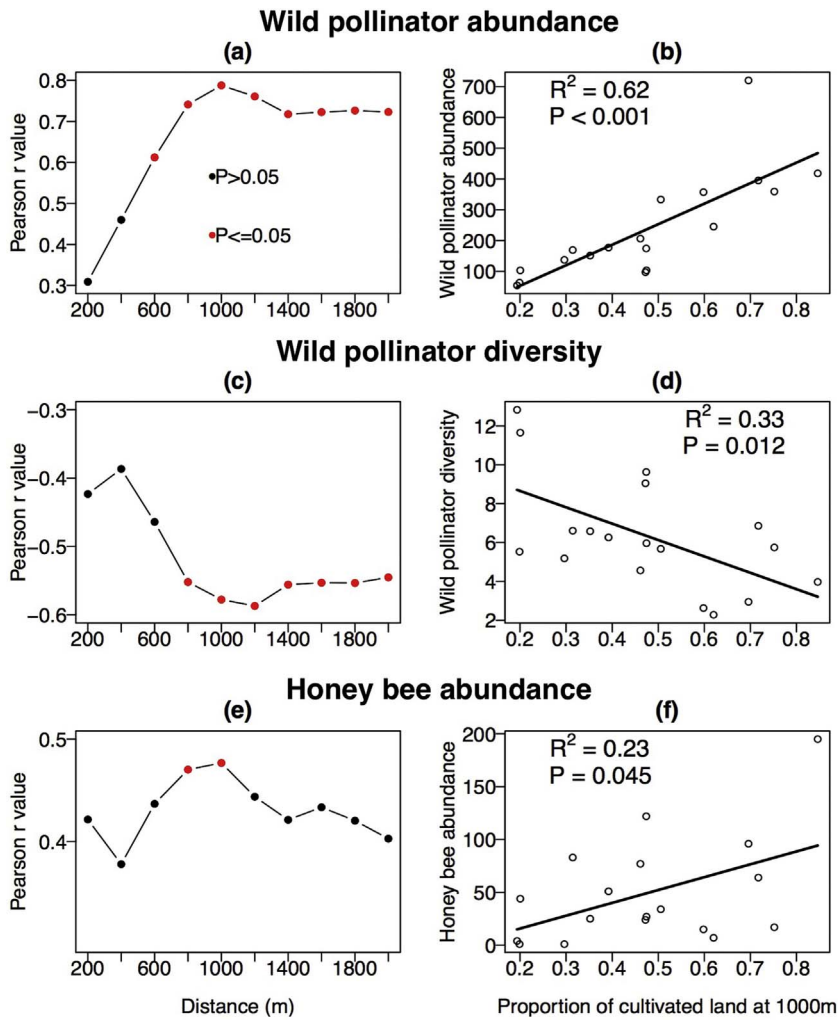


Fig. 2. Pearson r correlation coefficients between the proportion of cultivated land and the abundance (a) and diversity (c) of wild pollinators, and the abundance of honey bees (e) at spatial scales from 200 to 2000 m radius. Scatter plots show linear regressions of the abundance (b) and diversity (d) of wild pollinators, and the abundance of honey bees (f) and cultivated area at a scale of 1000 m radius.

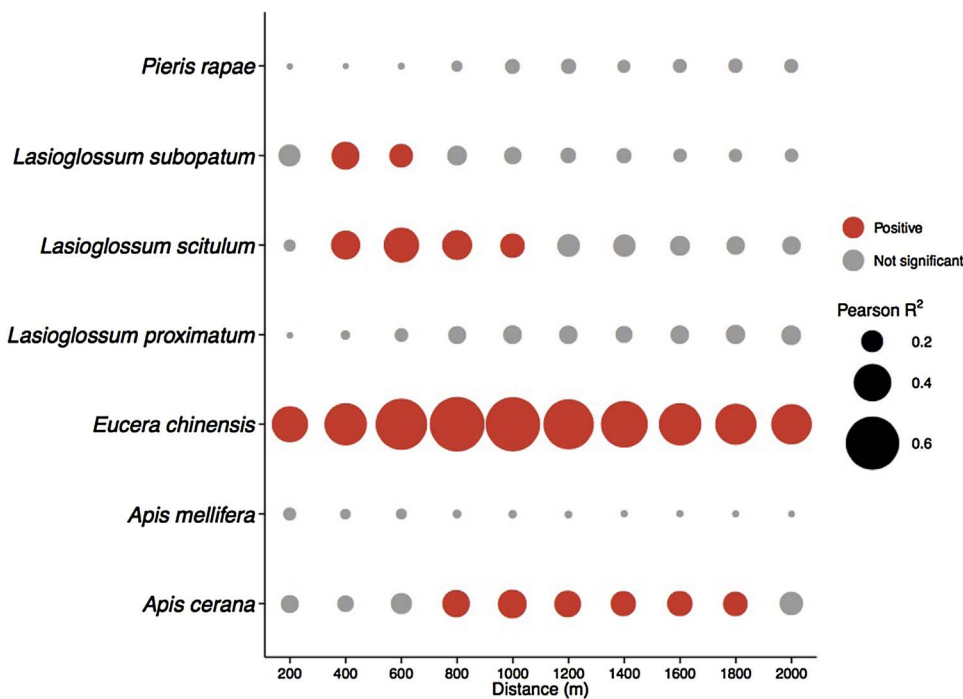


Fig. 3. Coefficient of determination (Pearson  $R^2$ ) between the abundance of the seven most common pollinator species and the proportion of cultivated land at scales of 200–2000 m radius. Size of circles indicates the value of  $R^2$  while the colour indicates sign of the relationship. Red markers represent positive correlations with P values  $\leq 0.05$  and grey markers represent  $P > 0.05$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Most parsimonious models for wild pollinator abundance, diversity and honey bee abundance for a 1000 m landscape radius. Models were selected based on AIC and only the three top ranked models are presented; df is degrees of freedom; logLik is the log likelihood of the model; R<sup>2</sup> is the explained deviance; ΔAIC is the difference in AIC between a model and the model with the lowest AIC, and the weight represents a degree of belief in the model (proportional to exp(-ΔAIC/2); Bolker, 2008). Dashes (-) indicate variables that were not included in the model. Significance levels are indicated by asterisks (\* P < 0.5, \*\* P < 0.01, \*\*\* P < 0.001).

Response variables	Model No.	Cultivated	Orchard	Distance to forest	Flower cover	df	logLik	R <sup>2</sup>	AIC	ΔAIC	weight
Wild pollinator abundance	1	3.05 ± 0.43***	-	-	-	15	-101.3	0.73	208.6	0	0.45
	2	2.96 ± 0.43***	-	-	0.83 ± 0.74	14	-100.7	0.74	209.5	0.9	0.28
	3	2.86 ± 0.46***	-	0.75 ± 0.8	-	14	-100.8	0.74	209.6	1	0.27
Wild pollinator diversity	1	-1.56 ± 0.51**	-	-	1.37 ± 0.8	14	-38.1	0.49	84.3	0	0.5
	2	-1.38 ± 0.51**	-	-	-	15	-39.6	0.35	85.2	0.9	0.31
	3	-1.63 ± 0.58**	-	0.26 ± 0.99	1.39 ± 0.81	13	-38.1	0.49	86.2	1.9	0.19
Honey bee abundance	1	2.81 ± 0.85**	17.53 ± 6.23**	-	8.55 ± 1.56***	13	-77.3	0.68	164.6	0	0.9
	2	2.03 ± 0.99*	-	-	7.31 ± 1.73***	14	-81.1	0.51	170.2	5.6	0.05
	3	-	12.75 ± 7.3	-	9.74 ± 1.77***	14	-81.1	0.51	170.3	5.7	0.05

rape-rice crop rotations have the capacity to support effective densities of pollinators in spite of the substantial period of rice cultivation, which is likely a period with low resource availability for pollinators.

The positive relationship between wild pollinator abundance and the proportion of cultivated land was driven by a few abundant species, while a few abundant species are likely supporting a majority of pollination services (Garibaldi et al., 2014; Kleijn et al., 2015; Lowenstein et al., 2015). The abundances of four of the seven most common pollinating bee species (*Eucera chinensis*, *Lasioglossum scitulum*, *L. subopatum* and *Apis cerana*) responded positively to the proportion of cultivated land, though at different spatial scales. The dominance of wild bees in pollinator communities has been observed before, but the spatial variability in the composition of pollinator communities can be high (Rader et al., 2016). Interestingly, the two honey bee species, the western honey bee (*A. mellifera*) and Chinese honey bee (*A. cerana*), showed contrasting responses to landscape context. Most commercial beekeepers prefer to keep *A. mellifera* because they produce more honey than *A. cerana* (Zheng et al., 2011). Most likely, most individuals of *A. cerana* were feral in our study region, while *A. mellifera* were mostly managed by bee keepers. The positive correlation between honey bee abundance and orchard land may reflect a preference of beekeepers to put *A. mellifera* hives near orchards.

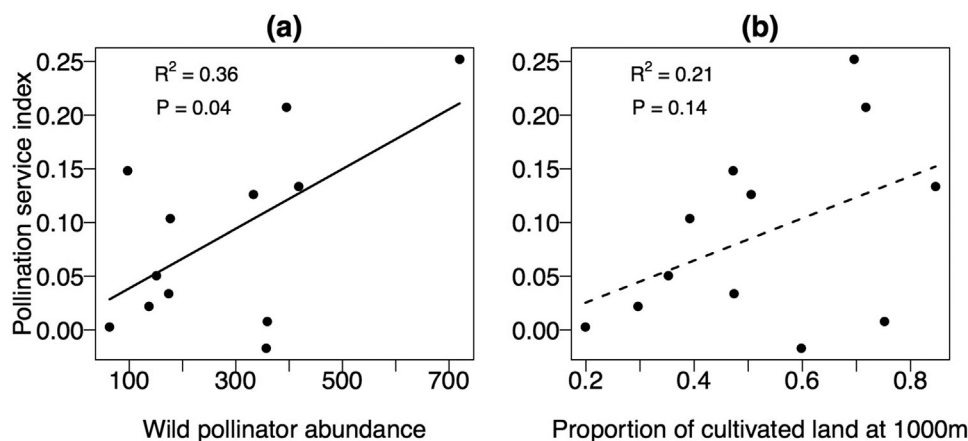
The high pollinator abundance in landscapes dominated by cultivated land is accompanied by a reduction in wild pollinator diversity. Contrasting responses of abundance and diversity have been reported for hoverflies (Meyer et al., 2009) and point to potential conflicts between agronomic and conservation interests (Kleijn et al., 2015). Thus, while small-holder cropping systems benefit especially dominant pollinator species, the inevitable reduction in semi-natural habitats still comes at the cost of an overall species loss. Semi-natural habitats, providing floral resources and nesting sites for a wide range of wild bee species (Kremen et al., 2004; Tscharntke et al., 2005; Mandelik et al., 2012; Woodcock et al., 2014), have been associated with species

richness in Europe and North America (Öckinger and Smith, 2007; Le Féon et al., 2010; Watson et al., 2011; Martins et al., 2015). The role of semi-natural habitats for the conservation of wild pollinators (Tscharntke et al., 2005) seems similarly important in small-scale agroecosystems of Southeast Asia.

Our results indicate that the functional spatial scale of insect pollinators in south China is approximately 1000 m, which corresponds well with maximal foraging distances for bee species (Steffan-Dewenter et al., 2001, 2002; Kremen et al., 2004; Chifflet et al., 2011; Danner et al., 2016). *Lasioglossum subopatum* and *L. scitulum* are solitary bees with a small body size and have a relatively short foraging range (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007), which explains the low correlation between cultivated land and the abundance of these two species at larger spatial scales. Although a small proportion of individuals forage relatively far from their nest, the nesting and foraging habitats should be much closer than the maximum distance to preserve a sustainable population size (Zurbuchen et al., 2010).

This study showed strong positive associations between (i) the proportion of cultivated land and pollinator abundance (Fig. 2b), and (ii) pollinator abundance and pollination services of oilseed rape (Fig. 4a). Nevertheless, pollination services were not significantly related to the proportion of cultivated land (Fig. 4b). The lack of significance might result from an insufficient statistical power of our study, or it might have been influenced by the presence of managed honeybees, *A. mellifera*, that are independent from landscape factors, even though honey bee abundance solely did not significantly contribute to pollination services. Possibly, the relationship between pollination services and pollinator community and landscape factors was masked by the ability of oilseed rape to self-pollinate and by local crop management (Marini et al., 2015). The likelihood of finding significant landscape effects on pollination could therefore be increased in future studies by using plants that depend entirely on pollination by insects.

We used pollinator sampled from pan traps as a proxy of pollinator



**Fig. 4.** Relationship between pollination service index and wild pollinator abundance (a) and with proportion cultivated land at 1000 m. Solid and dashed lines refer to significant (P < 0.05) and non-significant linear relationships, respectively.

abundance and diversity within the oilseed rape and the surrounding area. Catches in pan traps may under-represent certain pollinator species (Baum and Wallen, 2011). Nevertheless, the pollinator community structure within oilseed rape fields, as measured with these traps, reflected the pollinator potential of surrounding landscapes, thus validating the sampling method (see also Kovacs-Hostyanszki et al., 2013). Employing additional monitoring methods, such as transect walk observation and nest counting, can provide a more comprehensive view on landscape effects on pollinator communities and oilseed rape flower visitation. Combining results of multiple sampling methods may strengthen relationships as oilseed rape can be pollinated by a variety of generalist pollinators with different pollination efficiency (Rader et al., 2009; Jauker et al., 2012).

In conclusion, our study suggests that, in small-holder farming systems of South China, crop dominated landscapes supported an abundant, but relatively species poor pollinator communities. While our study is in line with findings of Garibaldi et al. (2016) who show that small farms benefit more from pollination services than large farms, our study shows that the positive association between small-holder agroecosystems and pollination services extends to the landscape scale. Conservation of natural and semi-natural habitats, however, is important for maintaining a high diversity of wild pollinators and should be considered as a part of sustainable agroecosystem management.

## Acknowledgements

We thank Riccardo Bommarco for kind suggestions during the experiment set up. We also thank Mario van Telgen, Daomeng Fu, Yongwei Yuan, Chao Zou, Yuekun Wu, Weizhao Sun and Xinlong Zhang for their help in fieldwork. We are also grateful for the kind help in bee identification by Huanli Xu from China Agricultural University. This study was financially supported by the Division for Earth and Life Sciences of the Netherlands Organization for Scientific Research (grant 833.13.004), the National Natural Science Foundation of P.R. China (31660539), the Agricultural Science and Technology Innovation Program (CAAS-ASTIP-2015-IAR), the Cultivation Plan for Young Scientists of Jiangxi Province (20153BCB23014) and External Cooperation Program of the Chinese Academy of Sciences (GJHZ1312).

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2017.05.035>.

## References

- Bartoń, K., 2015. MuMIn: Multi-Model Inference. R package version 1.13.4.
- Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, T., Roberts, S.P., Szentgyörgyi, H., Westphal, C., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ* 2, e328.
- Batary, P., Baldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. B* 278, 1894–1902.
- Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* 530, 85–88.
- Baum, K.A., Wallen, K.E., 2011. Potential bias in pan trapping as a function of floral abundance. *J. Kans. Entomol. Soc.* 84, 155–159.
- Beck, J., Schwanghart, W., 2010. Comparing measures of species diversity from incomplete inventories: an update. *Methods. Ecol. Evol.* 1, 38–44.
- Bolker, B.M., 2008. *Ecological Models and Data in R*. Princeton University Press, Princeton, pp. 396.
- Bommarco, R., Marini, L., Vaissière, B.E., 2012. Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025–1032.
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28, 230–238.
- Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyörgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissière, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agric. Ecosyst. Environ.* 133, 40–47.
- Chifflet, R., Klein, E.K., Lavigne, C., Le Féon, V., Ricroch, A.E., Lecomte, J., Vaissière, B.E., 2011. Spatial scale of insect-mediated pollen dispersal in oilseed rape in an open agricultural landscape. *J. Appl. Ecol.* 48, 689–696.
- Danner, N., Molitor, A.M., Schiele, S., Haertel, S., Steffan-Dewenter, I., 2016. Season and landscape composition affect pollen foraging distances and habitat use of honey bees. *Ecol. Appl.* 26, 1920–1929.
- Diekötter, T., Peter, F., Jauker, B., Wolters, V., Jauker, F., 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy* 6, 219–226.
- FAO, 2013. FAOSTAT, <http://faostat3.fao.org>, 1 January 2017.
- Fiedler, K., Truxa, C., 2012. Species richness measures fail in resolving diversity patterns of speciose forest moth assemblages. *Biodivers. Conserv.* 21, 2499–2508.
- Foldesi, R., Kovacs-Hostyanszki, A., Korosi, A., Somay, L., Elek, Z., Marko, V., Sarospataki, M., Bakos, R., Varga, A., Nyisztor, K., Baldi, A., 2016. Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. *Agric. For. Entomol.* 18, 68–75.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schuupp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611.
- Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Kremen, C., Morandin, L., Scheper, J., Winfree, R., 2014. From research to action: enhancing crop yield through wild pollinators. *Front. Ecol. Environ.* 12, 439–447.
- Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipólito, J., Freitas, B.M., Ngo, H.T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F.J.C., Oliveira da Silva, F., Devkota, K., Ribeiro M. d.F. Freitas, L., Gaglianone, M.C., Goss, M., Irshad, M., Kasina, M., Filho, A.J.S.P., Kiill, L.H.P., Kwapong, P., Parra, G.N., Pires, C., Pires, V., Rawal, R.S., Rizali, A., Saraiva, A.M., Veldtman, R., Viana, B.F., Witter, S., Zhang, H., 2016. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* 351, 388–391.
- Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71, 757–764.
- Gittleman, J.L., Kot, M., 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Syst. Zool.* 39, 227–241.
- Greenleaf, S., Williams, N., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596.
- Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biol. Rev.* 87, 526–544.
- Holzschuh, A., Dudenhöffer, J.-H., Tscharntke, T., 2012. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153, 101–107.
- Holzschuh, A., Dormann, C.F., Tscharntke, T., Steffan-Dewenter, I., 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* 172, 477–484.
- Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith, H.G., Vilà, M., Vujić, A., Steffan-Dewenter, I., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* 19, 1228–1236.
- Hudewenz, A., Pufal, G., Bögeholz, A.L., Klein, A.M., 2014. Cross-pollination benefits differ among oilseed rape varieties. *J. Agric. Sci.* 152, 770–778.
- Jauker, F., Wolters, V., 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156, 819–823.
- Jauker, F., Diekötter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecol.* 24, 547–555.
- Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.* 14, 81–87.
- Jost, L., 2006. Entropy and diversity. *Oikos* 113, 363–375.
- Jost, L., 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427–2439.
- 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.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., McGonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Baldi, A., Batary, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf,

- M., Sardinas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tschamtkke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C., Potts, S.G. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6, 7414.
- Klein, A.M., Steffan-Dewenter, I., Tschamtkke, T., 2003a. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.* 40, 837–845.
- Klein, A.M., Steffan-Dewenter, I., Tschamtkke, T., 2003b. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B* 270, 955–961.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtkke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* 274, 303–313.
- Kovacs-Hostyánszki, A., Haenke, S., Batary, P., Jauker, B., Baldi, A., Tschamtkke, T., Holzschuh, A., 2013. Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecol. Appl.* 23, 1938–1946.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.* 7, 1109–1119.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10, 299–314.
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities A large scale study in four European countries. *Agric. Ecosyst. Environ.* 137, 143–150.
- Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., Bommarco, R., 2016. Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 180, 759–769.
- Lowenstein, D.M., Matteson, K.C., Minor, E.S., 2015. Diversity of wild bees supports pollination services in an urbanized landscape. *Oecologia* 179, 811–821.
- Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. *Ecol. Appl.* 22, 1535–1546.
- Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindström, S.A.M., Zanetti, F., Mosca, G., Bommarco, R., 2015. Crop management modifies the benefits of insect pollination in oilseed rape. *Agric. Ecosyst. Environ.* 207, 61–66.
- Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2015. Pollination services are mediated by bee functional diversity and landscape context. *Agric. Ecosyst. Environ.* 200, 12–20.
- Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* 10, 178–186.
- Murakami, K., Itino, T., 1990. Foraging behaviour of pollinator bees on Chinese milk vetch, *Astragalus sinicus*, in relation to the diurnal nectar-secreting pattern of the flowers. *Honeybee Science* 11, 11–16.
- Öckinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J. Appl. Ecol.* 44, 50–59.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Partap, U., Ya, T., 2012. The human pollinators of fruit crops in Maoxian County Sichuan. *China. Mount. Res. Dev.* 32, 176–186.
- Phillips, B.W., Gardiner, M.M., 2015. Use of video surveillance to measure the influences of habitat management and landscape composition on pollinator visitation and pollen deposition in pumpkin (*Cucurbita pepo*) agroecosystems. *PeerJ* 3, e1342.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.
- R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A., Newstrom-Lloyd, L.E., Walker, M.K., Teulon, D.A., Edwards, W., 2009. Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *J. Appl. Ecol.* 46, 1080–1087.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jagger, S., Jauker, F., Klein, A.M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., de O. Pereira, N., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *PNAS* 113, 146–151.
- Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., Holzschuh, A., 2014. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecol.* 29, 425–435.
- Sabbahi, R., De Oliveira, D., Marceau, J., 2005. Influence of honey bee (Hymenoptera: Apidae) density on the production of canola (Crucifera: Brassicaceae). *J. Econ. Entomol.* 98, 367–372.
- 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.
- Stanley, D.A., Gunning, D., Stout, J.C., 2013. Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: ecological and economic incentives for pollinator conservation. *J. Insect Conserv.* 17, 1181–1189.
- Steffan-Dewenter, I., Munzenberg, U., Tschamtkke, T., 2001. Pollination, seed set and seed predation on a landscape scale. *Proc. R. Soc. B* 268, 1685–1690.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tschamtkke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Sutter, L., Albrecht, M., 2016. Synergistic interactions of ecosystem services: florivorous pest control boosts crop yield increase through insect pollination. *Proc. R. Soc. B* 283 20152529.
- Tschamtkke, 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.
- Tscheulin, T., Neokosmidis, L., Petanidou, T., Settele, J., 2011. Influence of landscape context on the abundance and diversity of bees in Mediterranean olive groves. *Bull. Entomol. Res.* 101, 557–564.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth ed. Springer, New York.
- Watson, J.C., Wolf, A.T., Ascher, J.S., 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environ. Entomol.* 40, 621–632.
- Westphal, C., Steffan-Dewenter, I., Tschamtkke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* 6, 961–965.
- Williams, I.H., Martin, A.P., White, R.P., 1986. The pollination requirements of oil-seed rape (*Brassica napus* L.). *J. Agr. Sci.* 106, 27–30.
- Williams, P., Ya, T., Jian, Y., Cameron, S., 2009. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Syst. Biodivers.* 7, 101–187.
- Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S., Kremen, C., 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania. *USA. J. Appl. Ecol.* 45, 793–802.
- Woodcock, B.A., Savage, J., Bullock, J.M., Nowakowski, M., Orr, R., Tallowin, J.R.B., Pywell, R.F., 2014. Enhancing floral resources for pollinators in productive agricultural grasslands. *Biol. Conserv.* 171, 44–51.
- Woodcock, B.A., Bullock, J.M., McCracken, M., Chapman, R.E., Ball, S.L., Edwards, M.E., Nowakowski, M., Pywell, R.F., 2016. Spill-over of pest control and pollination services into arable crops. *Agric., Ecosyst. Environ.* 231, 15–23.
- Zheng, H., Wei, W., Hu, F., 2011. Beekeeping industry in China. *Bee World* 88, 41–44.
- Zou, Y., Xiao, H., Bianchi, F.J.J.A., Jauker, F., Luo, S., van der Werf, W., 2017. Wild pollinators enhance oilseed rape yield in small-holder farming systems in China. *BMC Ecol.* 17, 6.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol. Conserv.* 143, 669–676.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media, Stanford.