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Pollination efficiency and foraging behaviour of honey bees and non-*Apis* bees to sweet cherry

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Abstract

1 Crop pollination generally increases with pollinator diversity and wild pollinator visitation. To optimize crop pollination, it is necessary to investigate the pollination contribution of different pollinator species. In the present study, we examined this contribution of honey bees and non-*Apis* bees (bumble bees, mason bees and other solitary bees) in sweet cherry.

2 We assessed the pollination efficiency (fruit set of flowers receiving only one visit) and foraging behaviour (flower visitation rate, probability of tree change, probability of row change and contact with the stigma) of honey bees and different types of non-*Apis* bees.

3 Single visit pollination efficiency on sweet cherry was higher for both mason bees and solitary bees compared with bumble bees and honey bees. The different measures of foraging behaviour were variable among non-*Apis* bees and honey bees. Adding to their high single visit efficiency, mason bees also visited significantly more flower per minute, and they had a high probability of tree change and a high probability to contact the stigma.

4 The results of the present study highlight the higher pollination performance of solitary bees and especially mason bees compared with bumble bees and honey bees. Management to support species with high pollination efficiency and effective foraging behaviour will promote crop pollination.

Keywords *Apis mellifera*, bumble bees, fruit set, *Osmia cornuta*, *Prunus avium*, solitary bees.

Introduction

The western honey bee (*Apis mellifera*) is the principal insect species used for pollination of agricultural crops. Yield of crops that depend on insect mediated pollination increases with pollinator diversity and crop visitation rates of wild pollinating insects, whereas honey bee visitation rates only show a significant positive relationship in three of the 22 studied crops (Garibaldi *et al.*, 2013). Currently, consensus about clear management strategies to optimize insect mediated crop pollination is lacking (Isaacs *et al.*, 2017; Rollin & Garibaldi, 2019). To optimize crop pollination, it is necessary to identify which pollinator species contribute significantly to the pollination of certain crops. Consequently, when these efficient pollinator species are identified, targeted measures in and around crop fields can be implemented to support these species and their corresponding pollination service (Garibaldi *et al.*, 2014).

Different parameters can determine the pollination performance of a pollinator species. First, at the level of a single flower, pollination efficiency and flower handling can indicate which pollinator species a flower visit will result in a successful pollination of that flower. In several studies, the pollination efficiency on a single visit basis for certain wild bee species was found to be higher compared with that of honey bees in certain crop systems (Kendall & Smith, 1975; Kuhn & Ambrose, 1984; Bosch & Blas, 1994; Vicens & Bosch, 2000a; Monzon *et al.*, 2004; Greenleaf & Kremen, 2006; Zhang *et al.*, 2015). In addition, compared with honey bees, both pollen deposition on the stigma and the growth of the pollen tube were found to be more favourable for certain wild pollinators in a variety of crops (Willmer *et al.*, 1994; Thomson & Goodell, 2001; Javorek *et al.*, 2002; Winfree *et al.*, 2007; Brittain *et al.*, 2013; Zhang *et al.*, 2015). However, honey bees are also found to enhance pollen deposition in a number

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of crop systems compared with certain wild pollinators (Rader *et al.*, 2009; Wist & Davis, 2013; Sáez *et al.*, 2014). It is clear that this pollination efficiency depends on the specific crop and also on the pollinating insects for which this comparison is made. Clearly, the deposition of compatible pollen and a morphological match between the crop flower and the pollinating insect are important aspects for understanding the pollination efficiency of a pollinator species (Free, 1993; Blüthgen & Klein, 2011; Garibaldi *et al.*, 2015). In a variety of Rosacea fruit crops, certain solitary bees (*Osmia* spp. and *Andrena* spp.) also handle flowers more effectively compared with honey bees because these solitary bees make more contact with the floral stigma to facilitate pollen deposition (Free, 1993; Bosch & Blas, 1994; Vicens & Bosch, 2000a; Monzon *et al.*, 2004; Martins *et al.*, 2015). The foraging behaviour of pollinators is another aspect to keep in mind when considering pollination performance of different pollinator species. For fruit crops that depend on insects to facilitate cross-pollination, compatible pollinizer cultivars are planted interspersed in the same rows or in different rows of the commercial cultivar (e.g. almond, apple, sweet cherry, strawberry, etc.). In such cropping systems, it is vital that pollinating insects visit flowers of different plants to exchange compatible pollen and successfully pollinate flowers. In these crop systems, bumble bees and mason bees have been shown to change trees or plants within and between rows more often compared with honey bees (Bosch & Blas, 1994; Willmer *et al.*, 1994; Vicens & Bosch, 2000a; Monzon *et al.*, 2004; Brittain *et al.*, 2013). Visitation rate is another important behavioural parameter because it determines the number of flowers a certain species can pollinate per unit of time. Visitation rate has been studied in a number of crops systems and the parameter is variable between honey bees and non-*Apis* bees and also among non-*Apis* bees there are clear differences (Chagnon *et al.*, 1993; Vicens & Bosch, 2000a; Thomson & Goodell, 2001; Javorek *et al.*, 2002; Rader *et al.*, 2009; Martins *et al.*, 2015).

In addition to the abundance of honey bees, the community of pollinating insects in agricultural crops is often very diverse (Winfree *et al.*, 2011). With the increasing importance of sustainable crop pollination, it is necessary to investigate the pollination performance of the entire community of pollinating insects to develop management guidelines for crop pollination (Garibaldi *et al.*, 2013). Previous studies in sweet cherry have highlighted the contribution of wild pollinators to sweet cherry production (Holzschuh *et al.*, 2012; Eeraerts *et al.*, 2017; Eeraerts *et al.*, 2019b). These studies revealed that bumble bees and different solitary bee species (*Andrena* spp. and *Osmia* spp.) make up a significant part of the pollinator community next to the ever-present honey bees. However, most studies in Rosacea fruit crops that investigate the pollination performance of bees only compare honey bees with one species of bumble bee or solitary bee (mainly *Osmia* spp.) (Kuhn & Ambrose, 1984; Bosch & Blas, 1994; Willmer *et al.*, 1994; Vicens & Bosch, 2000a; Monzon *et al.*, 2004; Brittain *et al.*, 2013; Zhang *et al.*, 2015). To assess the potential role of wild pollinators of sweet cherry, we compared the pollination performance of honey bees and different non-*Apis* bees in sweet cherry orchards (*Prunus avium*). Sweet cherry can serve as a model system for other fruit crops that rely on cross pollination and that have a similar flowering phenology (almond, apple, pear, etc.). Pollination performance was measured as foraging behaviour (flower visitation rate, probability of tree change, probability of row change and contact between pollinator and the stigma) and as pollination efficiency (fruit set of flowers that received only one visit). We compared these pollination performance parameters between different types of bees: bumble bees (*Bombus* spp.), honey bees, the European orchard bee (*Osmia cornuta*) and other solitary bees (mainly mining bees, *Andrena* spp.).

Materials and methods

Study system

The study was conducted on a commercial multi-crop farm in Baardegem, Belgium, which contains a 1-ha sweet cherry orchard. All sampling was conducted in 2018 and 2019 on the sweet cherry cultivars Kordia and Regina, which are the most abundant cultivars in the study orchard (11 out of 20 rows) and in European and North-American sweet cherry production in general (Quero-Garcia *et al.*, 2017). Given the excellent quality of the cherries, Kordia and Regina are the two cultivars of the most commercial interest. Yet, these two cultivars are highly dependent on insect mediated pollination because they are self-incompatible, and they require pollen from a compatible cultivar to set fruit (Lech *et al.*, 2008). Sweet cherry has hermaphroditic flowers with an open flower and so the stigma and the anthers are easily accessible to pollinators and, as such, pollen and nectar are easy to collect. To facilitate cross-pollination, fruit growers plant compatible pollinizer cultivars in separate rows of the commercial cultivars or in between the rows of the commercial cultivars (one pollinizer tree for every four or five commercial trees). Other cultivars within the study orchard are Vanda, Canada Giant, Earlise, Bellise, Merchant, Sylvia and Lapins (all cultivars are planted in full rows; see Supporting information, Fig. S1). The blooming period of Kordia overlaps partially with that of Regina and the blooming period of Sylvia overlaps with both the blooming periods of both Kordia and Regina. Vanda, Canada Giant, Earlise, Bellise, Merchant and Lapins have flowering periods earlier than that of Kordia and Regina. Depending on the weather and the cultivar, it takes approximately 8–12 weeks for the cherries to develop and ripen. No manual/chemical thinning like in other fruit crops (apple, pear) is applied in sweet cherry cultivation. Flowers/unfertilized fruit fall occurs 2–3 weeks after bloom and, after these 3–4 weeks, fruit set stabilizes and the reduction as a result of natural abortion of cherries is very low (Hedhly *et al.*, 2007).

Previous studies in 2015 and 2017 indicated that a pollinator community rich in bumble bees and solitary bees (*Andrena* spp.) occurred in this specific orchard (Eeraerts *et al.*, 2017; Eeraerts *et al.*, 2019b). It is common practice to place honey bee hives in sweet cherry orchards during full bloom, and so honey bees were also placed in the study orchard (three honey bee hives in 2018 and five hives in 2019). Each year, two standard bumble bee hives were also placed in the centre of the orchard. In addition, we placed eight trap nests for mason bees in and around the study orchard. Both in 2018 and in 2019, we released 1500 cocoons of the European orchard bee at the start of blooming of the first sweet cherry cultivars (Earlise and Bellise), which is approximately 7–10 days and 10–14 days before full bloom of Kordia and Regina, respectively.

Data collection

To measure single flower visit (SFV) pollination efficiency, branches of approximately 1 m were covered before bloom in fine mesh bags with 1-mm^2 openings to prevent insect visitation. When open flowers were available, the branches were uncovered and watched continuously until a bee visited a certain flower once. Only legitimate flower visits were considered (i.e. when a flower visiting bee was extracting nectar and/or pollen). If a bee landed on a flower to rest or sunbathe, this was not considered as a legitimate flower visit and this flower was removed. One person uncovered and observed not more than three or four branches at the same time. After a flower was visited once, this specific flower was labelled, the type of bee that visited the flower was recorded (bumble bee, honey bee, mason bee or other solitary bee) and the flower was again covered with the fine mesh bag to prevent subsequent insect visitation. Bee specimens were identified in the field by the authors (M. Eeraerts and R. Vanderhaegen) using the identification key of Falk *et al.* (2017). Fruit set was measured 8 weeks after bloom. Fruit set is defined as the probability that a single visited flower became a red cherry or not. The relationship between fruit set and the type of pollinator allows to infer the SFV pollination efficiency per type of pollinator.

Data were collected on four characteristics of foraging behaviour of bees: visitation rate, the probability of a tree change, the probability of row change and contact with the flower stigma. For the first three characteristics, transects were walked at a slow pace between rows of cherry trees that were in full bloom. When a foraging bee was encountered, the type of pollinating insect of this individual was determined (bumble bee, honey bee, mason bee or other solitary bee). The encountered bee was followed and every time it visited another flower this was noted. Different movements were distinguished as the subsequent flower could be (i) a flower on the same tree; (ii) a flower on another tree in the same row, or (iii) a flower on another tree in another row that was in full bloom. Again, only legitimate flower visits were taken into account (see above). Every foraging bee was followed as long as possible until it was out of sight, and another foraging bee was looked for. The length of time for which every foraging bee was followed was recorded with a chronometer. Foraging bees had to visit at least three flowers to be included in the dataset. Data concerning whether a certain pollinating bee touched the stigma were collected simultaneously with the SFV data collection. More specifically, when a certain bee visited a sweet cherry flower, a record was made of whether this bee touched the stigma of that flower.

All of the data concerning pollinating insects (SFV experiment and foraging behaviour experiment) were collected in the orchard during full bloom of sweet cherry cultivars Kordia and/or Regina in April 2018 and April 2019. A schematic overview of the orchard and the locations of the transects is provided in the Supporting information (Fig. S1). To ensure adequate bee activity, pollinator surveys were conducted between 10.00 h and 18.00 h, only when weather conditions were suitable for bee sampling in spring (no or calm wind, no rain and temperatures above 13 °C).

Statistical analysis

Differences between pollinator type (bumble bee, honey bee, mason bee or solitary bee) on SFV pollination efficiency were analyzed with a generalized linear model. SFV pollination efficiency is defined as the probability that a flower became a red cherry or not (a flower becomes a cherry = 1 or no cherry = 0). SFV pollination efficiency was modelled with a binomial distribution and a complementary log–log link function (Zuur *et al.*, 2009). For SFV pollination efficiency, pollinator type, year and cultivar were included in the generalized linear model as fixed factors. For pollinator visitation rate, differences between pollinator type were analyzed with a linear model. Visitation rate is defined as the mean number of flowers a pollinator specimen visited per minute. Visitation rate was checked for outliers and for normality and a log transformation was applied to improve normality. For visitation rate, the model included pollinator type and year as fixed factors. We used a generalized linear mixed effect model to study differences between the probability of tree changes (PTC) and the probability of row changes (PRC) when foraging between different pollinator types. A single specimen receives a scoring each time it changes a flower. For PTC, a flower change on the same tree and a flower change to another tree in a different row are marked as zero, and only a flower change to a tree in the same row is recorded as one. For PRC, a flower change on a tree and between trees in the same row are zero, and only a flower change to another tree in a different row is recorded as one. Both PTC and PRC were modelled with a binomial distribution with a complementary log–log link function (Zuur *et al.*, 2009). For PTC and PRC, the mixed model included pollinator type and year as fixed factors and pollinator ID as random factor. The effect of pollinator type on stigma contact (contact with the stigma = 1 and no contact = 0) was analyzed with a generalized linear model. Here, the model included pollinator type and year as fixed factor.

For each of the above parameters measuring pollination performance, the general model was tested with pollinator type as a fixed factor and the above mentioned fixed (and random factor) included in the model. This was followed by testing a model for

Table 1 The amount of red cherries (*n_rc*) and the amount single visited flowers (*n*) and the corresponding percentage single flower visit (SFV) pollination efficiency per pollinator type and per year on sweet cherry

Type of pollinator	Year	*n_rc/n*	SFV efficiency (%)
Bumble bees	2018	0/16	0.0
	2019	0/14	0.0
Honey bees	2018	1/27	3.7
	2019	14/152	9.2
Mason bees	2018	5/22	22.7
	2019	18/70	27.1
Solitary bees	2018	4/27	14.8
	2019	31/112	27.7

Table 2 The number of observations and corresponding mean value for the different parameters measuring foraging behaviour per pollinator type and per year on sweet cherry

		Visitation rate		Tree change		Row change		Stigma contact	
Type of pollinator	Year	*n*	Mean (flowers per min)	*n_tc/n*	Mean (%)	*n_rc/n*	Mean (%)	*n_sc/n*	Mean (%)
Bumble bees	2018	27	10.4	21/625	3.4	14/625	2.2	4/12	33.3
	2019	66	13.1	70/1355	5.2	23/1355	1.7	7/11	63.6
Honey bees	2018	46	6.1	17/563	3.0	4/563	0.7	16/20	80.0
	2019	46	5.4	25/687	3.6	6/687	0.9	50/62	80.6
Mason bees	2018	25	12.0	11/285	3.9	4/285	1.4	20/21	95.2
	2019	53	9.7	43/716	6.0	13/716	1.8	29/30	96.7
Solitary bees	2018	10	4.4	7/84	8.3	0/84	0.0	13/17	76.5
	2019	23	4.6	7/173	4.0	2/173	1.2	64/72	88.9

For visitation rate, the total amount of observed specimens (*n*) and the mean value is given. For tree changes, row changes and stigma contact the number of observations (*n*) and the number of successful tree changes (*n_tc*), the amount of successful row changes (*n_rc*), the amount of successful stigma contacts (*n_sc*) and the mean values are given.

each possible comparison between every specific pollinator type combination with pollinator type as a fixed factor and the above mentioned fixed (and random factor) again included in the model. All analyses were performed in R, version 3.5.1 (R Development Core Team, 2018).

Results

In total, 92 and 348 flowers received only one visit of a certain pollinator type for the SFV experiment in 2018 and 2019, respectively. In 2018, this resulted in 11 pollinated flowers or red cherries; in 2019, this was 63 red cherries. The total number of flowers visited and the corresponding SFV pollination efficiency per type of pollinator and per year are shown in Table 1. For the SFV experiment, 85% of the solitary bees were species of the genus *Andrena* spp. (i.e. three specimens of *A. dorsata*, seven of *A. carantonica*, 30 of *A. fulva* and 78 of *A. haemorrhoa*). Other solitary bees could clearly be distinguished as bees of the genus *Andrena* spp. and *Lassgioglossum* spp. But, unfortunately, they could not be caught to be identified to species level. The bumble bee visits consisted of 19 bumble bees workers of the commercial nest (*Bombus terrestris*) and 11 bumble bee queens (two specimens of *B. pascuorum*, two of *B. pratorum*, one of *B. lapidarius* and six of *B. terrestris* agg.). Distinction between commercial worker *B. terrestris* and wild *B. terrestris* agg. (‘agg.’ refers to the *Bombus terrestris/lucorum* complex) queens could be made based on the size (big queens, wingspan > 15 mm). At the time of sampling, wild *B. terrestris* agg. were still in the stage of foraging queens and wild workers were not yet present. In total, the foraging behaviour was described for 296 foraging bees, accounting for 4488 flower visits; 201 flowers were visited for which a change to a tree in the same row was executed and 66 flower visits for which a change to a different row was executed. The mean time a foraging bee was followed was 127 ± 123 s (mean ± sd). For the stigma contact, 245 observations were made in total during the SFV experiment, for which 203 specimens effectively made contact with the flower’s stigma. The number of bees for which any of the four different foraging parameters has been described is listed per pollinator type and per year in Table 2.

Table 3 Generalized linear model (calculated F-statistic and *P*-value) of the effect of pollinator type (B, bumble bees; H, honey bees; M, mason bees; S, solitary bees), cultivar and year on single flower visit (SFV) pollination efficiency

		SFV efficiency	
Pollinator type comparison	Factor	*F*	*P*
B – H	Pollinator type	1.53	0.22
	Cultivar	0.36	0.55
	Year	2.68	0.10
B – M*	**Pollinator type**	**10.99**	**< 0.01**
	Cultivar	3.05	0.06
	Year	0.31	0.57
B – S*	**Pollinator type**	**6.65**	**0.01**
	Cultivar	0.76	0.19
	Year	0.64	0.43
H – M*	**Pollinator type**	**17.82**	**< 0.001**
	Cultivar	2.23	0.14
	Year	2.72	0.10
H – S*	**Pollinator type**	**9.10**	**< 0.01**
	Cultivar	3.92	0.05
	Year	1.12	0.29
M – S	Pollinator type	1.71	0.19
	Cultivar	1.15	0.28
	Year	2.52	0.11

An asterisk (*) is placed next to the best performing bee in the case of a significant pollinator type effect.

Pollinator type significantly affected SFV pollination efficiency, whereas year and cultivar had no effects (generalized linear model, pollinator type: $F_{3,434} = 9.46$, $P < 0.001$, year: $F_{1,434} = 2.31$, $P = 0.13$ and cultivar: $F_{1,434} = 1.16$, $P = 0.28$). SFV pollination efficiency was higher for both mason bees and solitary bees compared with bumble bees and honey bees (Table 3). The linear model showed that pollinator type significantly affected flower visitation rate, whereas year showed no effect (pollinator type: $F_{3,291} = 79.8$, $P < 0.001$ and year: $F_{1,291} = 0.03$, $P = 0.38$) (Fig. 1). The exact differences between pollinator types are shown in Table 4. Both bumble bees and mason bees visited more flowers per minute compared with solitary bees and honey bees, with the latter also visiting more flowers per minute than solitary bees. No significant differences were

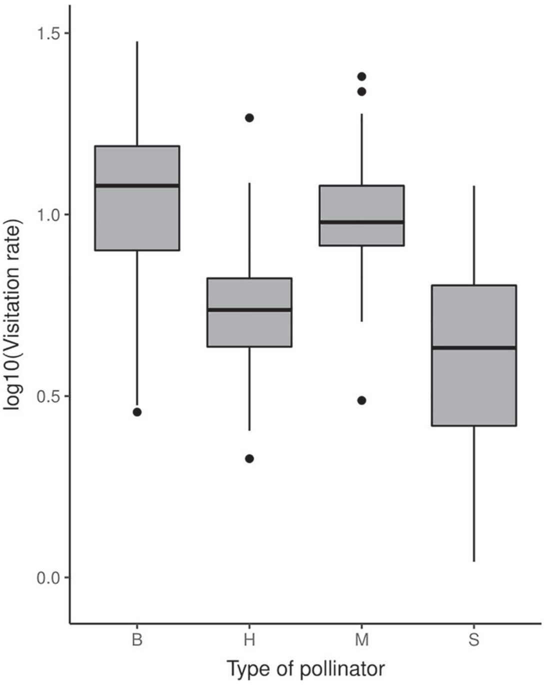

Figure 1 Visitation rate (log transformed values) for different pollinator types (B, bumble bees; H, honey bees; M, mason bees; S, solitary bees) on sweet cherry blossoms.

detected for the probability of tree changes (PTC, pollinator type: $z = 1.7$, $P = 0.24$ and year: $z = 2.0$, $P = 0.06$) and the probability of row changes (PRC, pollinator type: $z = 1.3$ $P = 0.18$ and year: $z = 0.1$, $P = 0.94$) with pollinator type and year as fixed factors. However, as a result of differences between pollinator types concerning PTC and PRC in a previous study (Eeraerts *et al.* n.d.), we tested the multiple comparison. With these comparisons, we did detect a higher PTC for mason bees compared with honey bees and a higher PRC for bumble bees compared with honey bees (Table 4). Contact with the flower's stigma was affected by pollinator type but not by year (generalized linear mixed effect model, pollinator type: $F_{3,240} = 10.1$, $P < 0.001$ and year: $F_{1,240} = 2.3$, $P = 0.13$). More specifically, honey bees, mason bees and solitary bees contacted the flower's stigma more often than bumble bees, and mason bees also made more stigma contact compared with honey bees (Table 4).

Discussion

In addition to the presence of pollinizer cultivars, the degree of self-incompatibility of the commercial cultivar and resource availability (weather, nutrients, etc.), crop yield also depends on the pollinator community composition (Melathopoulos *et al.*, 2015; Tamburini *et al.*, 2019). Similar to many other fruit crops, sweet cherry is self-incompatible and requires insect-mediated cross pollination. Here, an effective pollinator should visit a lot of flowers of different trees in an orchard and it should contact the stigma of these flowers to deposit the pollen of compatible cultivars that it carries on its body. On the level of a single flower, the SFV efficiency is an essential measure for ranking the pollination performance of different types of bees (Spears Jr, 1983; King *et al.*, 2013). However, the measures describing the foraging behaviour can be useful in combination with SFV efficiency data to scale up from a single visit at the flower level (Ne'Eman *et al.*, 2010). Based on our results, the European orchard bee (*Osmia cornuta*) emerges as very effective pollinator species for sweet cherry pollination (Tables 1 and 3). The high SFV efficiency of mason bees might be explained by the extent that the species touches the stigma of the flower it visits (Tables 2 and 4). Next to its high SFV efficiency, mason bees also have a high visitation rate and change trees within the same row more often than honey bees (Fig. 1 and Tables 2 and 4). With these results, our study confirms previous studies that have concluded the superior pollination performance of mason bees (*Osmia* spp.)

Table 4 Test statistics for the different multiple comparisons the different foraging behaviour parameters (VR, flower visitation rate per minute; PTC, probability of tree change; PRC, probability of row change; SC, stigma contact between the pollinator and the flower's stigma) between the different years and the different pollinator types (B, bumble bees; H, honey bees; M, mason bees; S, solitary bees)

		VR		PTC		PRC		SC	
Pollinator type comparison	Factor	*F*	*P*	*z*	*P*	*z*	*P*	*F*	*P*
B* – H$^{\#}$	Type	**136.9**	**< 0.001***	1.6	0.11	**2.5**	**0.02***	**10.59**	**< 0.01$^{\#}$**
	Year	0.4	0.53	1.6	0.10	0.7	0.47	0.89	0.35
B – M*	Type	3.6	0.07	0.7	0.49	0.5	0.62	**35.14**	**< 0.001***
	Year	0.1	0.91	**2.1**	**0.04**	0.6	0.54	1.93	0.17
B* – S$^{\#}$	Type	**103.8**	**< 0.001***	0.4	0.66	1.3	0.21	**19.23**	**< 0.001$^{\#}$**
	Year	1.2	0.28	1.0	0.34	0.7	0.49	3.3	0.05
H – M*	Type	**124.2**	**< 0.001***	**2.04**	**0.04***	1.6	0.12	**6.72**	**0.01**
	Year	**7.7**	**0.01**	1.3	0.18	0.3	0.73	0.02	0.88
H* – S	Type	**15.6**	**< 0.001***	1.6	0.11	0.1	0.97	1.12	0.29
	Year	1.8	0.19	0.1	0.96	0.4	0.70	0.82	0.37
M* – S	Type	**101.6**	**< 0.001***	0.3	0.96	−1.0	0.32	1.13	0.29
	Year	**4.5**	**0.04**	0.3	0.62	0.7	0.50	0.82	0.37

Model type for VR multiple comparison: linear model, model type for PTC and PRC multiple comparison: generalized linear mixed effects model and model type for SC multiple comparison: generalized linear model. *F* and *z* are the calculated test statistic and *P* = *P*-value.
A asterisk (*) or hash ($^{\#}$) symbol and the corresponding *P*-value is placed next to the best performing bee in the case of a significant pollinator type effect.

compared with honey bees (*Apis mellifera*) in Rosacea fruit tree crops (apple: Kuhn & Ambrose, 1984; almond: Bosch & Blas, 1994; apple: Vicens & Bosch, 2000a; pear: Monzon *et al.*, 2004; almond: Brittain *et al.*, 2013). In addition to this high pollination efficiency and intense foraging activity, mason bees are also active in poor weather conditions (Vicens & Bosch, 2000b). With respect to this combination, mason bees can be regarded as very efficient pollinators of sweet cherry and other similar Rosacea crops that bloom early in spring, such as almond, apple, etc. (Bosch & Kemp, 2002; Bosch *et al.*, 2006). Next to mason bees, other solitary bees also had a high SFV pollination efficiency, although solitary bees have the lowest visitation rate (Tables 2 and 4). Yet, this high SFV pollination efficiency implies that, if these species are abundant in certain fields, they will contribute significantly to crop yield despite a lower visitation rate.

The results of the present study also show that the direct contribution of bumble bees to pollination of sweet cherry is very low at the single flower level, with a SFV pollination efficiency of zero (Tables 1 and 3). This can possibly be explained by the low contact that bumble bees make with the stigma (Tables 2 and 4). In apple and peach, however, the pollination efficiency of bumble bees was found to be higher compared with honey bees (Thomson & Goodell, 2001; Zhang *et al.*, 2015). Our result indicating a very low pollination efficiency for bumble bees can be explained by the flower size; flowers of sweet cherries are just over half the size than flowers of apple and peach (Godet, 1985). Because bumble bees are large bees, this might create a morphological mismatch between pollinator and flower (but see Blüthgen & Klein, 2011; Garibaldi *et al.*, 2015). In addition, similar to honey bees, bumble bees also collect pollen in their tibial corbicula and moisten this pollen with nectar. Doing so, they carry less dry pollen on their bodies that is available for pollination compared with solitary bees (Free, 1993; Martins *et al.*, 2015). Moreover, it has been found that this grooming behaviour inactivates pollen from being available for pollination (Parker *et al.*, 2015). However, with their intense foraging behaviour (high visitation rate and high probability of row change), bumble bees might contribute indirectly to crop pollination through direct interactions with other pollinators, where the latter change trees or rows after such an interaction (Greenleaf & Kremen, 2006; Carvalheiro *et al.*, 2011).

The direct contribution of individual honey bees on the other hand is lower compared with mason bees and solitary bees and they also visit fewer flowers per minute compared with mason bees and bumble bees (Fig. 1 and Tables 1 to 4). Despite high rates of stigma contact of approximately 80%, honey bee SFV pollination efficiency was only 3.7% and 9.2% in 2018 and 2019, respectively. As previously noted, the intense grooming behaviour of honey bees involves them mixing pollen with nectar and transfering this pollen to the tibial corbicula, and so there is only a small amount of dry 'free pollen' on their body available for pollen deposition (Martins *et al.*, 2015; Parker *et al.*, 2015). Contact with the stigma is therefore less likely to lead to the deposition of pollen on the stigma. By contrast, mason bees and other solitary bees collect and carry dry pollen with the abdominal corbicula, the femoral corbicula, the basitarsal scopa or the propodeal corbicula (Michener, 1999). This possibly explains the differences in SFV pollination efficiency between bumble bees and honey bees on the one hand and mason bees and solitary bees on the other hand. We do not doubt that managed honey bees are a useful and even necessary tool for growers to improve the yield of many pollination dependent crops. It is rather a matter of determining the optimal honey bee density for specific crops (Isaacs *et al.*, 2017; Rollin & Garibaldi, 2019). This is an important area for future research because high densities of honey bees sometimes can displace wild pollinators form crops, which might reduce the total pollination service (Lindström *et al.*, 2016; Mallinger *et al.*, 2017).

A limitation of the present study is that it was only conducted at one single farm and that the effects of the surrounding landscape might alter the performance of pollinators. The main trends of our results are in line with previous research and can be regarded as a general conclusion for the pollination performance for the different species at hand. We argue that landscape context will mainly influence the diversity of the pollinator community (Garibaldi *et al.*, 2011; Kennedy *et al.*, 2013) and it is mainly this diversity that can influence the pollination performance of different pollinators. Indeed, Woodcock *et al.* (2013) did not find pollination performance (visitation rate, stigma contact, row changes and pollen collection) of honey bees and wild pollinators to be influenced by landscape structure. However, empirical evidence about the effects of pollinator diversity on pollination performance in crops is scarce (but see Brittain *et al.*, 2013). We are currently conducting a separate study aiming to directly investigate the influence of pollinator diversity on pollination performance in sweet cherry.

Despite the significant contribution of wild pollinator abundance and pollinator diversity for pollinator dependent crops worldwide (Garibaldi *et al.*, 2013; Kleijn *et al.*, 2015; Rader *et al.*, 2016), only the abundance of a few pollinator species is commonly managed for greater yield. Our results suggest that both the direct contribution to crop pollination (i.e. SFV efficiency) and the foraging behaviour are different among different pollinator species. More specifically, the present study shows that especially mason bees and solitary bees can be very efficient pollinators. As such, we elaborate on previous studies that investigate pollination efficiency and foraging behavior in crops (an aspect that is very important in crops that rely in cross-pollination to set fruit) by taking more than two types/species of pollinator into account. Indeed, the pollinator communities in many fruit crops comprise a significant amount of different solitary bees (*Andrena* spp., *Osmia* spp., *etc*.), bumble bees and other pollinator species, such as hoverflies for example (Chagnon *et al.*, 1993; Martins *et al.*, 2015; Alomar *et al.*, 2018). Our results emphasize the importance of investigating the pollination performance of different pollinator species instead of comparing honey bees with one species of pollinator. The potential of different non-*Apis* bees to provide full pollination at the crop level will ultimately depend on their abundance and on the total diversity of the pollinator community on each specific farm. The identification and implementation of targeted and cost-effective measures to promote wild pollinators may be a good way of enhancing and optimizing the crop yield in sweet cherry.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Overview of the orchard layout and experimental set-up. Solid red lines indicate the locations of the transect for data collection of specific foraging characteristics: visitation rate, probability of tree change and the probability of row change. The zone in the dashed square indicates the zone in which data were collected for the single flower visit pollination efficiency and for the stigma contact. Cultivars are planted in full rows except for row 1 and row 20. Numbers of each row indicate the cultivars in that row: 1 – Earlise +6 trees of Bellise; 2 – Lapins; 3 – Vanda; 4 – Summit; 5 – Merchant; 6 – Canada Giant; 7 – Kordia; 8 – Regina; 9 – Sylvia; 10 – Regina; 11 – Kordia; 12 – Kordia; 13 – Sylvia; 14 – Regina; 15 – Regina; 16 – Kordia; 17 – Kordia; 18 – Regina; 19 – Regina; and 20 – Merchant +6 trees of Earlise.

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