



# Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry

Andrea Holzschuh<sup>a,b,\*</sup>, Jan-Hendrik Dudenhöffer<sup>b</sup>, Teja Tscharntke<sup>b</sup>

<sup>a</sup> Animal Ecology and Tropical Biology, Theodor-Boveri-Institute, Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany

<sup>b</sup> Agroecology, Georg-August-University Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany

## ARTICLE INFO

### Article history:

Received 11 October 2011

Received in revised form 17 April 2012

Accepted 27 April 2012

Available online 29 June 2012

### Keywords:

Bees

Cherry

Fruit set

Landscape

Pollination

Semi-natural habitats

## ABSTRACT

More than 70% of the leading global food crops, accounting for 35% of the global food production, are affected by pollination of flower-visiting animals, but the main pollinators – managed honey bees and wild bees – are currently declining in many regions worldwide. For the vast majority of crops it is unknown whether managed honey bees or wild bees are the most efficient pollinators, and how the pollination service provided by wild bees can be ensured.

**We assessed in a landscape-scale study how** sweet cherry production is influenced (1) by high-diversity bee habitats, and (2) by flowering ground vegetation which might compete with cherry for pollinators or might facilitate cherry pollination.

Cherry was highly dependent on insect pollination with bagged flowers producing only 3% of the fruits produced by open-pollinated flowers. Although two thirds of all flower visitors were honey bees, fruit set was related to wild bee visitation only, presumably due to their higher pollination efficiency. Initial fruit set and final cherry yield were closely correlated. **Wild bee visitation increased with the proportion of high-diversity bee habitats in the surrounding landscape** (1 km radius). An increase of high-diversity bee habitats in the landscape from 20% to 50% enhanced fruit set by 150%, which was experimentally shown to be due to pollen limitation. **Neither flower cover of ground vegetation nor bee densities on ground transects were related to flower visitation in trees or fruit set.**

Our results show that pollination services by wild bees in cherry surpassed pollination by honey bees. Hence, farmers need to protect semi-natural habitats in their landscapes to guarantee pollination and high yields. The conservation of semi-natural habitats, which provide nesting sites and additional food resources before and after cherry flowering enhances gratis ecosystem services, and thereby, the farmer's yield.

© 2012 Elsevier Ltd. All rights reserved.

## 1. Introduction

Agricultural production is crucially dependent on gratis ecosystem services provided by insects ([Zhang et al., 2007](#)). More than 70% of the leading global food crops – accounting for 35% of the global food production – are affected by pollination of flower-visiting animals ([Klein et al., 2007](#)). The economic value of global insect pollination has been estimated at €153 billion or USD 200 billion per year ([Gallai et al., 2009](#)). Most of the pollination service in pollinator-dependent crops is provided by managed honey bees and by wild bees, which predominantly nest in (semi-) natural habitats and fly into crop fields for foraging ([Allen-Wardell et al., 1998](#)). Populations of both managed and wild bees are currently

exposed to multiple risks, which has resulted in severe pollinator declines in many regions worldwide ([Potts et al., 2010](#)). Understanding the drivers of pollinator decline is therefore crucial for preventing or mitigating pollinator losses, and for maintaining or enhancing food production.

The importance of honey bees vs. other bees for crop pollination has been rated differently by different authors ([Aebi et al., 2012](#); [Breeze et al., 2011](#); [Ollerton et al., 2012](#)). The loss of (semi-) natural habitat providing nesting sites has been identified as one of the main drivers of the decline in crop-visiting wild bees worldwide ([Ricketts et al., 2008](#)) and of severe yield losses in pollinator-dependent crops ([Garibaldi et al., 2011](#)). However, pollination services provided by managed honey bees, which do not depend on (semi-) natural habitats for nesting, might buffer yield losses ([Ghazoul, 2005](#)). In accordance with this hypothesis, [Ricketts et al. \(2008\)](#) found in their meta-analysis that yield declines in the absence of (semi-) natural habitats were lower than expected from the declines in wild bees, but there have been few published

\* Corresponding author at: Animal Ecology and Tropical Biology, Theodor-Boveri-Institute, Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany. Tel.: +49 (0)931 31 82380; fax: +49 (0)931 31 84352.

E-mail address: [andrea.holzschuh@uni-wuerzburg.de](mailto:andrea.holzschuh@uni-wuerzburg.de) (A. Holzschuh).

studies assessing the relative impact of honey bees vs. other bees in crop pollination (but see [Javorek et al., 2002](#); [Williams and Thomson, 2003](#); [Wilson and Thomson, 1991](#); [Winfree et al., 2007](#)). Results from one crop can hardly be transferred to another crop, because honey bees can be as good pollinators as wild bees in one crop, but bad pollinators in another crop ([Wilson and Thomson, 1991](#)). Studies on the impact of (semi-) natural habitats on crop visitation of wild bees and on the potential of honey bees to provide comparable pollination services in the absence of wild bees are lacking for the majority of cash crops ([Garibaldi et al., 2011](#); [Ricketts et al., 2008](#)).

In this study, we examined the effects of honey bees and wild bees on fruit set in sweet cherry, and the effects of (semi-) natural habitats on bee visitation. Cherry is with a production of more than 2 million metric tons annually ([FAOSTAT, 2010](#)) one of the leading global food crops which greatly depend on animal pollination ([Klein et al., 2007](#)). Honey bees have been assumed to be the main pollinators in cherry ([Free, 1993](#)), but there is anecdotal evidence that wild bees provide better pollination services than honey bees in cherry ([Bosch et al., 2006](#)). Although cherry producers might strongly depend on pollination services provided by bees, there has been no replicated study assessing the relative importance of honey bees and wild bees for cherry production to date.

The mass-flowering of cherry trees lasts every year for a short period only. Before and after that period, bees require alternative food resources, which they might find in (semi-) natural habitats in the surrounding of the orchard or in the flowering ground vegetation in the orchard. Flowering non-crop plants between the cherry trees could serve as magnets which attract pollinators to orchards, and subsequently to the crop, as shown for non-crop plants which enhanced yield in sunflower fields ([Carvalho et al., 2011](#)). Besides facilitation of overall bee densities and cherry pollination by the ground-flowering vegetation, also negative effects of non-crop plants on cherry pollination are plausible. Non-crop plants which flower simultaneously to the crop might provide a disservice to crop production by competing with the crop for pollinators ([Free, 1993](#)). Although a published study on the effects of flowering wild plants on cherry pollination has been lacking, [Somerville \(1999\)](#) recommended complete removal of the ground vegetation because it might distract bees from the cherry blossom.

We conducted a landscape-scale study assessing how cherry production is influenced by the flower visitation of honey bees and wild bees, by semi-natural bee habitats and by flowering ground vegetation. We tested the following hypotheses:

- (1) Insect pollination enhances fruit set in cherry trees compared to fruit set after wind pollination.
- (2) Honey bees and wild bees are similarly effective in providing pollination services and enhancing cherry fruit set.
- (3) Fruit set of cherry trees increases with increasing proportion of semi-natural high-diversity bee habitats in the landscape mediated by increasing bee visitation rates in cherry trees.
- (4) Flowering ground vegetation affects fruit set negatively or positively supporting a competition or facilitation hypothesis.

## 2. Methods

### 2.1. Study sites

The study was conducted in the region around the town of Witzhausen, Northern Hesse, Germany (51°20'23"N, 9°51'20"E). This region is characterized by relatively heterogeneous landscapes consisting of intensively managed orchards, traditional orchard meadows, forest fragments, intensively managed crop fields, grasslands and semi-natural habitats like calcareous grasslands and hedgerows.

We selected eight landscape circles with 1 km radius. The study landscapes encompassed a gradient from little to high amounts of typical bee-nesting habitats. Based upon the habitat requirements of solitary bees ([Westrich, 1990](#)), we classified hedgerows, old fallows, orchard meadows and other non-intensively managed grasslands as major bee-nesting habitats. These habitats can be considered to be high-diversity sources of bee populations, which forage in multiple habitats at the landscape scale to collect pollen for larvae provision in the nesting habitats (hereafter referred to as 'high-diversity habitats'). Landscape circles were located within an area of 8 km × 10 km.

The study orchards were located in the centers of the landscape circles (one orchard per landscape, distance between study orchards > 1.2 km). Orchards had been planted with sweet-cherry trees (*Prunus avium*, half-standard size, i.e. stem height < 1.35 m), and were managed conventionally for commercial cherry production.

Orchard areas ranged between 1.16 ha and 5.04 ha (3.59 ha ± 1.18 ha; mean ± SE). Trees had been planted in rows of a single cultivar. Distances between neighboring rows were 2–3 m, between neighboring trees within a row 1.5–2 m. Ground vegetation between tree lines was mown after cherry flowering, with exception of two orchards which were mown before or during cherry flowering. Vegetation growing directly under the trees was not mown. Species richness of flowering plants on the ground was generally low and ranged between 3 and 9 species (5 ± 0.9). Species richness of flowering plants, orchard area or number of sweet cherry trees per orchard were not related to bees or fruit set.

We studied the most common sweet-cherry cultivars in the region ("Regina" and "Kordia"), which could be found in all eight orchards (in six orchards both cultivars were present, in two orchards either Regina or Kordia). Both cultivars are self-sterile (S-alleles: Regina S<sub>1</sub>S<sub>3</sub>, Kordia S<sub>3</sub>S<sub>6</sub>), and successful fruit development depends on pollination with pollen of a compatible cultivar ([Lech et al., 2008](#)). Compatible pollinator cultivars were present in all orchards. We randomly chose four plots per orchard, each consisting of three neighboring trees. If the cultivars Regina and Kordia were both present in the orchard, two plots were chosen per cultivar.

Farmers are aware that yield depends on insect pollination and place honey-bee hives in the orchard or the vicinity, or trust in long-distance foraging of honey bees within the region.

### 2.2. Pollination treatments and quantifying fruit set

We compared three pollination treatments to determine the relative impact of wind, insect and optimal pollination on the fruit set: fruit set of (1) bagged flowers (wind pollination only), (2) open flowers (wind and insect pollination), (3) hand-pollinated open flowers ("optimum" pollination). Treatments were randomly assigned to the three trees of a plot, resulting in 32 replicates per treatment (four plots per orchard; eight orchards). One branch per tree was marked and treated. During the experiment, markings of eight hand-pollinated branches were lost, reducing the number of replicates for that treatment from 32 to 24.

For the treatment "bagged flowers", branches were covered with polyethylene tulle bags (mesh size 3 mm) for the whole duration of flowering. Bags prevented access of pollinating insects, but allowed pollen grains to pass through. We removed bags immediately after petal abscission to avoid shading of the developing fruits.

For the treatment "insect pollination", the marked branches were freely exposed to insect pollinators.

For the treatment "hand pollination", all flowers of a branch were freely exposed to insect pollinators and were additionally hand-pollinated directly after they had opened by touching each of them with three flowers of a compatible cultivar to test for

pollen limitation. The number of flowers was counted for all treated branches, when flower buds became visible.

To quantify fruit set, the number of developing cherry fruits was counted in all treatments 4 and 9 weeks after flowering (7 and 2 weeks before harvest). In the further analysis, we focused on fruit set after 9 weeks only, because these data represent the economically interesting fruit yield. Pollen limitation was calculated for each pair of hand- and open-pollinated trees (i.e. trees of the same plot) as fruit set after hand pollination divided by fruit set after open pollination. Values larger than 1 indicate a higher fruit set in the hand pollination treatment, i.e. pollen limitation occurred, a value of 1 indicates no difference between treatments, i.e. the absence of pollen limitation, and values below 1 indicate higher fruit set after hand pollination. Values below 1 should not occur under optimal circumstances, because the supplement treatment (additional hand pollination of open flowers) is expected to increase pollen deposition and subsequently fruit set compared to the open pollination treatment. However, there are multiple reasons why hand pollination of open flowers can result in lower fruit set than insect pollination of open flowers (Young and Young, 1992).

### 2.3. Pollinators in cherry trees

Flower-visiting pollinators (honey bees, wild bees and hover flies) were recorded from 20th April to 7th May 2008 during the flowering period of sweet cherry trees. Hoverflies were excluded from the analyses, because only five individuals were observed. Although honey bees are native to the region, no wild honeybee populations exist anymore. Thus, all honey bees recorded in our study came from managed populations, and the group of wild bees comprises all other bees besides the honey bees. Three survey rounds per orchard were conducted between 10:00 and 17:00, when conditions were suitable for pollinator activity (temperature > 18 °C, wind speed < 3 bft, sunny weather). All orchards were surveyed once in the morning, around noon, and in the afternoon on three non-consecutive days. The first round started one day after bud opening.

Flower-visiting pollinators were recorded in all trees which had been marked for the open pollination treatment for 5 min per tree and survey round (=altogether 15 min per tree, four trees per orchard). Because of the relatively small size of trees, all flower-visitors of a tree were captured during walking slowly around the tree. Wild bees that could not be identified in the field were brought to the lab for further species identification. Bees that could be identified in the field were stored until the end of the observation round to avoid multiple counts of one individual. Individuals that could not be captured were counted and identified to the genus level if possible. For calculating visitation rates, the number of pollinators per tree was divided by the number of flowers in the tree. Visitation rates were cumulated for the three rounds.

The species richness of wild bees was positively related to the visitation rates (linear mixed-effect model with orchard as random factor:  $F_{1,5} = 19.8$ ,  $P = 0.007$ ) and was therefore not analyzed separately.

### 2.4. Pollinators around trees: the effects of additional floral resources

To investigate whether floral resources around cherry trees reduce or enhance flower visitation in cherry trees, plants and pollinators were recorded along transects between the cherry trees. Transects were 50 m long and 2 m width, started at the orchard edge and led in the direction of the orchard center. Transects were walked at low speed for 15 min directly after the pollinator survey in the trees (15 min  $\times$  3 rounds = 45 min per orchard). All bees

sighted on the transect were captured or recorded. Percentage flower cover on the transect was recorded for every round by counting the number of flowers or flowering parts for each plant species, multiplying it with the estimated area of the flower/the flowering part and dividing it by transect area. Flower cover was not related to the diversity of flowering plant species or the orchard area. The species richness of wild bees was positively related to their abundance (linear mixed-effect model with orchard as random factor:  $F_{1,15} = 6.9$ ,  $P = 0.019$ ) and was therefore not analyzed separately.

### 2.5. Landscape parameters

Habitat types were mapped during field inspections on the basis of official topographical maps (Deutsche Grundkarte 1:5000) within a circle of 1 km radius around the orchard center. The 1 km radius was chosen, because solitary bees, which comprise most of the recorded bee species, are known to be influenced by landscape factors at small spatial scales up to 1 km (Gathmann and Tscharnkte, 2002; Steffan-Dewenter et al., 2002). The percentage area of the different habitat types was calculated for the landscape circles using the geographic information system ArcView 3.2 (ESRI Geoinformatik GmbH, Hannover, Germany). The proportion of high-diversity habitats did neither correlate with flower cover and species richness of flowering plants nor with the landscape parameters proportion of forest, proportion of annual crops, and proportion of mass-flowering annual crops (Spearman Rank Correlations,  $n = 8$ , all  $P > 0.3$ ), and it was marginally negatively related to the proportion of intensively used orchards in the landscape ( $n = 8$ ,  $R = 0.71$ ,  $P = 0.058$ ).

### 2.6. Statistical analysis

The relationship between fruit set 4 weeks after flowering and fruit set 9 weeks after flowering (representing yield) was evaluated with Spearman correlation analysis. Effects of additional insect and hand pollination on fruit set compared to effects of wind pollination were assessed in linear mixed-effects model with pollination treatment as predictor, and orchard and plot as random factors nesting trees within plots and plots within orchards. The effect of pollination treatment was further inspected using the contrasts between mean levels of the tree factor categories. The estimated contrasts were computed using the `glht` function in the R-package `multcomp` (Hothorn et al., 2008).  $P$ -values of multiple comparisons were corrected by the Holm correction.

The relationship between fruit set of open-pollinated flowers and pollen limitation (fruit set after hand pollination divided by fruit set after open pollination) was assessed in linear mixed-effect models with orchard as random factor nesting tree pairs (=plots) within orchard. Models were calculated for both all pairs, and for the subset of pairs where pollen limitation values were higher than or equal to 1 to exclude trees where the experimental supplement of pollen has probably failed (Larson and Barrett, 2000).

The following analyses were performed on the orchard level with data averaged over the trees of an orchard. Direct effects on fruit set were assessed in a linear regression model with the predictors wild bee visitation and honeybee visitation. Indirect bee-mediated effects of environmental variables on fruit set were assessed in a linear regression model with the predictors proportion of high-diversity bee habitats and flower cover of additional flower resources. Indirect effects of bees on ground transects on fruit set were assessed in a linear regression model with the predictors wild bee ground densities and honeybee ground densities.

The determinants of wild bee and honeybee visitation in trees and wild bee and honeybee densities on ground transects were assessed in linear regression models with the predictors proportion

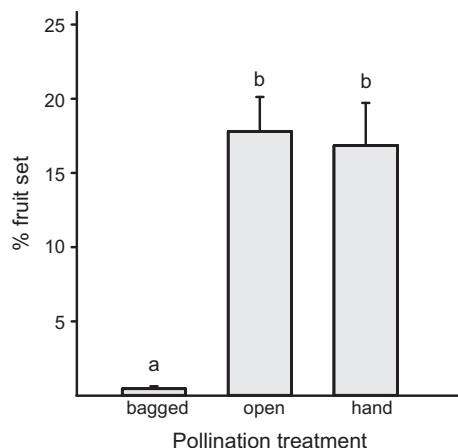
of high-diversity bee habitats and flower cover of additional flower resources. Visitation rates and ground densities were not related for wild bees (Spearman rank correlation,  $n = 8$ ;  $R = 0.08$ ,  $p > 0.8$ ), but for honey bees ( $R = 0.81$ ,  $p = 0.012$ ).

All models were computed in R (R Development Core Team, 2011, version 2.11.1). Predictors that did not contribute to the model with  $P < 0.05$  were removed by a stepwise backward procedure from the full model. F-tests (type I sums of squares) were used for the factor selection. Data were not transformed because they met the assumptions of normality and homoscedasticity (Zuur et al., 2009).

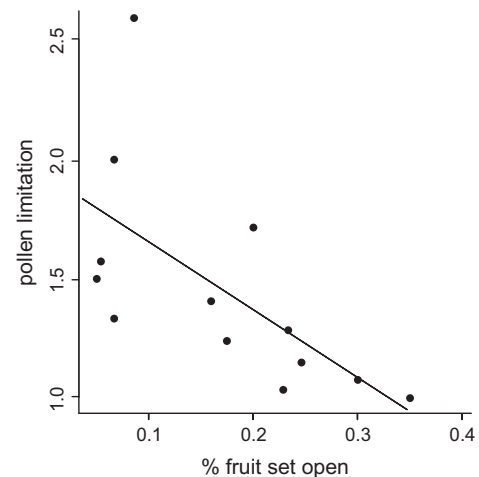
### 3. Results

Fruit set was lower 9 weeks after flowering (representing yield) than 4 weeks after flowering due to fruit abscission and fruit loss, but data sets were highly correlated (Spearman rank correlation:  $R = 0.95$ ,  $p < 0.001$ ,  $n = 88$  trees in six orchards). Bagged flowers (wind pollination only) produced less than 3% of the fruits produced by open-pollinated flowers (insect and wind pollination), showing a strong positive impact of insect pollination on fruit set (Fig. 1). When taking all sites together, open-pollinated and hand-pollinated flowers did not differ in fruit set (linear mixed-effects model:  $F_{2,58} = 55.2$ ,  $p < 0.001$ ,  $n = 88$  trees; post-hoc test: bagged vs. open or hand:  $p < 0.001$ , hand vs. open:  $p = 0.7$ ). However, pollen limitation – calculated as the quotient of fruit set after hand pollination and fruit set after open pollination – significantly decreased with increasing fruit set of open pollinated flowers, indicating high pollen limitation when fruit set was low, but low or no pollen limitation when fruit set was high (linear mixed-effects model:  $F_{1,17} = 8.6$ ,  $p = 0.009$ ,  $n = 24$  tree pairs in six orchards). The same patterns was found after exclusion of pollen limitation values below 1 (i.e. hand pollination < open pollination), which might have been resulted from experimental failure (Fig. 2; linear mixed-effects model:  $F_{1,7} = 7.5$ ,  $p = 0.029$ ,  $n = 13$  tree pairs in five orchards).

A total number of 712 bees was recorded during the sampling period, 165 bees in cherry trees (60 min per orchard) and 547 bees on flowers between tree lines (transects; 45 min per orchard). About two thirds of all bees were honey bees (67% in trees, 64% on transects). Virtually all wild bees were solitary bees, because social bumblebees were in the stage of colony establishment at the time of cherry flowering, and only single queens were present.



**Fig. 1.** Mean fruit set ( $\pm$ SE) for the pollination treatments. WP = wind pollination, OP = open pollination, HP = hand pollination. Different letters indicated significant differences ( $P < 0.5$ ). Results are from mixed effects models with the random factors orchard and plot, nesting trees within plots and plots within orchards.



**Fig. 2.** Relationship between pollen limitation (fruit set after hand pollination divided by fruit set after open pollination) and fruit set after open pollination. Data points represent pairs of hand-pollinated and open-pollinated trees where fruit set after hand pollination was higher than fruit set after open pollination. High values of pollen limitation in pairs with low fruit set of the open-pollinated tree indicate that low fruit set resulted from pollination deficits rather than from limitation of other resources. In linear mixed-effect models, pairs were nested within orchard by adding a random factor to the model.

Primitive-eusocial *Lasioglossum* bees were not found in cherry trees. The most common wild bee genus was *Andrena*, which provided 92% of wild bees in trees and 88% on transects. Bumblebees were represented by 4 individuals in trees and 15 individuals on transects.

Fruit set of cherry trees was enhanced by wild bee visitation in trees (direct effects, Table 1, Fig. 3a), but not by honeybee visitation ( $p > 0.3$ , Fig. 3b). The predictor wild bee visitation could be replaced by the proportion of high-diversity bee habitats (indirect effects, Table 1, Fig. 3c), because wild bee visitation in trees increased with the proportion of high-diversity bee habitats in the landscape in 1 km radius (Table 1, Fig. 3d). An increase in the proportion of high-diversity bee habitats from 20% to 50% resulted in an increase of 150% in fruit set (Fig. 3c). Wild bee densities on ground transects increased with flower cover on ground transects (Table 1,  $y = 98.08x + 0.15$ ), but neither flower cover nor transect densities of wild bees nor of honey bees were found to affect flower visitation in the trees or fruit set (all  $p > 0.2$ ).

### 4. Discussion

#### 4.1. Impact of insect pollination on cherry yield

We assessed the effects of local and landscape-scale factors on bee abundances, flower visitation and fruit set in cherry orchards. Bagged flowers (wind pollination only) produced only 3% of the fruits produced by open-pollinated flowers (insect and wind pollination). Our data show that pollination of sweet cherry strongly depends on insect pollination. Klein et al. (2007) classified sweet cherry as greatly dependent on pollinators based on the assumption that fruit set declines 40–90% in the absence of pollinators. Our data suggest that the decline in the studied cultivars is even higher and justifies categorization as essentially dependent on pollinators (sensu Klein et al., 2007: production reduction by  $\geq 90\%$ ).

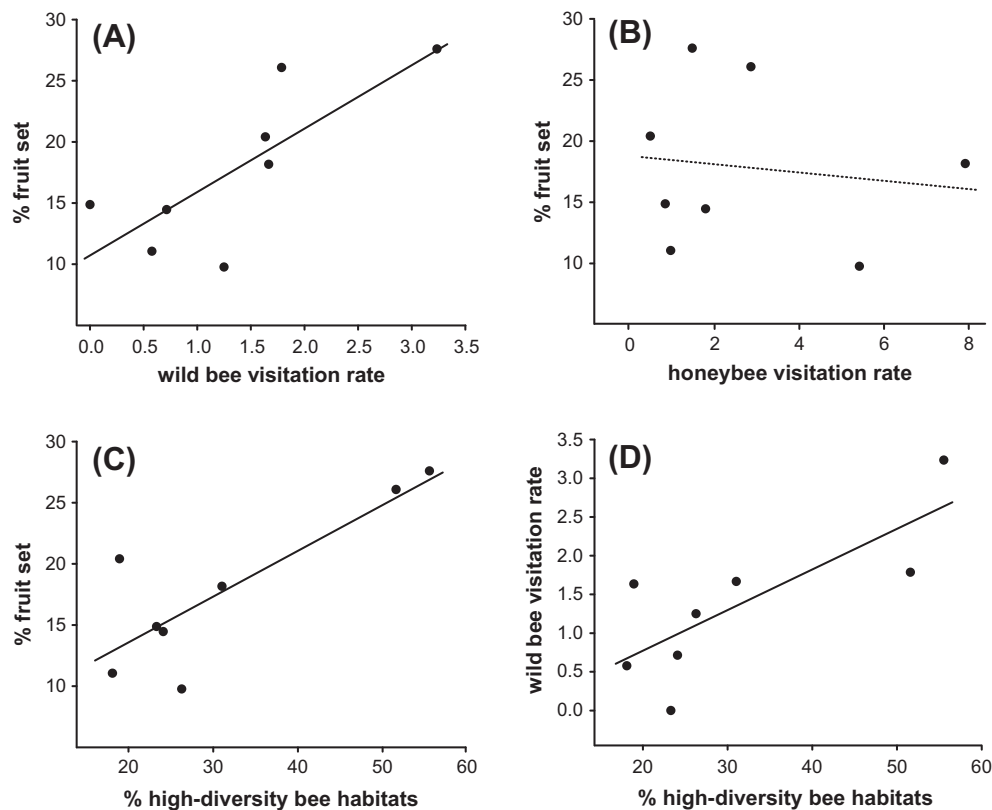
Pollen limitation was high when fruit set was low, but low or absent when fruit set was high. The negative relationship between fruit set and pollen limitation indicates that low fruit set was not



**Table 1**

Results from linear regression models assessing effects of bee visitation on fruit set (direct effects), and effects of high-diversity bee habitats in 1 km radius and of flower cover on ground transects on fruit set (indirect effects), bee visitation in cherry trees, and bee densities on ground transects ( $n = 8$  orchards).

Response variable	Fixed factor	Slope	$R^2$	$F_{1,6}$	$p$
Fruit set (direct effects)	Wild bee visitation (+)	0.05	0.54	9.1	0.024
Fruit set (indirect effects)	High-diversity habitats (+)	0.37	0.68	13.0	0.001
Wild bee visitation	High-diversity habitats (+)	5.25	0.53	8.9	0.024
Honey bee visitation	No model				
Wild bee transect densities	Flower cover (+)	98.1	0.43	6.3	0.046
Honey bee transect densities	No model				



**Fig. 3.** Effect of (A) wild bee visitation, (B) honeybee visitation, and (C) proportion of high-diversity bee habitats in 1 km radius on fruit set in cherry trees. (D) Effect of the proportion of high-diversity bee habitats in 1 km radius on wild bee visitation. Visitation rates are number of individuals per 1000 flowers in 60 min. Solid lines indicate significant regressions ( $p < 0.05$ ), dashed lines non-significant regressions ( $p > 0.05$ ). See Table 1 for the results from linear regression models with fruit set and visitation rates averaged per orchard.

subject to a lack of resources limiting fruit set, but was caused by a lack of pollinators (Burd, 1994).

#### 4.2. Pollination efficiency of wild bees vs. honey bees

Although honeybee abundances were twice as high as wild bee abundances, fruit set was significantly enhanced by wild bees, but not by honey bees, suggesting that wild bees are more efficient in pollinating sweet cherry than honey bees. To date, there has been only anecdotal evidence that solitary bees are more efficient in cherry pollination than honeybees provided by a study lacking replicates, controls and data on visitation rates (Bosch et al., 2006).

A higher pollination efficiency of solitary bees compared to honey bees can have three causes: more efficient pollen deposition, greater exchange of pollen between compatible cultivars, and indirect effects by interspecific interactions with honey bees.

In blueberry, solitary *Andrena* bees deposit four times as much pollen per visit as honey bees (Javorek et al., 2002). While solitary bees feed on nectar and collect pollen at the same time, thereby

getting in contact with the reproductive flower parts, nectar-collecting honey bees have less contact to the reproductive parts resulting in reduced pollen deposition. Also in watermelon, the number of deposited pollen grains increases with wild bee visitation, but not with honeybee visitation (Winfree et al., 2007). However, results from one crop can hardly be transferred to another crop because pollination efficiency of honey bees strongly depends on flower morphology (Wilson and Thomson, 1991). Besides pollen deposition per visit, the number of flowers visited per individual and day, and the amount of pollen that an individual removes from the system often differ between pollinator species (Ivey et al., 2003).

To enhance fruit set in a crop that depends on cross-pollination by a compatible cultivar, the frequent exchange of pollen between different plants, which, for example, grow in different rows, is even more important than a high amount of deposited pollen. Honey bees rarely change between fruit-tree rows during one foraging trip (Free and Spencer-Booth, 1966), and the solitary bee *Osmia cornuta* have been found to move more often between almond-tree

rows than nectar- or pollen-collecting honey bees (Bosch and Blas, 1994). However, movement frequencies differ among years and crops (Bosch and Blas, 1994; Vicens and Bosch, 2000), and have not been studied for honey bees vs. solitary bees in cherry. The frequency of movements between flowers or tree rows can be enhanced by interspecific interactions between wild bees and honey bees. Almost all honey bees visiting sunflower heads moved to another flower head when they had an interaction with a wild bee (Carvalho et al., 2011; Greenleaf and Kremen, 2006). That way, high wild bee abundances could contribute to pollination even if pollen deposition by wild bees was low.

We assume that the effect of honeybee pollination was masked by the higher pollination efficiency of wild bees in our study. Honey bees might have the potential to replace wild bees to a certain extent when the latter are rare. We found 15% fruit set even in the orchard where no wild bees were recorded. An increase of fruit set in that orchard compared to wind pollination might either indicate that honey bees were able to contribute to pollination and fruit set or that wild bees were present but that abundances were too low to be detected in our study. However, we can conclude from our data that honeybee abundances in the study orchards were not high enough to enhance cherry yield to values that were possible with contributions by wild bees.

#### 4.3. Landscape and local effects on flower visitation and fruit set

Our study provides new evidence that the absence of high-diversity habitat translates via reduced wild bee visitation into a decline in fruit set of an insect-pollinated crop. An increase in the proportion of high-diversity bee habitats in a 1 km radius from 20% to 50% resulted in an increase of fruit set by 150%. In a meta-analysis, fruit set of pollinator-dependent crops decreased by 16% at 1 km distance from the next natural habitat (Garibaldi et al., 2011). Further recent evidence for a positive effect of natural habitat on fruit set in crops comes from mango (Carvalho et al., 2010) and sunflower (Carvalho et al., 2011), whereas wild bees in watermelon and canola were found to be not significantly affected by natural habitats (Winfree et al., 2008; Arthur et al., 2010). Natural high-diversity habitats benefit wild bees by providing a variety of nesting sites and alternative flower resources beyond the short mass-flowering periods of crop plants (Krewenka et al., 2011; Roulston and Goodell, 2011). Our findings show that the increase of wild bee visitation and fruit set with the proportion of high-diversity habitats is linear up to a proportion of 55% of high-diversity habitats in the landscape circle. This is particularly remarkable because the study region is characterized by relatively high proportions of high-diversity habitats (>18%) compared to many other agricultural regions in central Europe. We conclude from our results that farmers cannot maximize yield by only ensuring small amounts of natural or semi-natural habitats in the surrounding of their orchards, and we expect that a decline in high-diversity habitats have an even stronger negative effect on yield in regions where the proportion of high-diversity habitats is already lower than in our study region.

Our third hypotheses stating that additional flower resources in the orchard reduce cherry fruit set was refuted, because we did not find an effect of flower cover on visitation in trees or on fruit set. This result contradicts the expectation of Somerville (1999) who recommended to farmers the removal of the ground vegetation because it might compete with cherry flowers for pollinators. Based on our results, there is no reason for removing flowering ground vegetation, which strongly enhanced bee abundances on the ground transects. Additional flower resources might help to build up pollinator populations in agricultural landscapes by providing valuable food resources in addition to the short-term flowering crops (Carvalho et al., 2011).

#### 4.4. Conclusion

Our results show that pollination services by wild bees in cherry surpassed pollination by honey bees. Higher visitation of cherry flowers by wild bees did not only enhance initial fruit set but also the economically important final cherry yield. Since wild bee visitation increased with the proportion of high-diversity bee habitats in the surrounding landscape, the conservation of high-diversity bee habitat is needed to enhance gratis pollination service provided by wild bees, and thereby, the farmers' yield. Farmers who pay attention to have their orchards surrounded by high-diversity bee habitats should gain a monetary advantage over competitors without high-diversity bee habitats in the surrounding. Based on our data, cherry yield cannot be maximized in our region if farmers rely on honeybee pollination only. Honey bees did not contribute significantly to the explanation of the great pollination differences between sites, although farmers had paid attention to having honey-bee colonies in the surrounding of their orchards.

#### Acknowledgements

We are very grateful to the farmers for their participation in the project. AH acknowledged funding from the Helmholtz Association (VH-NG-247), from the European Community's Seventh Framework Programme (FP7/2007–2013) under Grant Agreement No. 244090, STEP Project (Status and Trends of European Pollinators, [www.step-project.net](http://www.step-project.net)) and – together with TT – the German Science Foundation (Deutsche Forschungsgemeinschaft DFG).

#### References

- Aebi, A., Vaissière, B.E., vanEngelsdorp, D., Delaplane, K.S., Roubik, D.W., Neumann, P., 2012. Back to the future: *Apis* vs. non-*Apis* pollination. *Trends Ecol. Evol.* 72, 142–143.
- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G., Pavlik, B., Tepedino, V., Torchio, P., Walker, S., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12, 8–17.
- Arthur, A.D., Li, J., Henry, S., Cunningham, S.A., 2010. Influence of woody vegetation on pollinator densities in oilseed *Brassica* fields in an Australian temperate landscape. *Basic Appl. Ecol.* 11, 406–414.
- Bosch, J., Blas, M., 1994. Foraging behavior and pollination efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). *Appl. Entomol. Zool.* 29, 1–9.
- Bosch, J., Kemp, W., Trostle, G., 2006. Bee population returns and cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera: Megachilidae). *J. Econ. Entomol.* 99, 408–413.
- Breeze, T.D., Bailey, A.P., Balcombe, K.G., Potts, S.G., 2011. Pollination services in the UK: how important are honeybees? *Agric. Ecosyst. Environ.* 142, 137–143.
- Burd, M., 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Bot. Rev.* 60, 83–139.
- Carvalho, L.G., Seymour, C.L., Veldtman, R., Nicolson, S.W., 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *J. Appl. Ecol.* 47, 810–820.
- Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S., Nicolson, S.W., 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* 14, 251–259.
- FAOSTAT, 2010. <<http://www.faostat.fao.org>> (accessed March 2012).
- Free, J.B., 1993. *Insect Pollination of Crops*. Academic Press London, UK.
- Free, J.B., Spencer-Booth, Y., 1966. The foraging behaviour of honey-bees in an orchard of dwarf apple trees. *J. Hort. Sci. Biotechnol.* 39, 78–83.
- Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68, 810–821.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalho, L.G., Chacoff, N.P., Dudenhoefter, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyorgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072.
- Gathmann, A., Tschamtkke, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71, 757–764.

- Ghazoul, J., 2005. Buzziness as usual? Questioning the global pollination crisis. *Trends Ecol. Evol.* 20, 367–373.
- Greenleaf, S.S., Kremen, C., 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Nat. Acad. Sci. USA* 103, 13890–13895.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biometr. J.* 50, 346–363.
- Ivey, C., Martinez, P., Wyatt, R., 2003. Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). *Am. J. Bot.* 90, 214–225.
- Javorek, S., Mackenzie, K., Vander Kloet, S., 2002. Comparative pollination effectiveness among bees (Hymenoptera : Apoidea) on lowbush blueberry (Ericaceae : Vaccinium angustifolium). *Ann. Entomol. Soc. Am.* 95, 345–351.
- Klein, A.-M., Vaissiere, 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. Roy. Soc. B – Biol. Sci.* 274, 303–313.
- Krewenka, K., Holzschuh, A., Tscharntke, T., Dormann, C.F., 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biol. Conserv.* 144, 1816–1825.
- Larson, B.M.H., Barrett, S.C.H., 2000. A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society* 69, 503–520.
- Lech, W., Malodobry, M., Dziedzic, E., Bieniaszand, M., Doniec, S., 2008. Biology of sweet cherry flowering. *J. Fruit Ornam. Plant Res.* 16, 189–199.
- Ollerton, J., Price, V., Armbruster, W.S., Memmott, J., Watts, S., Waser, N.M., Totland, O., Goulson, D., Alarcón, R., Stout, J.C., Tarrant, S., 2012. Overplaying the role of honey bees as pollinators: a comment on Aebi and Neumann (2011). *Trends Ecol. Evol.* 27, 141–142.
- 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 Development Core Team, 2011 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, Ochieng, A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11, 499–515.
- Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56, 293–312.
- Somerville, D., 1999. Honey bees in cherry and plum pollination, NSW Agriculture Agnote DA1 126.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Vicens, N., Bosch, J., 2000. Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' apple. *Environ. Entomol.* 29, 235–240.
- Westrich, P., 1990. Die Wildbienen Baden-Württembergs, vol. 1, second ed. Ulmer Stuttgart, Germany.
- Williams, N.M., Thomson, J.D., 2003. Comparing pollinator quality of honey bees (Hymenoptera: Apidae) and native bees using pollen removal and deposition measures. In: Stickler, K., Cane, J.H. (Eds.), For nonnative crops, whence pollinators of the future? Entomological Society of America Lanham, Maryland, USA, pp. 163–179.
- Wilson, P., Thomson, J., 1991. Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* 72, 1503–1507.
- Winfree, R., Williams, N.M., Dushoff, J., Kremen, C., 2007. Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* 10, 1105–1113.
- 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.
- Young, H.J., Young, T.P., 1992. Alternative outcomes of natural and experimental high pollen loads. *Ecology* 73, 639–647.
- Zhang, W., Ricketts, T.H., Kremen, C., Carney, K., Swinton, S.M., 2007. Ecosystem services and dis-services to agriculture. *Ecol. Econ.* 64, 253–260.
- Zuur, F.A., Ieno, E.N., Walker, N., Saveliev, A.A., 2009. Mixed Effects Models and Extensions in Ecology with R (Statistics for Biology and Health), first ed. Springer, New York.