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Wild bees are less abundant but show better pollination behaviour for sweet cherry than managed pollinators

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Abstract

Pollinating insects provide pollination services to many crop species, including sweet cherry (*Prunus avium* L.), and this can be delivered by both managed and wild pollinators. Managed pollinators are often used to pollinate a range of fruit crops, but increasingly the role of wild insects is being studied. However, the importance of pollinator species depends on their relative abundance and pollination effectiveness, which depends on their foraging activity and their variability throughout the day. In this study, insect visitors of blossoms were observed in commercial sweet cherry orchards to explore abundance, diversity and pollination foraging behaviour of different insect pollinator groups throughout the day. A total of 1,174 pollinators from 31 different species were recorded visiting cherry blossoms over 2 years, of which 71.0% of total visits were by managed pollinators (western honeybee, *Apis mellifera* L. and buff-tailed bumblebee, *Bombus terrestris* L.) compared to 29.0% by wild pollinators. On average, solitary bees visited a sweet cherry blossom for the longest duration (20.7 (± 2.0 SE) seconds), whereas wild queen bumblebees visited the greatest number of flowers per minute (mean of 19.0 (± 1.3 SE)). As both these pollinator groups contacted cherry stigmas more often and moved more frequently between tree rows than managed bees and hoverflies, they are more likely to facilitate cross-pollination. The different pollinator groups also showed variation in behavioural parameters throughout the day, but less variation was recorded when all pollinator groups were considered altogether. This suggests diverse pollinator communities might be expected to provide a more stable pollination service to sweet cherry. This study demonstrates that whilst cherry blossoms were more frequently visited by managed pollinators, wild solitary bee and bumblebee behaviours are likely to be more effective at enhancing pollination in sweet cherry orchards, which, in turn, might lead to increased yields.

KEYWORDS

nectar and pollen, orchard, pollinator diversity, pollinator management, stigma contact, sustainability

1 | INTRODUCTION

Sweet cherry (*Prunus avium* L.) is an important pollinator-dependent crop, cultivated globally, with many cultivars being self-incompatible (Lech et al., 2008). Thus, insect pollinators are required for cross-pollination (compatible pollen delivery) to achieve marketable yields (Eeraerts, Smagghe, et al., 2020; Koumanov & Long, 2017). To reduce the risk of insufficient pollination, managed insect pollinators are routinely used in commercial sweet cherry orchards (Koumanov & Long, 2017). The western honeybee (*Apis mellifera* L.) is most commonly used, but can have a limited pollination capacity (Güler & Dikmen, 2013). In recent years, this has driven research on sweet cherry pollination and the associated pollinating insects. After much focus on honeybees, some studies have compared fruit set and yield achieved by using alternative managed pollinators, including bumblebees such as the buff-tailed bumblebee (*Bombus terrestris* L.) (Kwack et al., 2012; Sergeevna, 2018) or solitary bees including *Osmia lignaria* Say (Bosch & Kemp, 1999; Bosch et al., 2006) and *O. bicornis* (L.) (Ryder et al., 2020). These different groups of managed pollinators showed higher efficiency than honeybees leading to greater yields, except for Kwack et al. (2012) where fruit set was similar and Ryder et al. (2020) where solitary bees were investigated to supplement wild bees.

Wild pollinators, in turn, have also been investigated as pollinators of sweet cherry, with a focus on the dependence of wild pollinators on semi-natural habitats and influences at the landscape scale on commercial fruit set (Eeraerts et al., 2017; Schuepp et al., 2014). Landscape context has been associated with wild pollinator abundance and diversity, since it affects pollinator resources including nesting sites and the availability of additional forage (Eeraerts, Piot, et al., 2021; Eeraerts, Van Den Berge, et al., 2021; Kay et al., 2020). Other studies demonstrated greater pollination services, improved fruit set and greater yields in sweet cherry orchards when wild pollinator diversity was enhanced even in the presence of honeybees (Eeraerts et al., 2019; Holzschuh et al., 2012). This indicated that some wild species can be more effective than honeybees. Thus, the importance of wild pollinators and the impacts of their decline on sweet cherry production have been considered (Reilly et al., 2020).

Due to the potentially significant contribution of wild pollinating insects to sweet cherry pollination, their diversity and abundance have been investigated globally (Dar et al., 2018; Güler & Dikmen, 2013; Güler et al., 2015; Rosas-Ramos et al., 2020; Sharma et al., 2016; Tepedino et al., 2007). The identification of wild insect pollinators that enhance pollination services, by complementing or replacing honeybees under potential pollinator management approaches, has therefore been well documented. In contrast, the pollination behaviour and effectiveness of different pollinator groups, such as bumblebees (Eeraerts, Smagghe, et al., 2020), hoverflies (Bakshi et al., 2018), or multiple groups, including solitary bees (Abrol, 2005; Eeraerts, Vanderhaegen, et al., 2020), in sweet cherry orchards is less well studied. However, Eeraerts, Vanderhaegen, et al. (2020) explored the efficiency of single visits by pollinators and revealed greater pollination efficiency with managed *O. cornuta*

(Latreille) and wild solitary bees compared to managed bumblebees and honeybees.

The study of pollination behaviour and effectiveness is important since the successful transfer of compatible pollen between flowers depends on the behaviour of pollinating insects (Eeraerts, Vanderhaegen, et al., 2020). Pollination foraging behaviour (henceforth pollination behaviour) thus contributes to pollination success (i.e. stigmatic pollen deposition) (Ne'eman et al., 2010). Pollination behaviour includes the time spent visiting flowers, stigma contact, visitation rate (flowers visited per minute) (Vicens & Bosch, 2000) and movement between trees or tree rows for cross-pollination (Brittain, Williams, et al., 2013). Pollination behaviour can also differ between groups, for example wild bee pollinators move more frequently between tree rows than honeybees (Eeraerts, Smagghe, et al., 2020). Compared to solitary bees, honeybees make fewer stigma contacts in apple blossoms and as a consequence their pollination efficacy is lower (Vicens & Bosch, 2000), although this is compensated for by higher visitation rates (Garratt et al., 2016; Vicens & Bosch, 2000). Additionally, the diversity and abundance of wild pollinators can influence pollination behaviour, and therefore pollination efficiency, particularly of honeybees (Brittain, Williams, et al., 2013; Carvalheiro et al., 2011; Eeraerts, Smagghe, et al., 2020).

Pollinators also respond differently to environmental factors (e.g. temperature, humidity and wind speed), directly affecting pollinator abundance and behaviour throughout the day (Chang et al., 2016; Sgolastra et al., 2016). A diverse wild pollinator community can therefore underpin successful crop pollination because some wild pollinators are more active in poor weather conditions compared to honeybees (Brittain, Kremen, et al., 2013; Földesi et al., 2016; Güler & Dikmen, 2013). Pollination by a diverse community of wild pollinators also provides a more resilient service in the context of climate change (Bartomeus et al., 2013; Senapathi et al., 2021). Different pollinator species can be active before and after flowering time if flowering is either advanced or delayed, then a diverse pollinator community increases the likelihood of overlap between crop flowering and the activity of its pollinators (Bartomeus et al., 2013; Senapathi et al., 2021). Environmental factors also have indirect effects on pollination by altering pollen, nectar and water concentrations in the flower, directly influencing the number of visits to blossoms (Corbet et al., 1979; Kearns & Inouye, 1993). For example, honeybees may prefer nectar collection, but lower nectar quality might induce a preference for pollen foraging (Arenas & Kohlmaier, 2019). Collection of either nectar or pollen by bees might also determine how they land on the flower and thus contact the stigma (Bakshi et al., 2018; Martins et al., 2015). Consequently, crop pollination and crop yield can be affected by environmental factors (Tuell & Isaacs, 2010). This is particularly important for sweet cherry because the crop blooms early in the season under variable weather conditions (Fadón et al., 2015), and for short periods, typically lasting 2–5 weeks if different early, mid and late flowering cultivars are combined (Christensen, 1996).

Given the reliance of fruit growers on managed pollinators, sub-optimal pollination may result in an ongoing threat to the economic viability of sweet cherry production and other pollinator-dependent

crops. To reduce the risk of pollination deficits in sweet cherry, it is important to understand the potential contribution of different managed and wild pollinator groups by evaluating their pollination behaviour throughout the day. This might enable a targeted approach to the management of this service, either through the deployment of appropriate managed species or by promoting wild pollinator species through agri-environment actions (Albrecht et al., 2020; Isaacs et al., 2017).

Consequently, the aims of this study were to (a) investigate the abundance, diversity and pollination behaviour of different pollinator groups as a proxy for pollination effectiveness in sweet cherry orchards and (b) compare how this was influenced by time of the day.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

Five sites in the West Midlands, UK, were selected for the study conducted in 2018 and 2019. Three sites were located in Herefordshire and two in Staffordshire (minimum distance between sites of 2.8 km apart). At each of the five sites, two orchards were used, and three different alleyways were selected in each orchard. For each alleyway, one row of trees containing the cultivar Kordia (self-incompatible) was selected for study. As all five sites included self-incompatible cultivars, there were also two to six alternating cultivars every two or three rows. To account for any potential edge effects due to the use of polytunnels (protective plastic covers) (Hall et al., 2020), four Kordia cherry trees in each of the 30 rows of trees were selected for study at approximately 10, 29, 48 and 67 m from the orchard edge. In total, 120 trees were used for data collection each year. All five sites were managed for the commercial production of sweet cherry; four of the sites were covered with polytunnels during the cherry blossom, whilst one in Herefordshire (Site 3) was covered after blossom. In the eight orchards at the four sites where polytunnels were used, growers used a combination of honeybees and buff-tailed bumblebees as managed pollinators. However, at Site 3 (two non-covered orchards), a combination of honeybees and buff-tailed bumblebees was used in one of its orchards, whilst in the second one, only honeybee hives were deployed.

2.2 | Pollinator surveys

To investigate the abundance, diversity and pollination behaviour of insects visiting cherry blossoms, stationary timed visitation surveys were conducted (Garratt et al., 2014). Each of the 120 cherry trees was observed for 4 min. Surveys were conducted once the cherry blossoms started to open (balloon stage) until the end of the cherry blossom; stages 59–69 on the BBCH scale (Fadón et al., 2015). The cherry blossom period (flowering phenology) varied between years, from 23 April to 14 May in 2018, and from 7 April to 1 May in 2019. Surveys were conducted every day during the blossom period,

except when raining or when temperatures (measured with a Kestrel 3500 weather meter) were below 8°C. Average temperatures of 18.1°C (± 0.3 SE) were recorded in 2018 and 17.4°C (± 0.2 SE) in 2019. To investigate whether time of day (Pisanty et al., 2016) affected the abundance and behaviour of pollinating insects, surveys for each tree row (all four trees) took place within discrete 30-min time periods between 10:30 and 17:00 hr. All trees were surveyed at least five times each year alternating which trees were observed between time periods to avoid temporal bias.

Pollination behaviour was determined by recording visitation time (duration of pollinator visit per flower), visitation rate (flowers visited per minute) and stigma contact (Eeraerts, Vanderhaegen, et al., 2020; Vicens & Bosch, 2000). Due to the importance of cross-pollination in sweet cherry, the location of the tree subsequently visited (flying behaviour for cross-pollination) was recorded according to one of four categories: (a) 'stayed on tree': the pollinator was caught for identification or remained on the tree; (b) 'same tree row': the pollinator moved to a tree in the same row; (c) 'adjacent tree row': the pollinator moved to the adjacent row; and (d) 'flew away': the pollinator flew away. The part of the pollinator (head, sternum and legs) that made contact with the stigma and what substance (pollen, nectar or both) the insect was feeding on (pollinator feeding) were also recorded (Eeraerts, Vanderhaegen, et al., 2020; Vicens & Bosch, 2000). Percentage values for each body part contacting the stigma were calculated, considering only the pollinators that made contact with the stigma for each pollinator group. Due to pollinators making contact with more than one body part during the same visit, total values can exceed 100%.

Pollinators were identified to species (catching them if necessary for confirmation under a microscope) and then grouped into five pollinator groups: (a) honeybees, (b) buff-tailed bumblebees, (c) wild bumblebees, (d) solitary bees and (e) hoverflies. Honeybees and buff-tailed bumblebees were used by growers as managed pollinators, whilst wild bumblebees, solitary bees and hoverflies were specified as wild pollinator groups. As the cherry blossom occurs in early spring, queen buff-tailed bumblebees were recorded under the wild bumblebee group, whereas worker buff-tailed bumblebees were assumed to have originated from the commercial bumblebee boxes and were recorded under the buff-tailed bumblebee group. We used bumblebee size to distinguish queens from workers and colour markings for queens in the field (Falk, 2015).

2.3 | Statistical analysis

Data were analysed with generalized linear mixed-effect models (package lme4; Bates et al., 2015) using the software R (version R-3.6.1; R Core Team, 2019). Generalized linear mixed-effect models with negative binomial error structures (function =GLMER.NB) were used to analyse pollinator abundance, visitation time and visitation rate. Stigma contact, pollinator feeding and flying behaviour for cross-pollination were analysed using generalized linear mixed-effect models with binomial error structures (function =GLMER,

family = binomial). Each parameter was the response variable for its global model, whilst pollinator group, survey time and their interaction were specified as fixed effects (global models without the interaction were also studied). To analyse differences in pollinator abundance and behaviour according to time of day, the 12 time periods were grouped into four categorical variables: late morning (10:30–12:00 hr), early afternoon (12:00–13:30 hr), late afternoon (14:00–15:30 hr) and early evening (15:30–17:00 hr). Trees, tree rows and orchards were specified as nested random effects (*response variable* ~ *pollinator group* × *time period* + (*random: orchard/tree row/tree*)).

For each model, the relative importance of the model terms (fixed effects) was calculated by taking an information theoretic approach using the Akaike information criterion (AIC) (Burnham & Anderson, 2002). Each of the fixed effects was individually removed from the global model, and the difference in AIC values was calculated for the reduced model (ΔAIC). $\Delta\text{AIC} > 2$ was considered to have a substantial level of empirical support (Burnham & Anderson, 2002). Tukey's *post hoc* tests (multcomp package; Hothorn et al., 2008) were subsequently used for pairwise comparisons between pollinator groups and time periods. Spearman's rank correlation coefficients were calculated to investigate relationships between feeding behaviours and stigma contact.

3 | RESULTS

Across all stationary timed visitation surveys conducted in 2018 and 2019, a total of 1,174 pollinating insects were recorded. This included 535 honeybees, 298 buff-tailed bumblebees, 115 wild bumblebees (all queens except for two *B. pratorum* (L.) and one *B. hypnorum* L.), 134 solitary bees, and 92 hoverflies (Table S1). This was made up of 31 pollinator species; the western honeybee, 7 bumblebees (including buff-tailed bumblebee, which was recorded as managed and wild), 9 solitary bees and 14 hoverflies. Three solitary bees and five hoverflies were caught for confirmation under a microscope. Managed pollinators (honeybees and buff-tailed bumblebees) were recorded more frequently than wild pollinators with 833 (71.0%) individuals visiting cherry blossoms compared to 341 (29.0%), respectively. Wild *B. terrestris* (buff-tailed bumblebee) and *B. lapidarius* (L.) were the most frequently recorded wild bumblebees visiting the greatest number of blossoms, contributing 3.8% and 3.0% of the total records, respectively. Of the solitary bees, the genus *Andrena* Fabricius made up 96.3% of all solitary bee records, with *A. haemorrhua* (Fabricius) (3.7% of the total visits) and *A. cineraria* (L.) (2.6%) being the most frequently recorded species. The hoverfly *Eristalis pertinax* (Scopoli) contributed 3.3% of all recorded pollinator visits. The sum of these six species (managed and wild) represented 87.5% of all visitation records.

Pollinator abundance differed between pollinator groups but was consistent throughout the day (Table 1). Of the 683 surveys where pollinators were recorded visiting cherry blossoms, honeybees were recorded on 327 surveys, followed by buff-tailed bumblebees (253), then solitary bees (118), wild bumblebees (102) and

hoverflies (83). Consequently, on average, honeybees were the most abundant (Figure 1A). Despite some variation in abundance at different times of day for each pollinator group, none was significantly affected (Figure S1A).

3.1 | Visitation time (duration of pollinator visit per flower)

The time that pollinators spent on a single flower differed between pollinator groups (Table 1). On average, solitary bees and hoverflies spent more time per flower than other pollinator groups at 20.7 (± 2.0 SE) and 14.8 (± 3.3) seconds per flower, respectively (Figure 1B). In contrast, wild bumblebees spent the shortest time at 4.8 (± 0.3) seconds per blossom. Although some pollinator groups showed variation in the time spent on cherry blossoms (Figure S1B), the duration of visits for all pollinator groups combined was not significantly affected by the time of day surveyed (Table 1).

3.2 | Visitation rate (flowers visited per minute)

Visitation rates differed according to pollinator group and were not consistent throughout the day, with a significant interaction between pollinator groups and time of day found (Table 1). Wild bumblebees visited significantly more cherry flowers per minute, with a mean of 19.0 (± 1.3) (Figure 1C). In contrast, solitary bees visited an average of 6.9 (± 0.7) flowers per minute. Overall, Tukey tests did not support significant effects of the time of day on visitation rates for all pollinators combined, but solitary bees visited significantly more flowers per minute in early afternoon compared to late morning (Tukey test: $Z = 2.98$, $p < 0.05$; Figure S1C).

3.3 | Stigma contact

The number of times pollinators contacted the stigma varied between pollinator groups but was not significantly affected by the time of day surveyed (Figure S1D; Table 1). When visiting cherry blossoms, wild bumblebees and solitary bees contacted the stigma more frequently than the other pollinator groups (Figure 1D). Solitary bees also contacted stigmas with more body parts than the other pollinator groups, particularly with the head (Table 2). Hoverflies contacted the stigma on almost every visit, primarily with the legs, whilst both managed pollinator species contacted the stigma a similar number of times, predominantly with the legs and sternum.

3.4 | Pollinator feeding on pollen and/or nectar

The feeding behaviour of pollinators differed between pollinator groups (Table 1). Buff-tailed bumblebees and solitary bees had similar feeding behaviours and about 30% were recorded collecting nectar,

TABLE 1 Comparisons in the generalized linear mixed-effect models using the Akaike information criterion (AIC). Fixed factors are removed in each reduced model to determine significant differences. Models include degrees of freedom (df) and the difference between models (Δ AIC). Δ AIC > 2 was accepted to be significantly different

Parameter	Omitted terms in the models	df	AIC	Δ AIC
Pollinator abundance	Global model		2,182.1	
	Pollinator group	4	2,208.6	26.5
	Time of day surveyed	3	2,180.3	-1.8
Visitation time	Global model		5,535.2	
	Pollinator group	4	5,760.0	224.8
	Time of day surveyed	3	5,536.9	1.7
Visitation rate	Global model		6,269.8	
	Pollinator group: Time of day surveyed	12	6,277.3	7.5
Stigma contact	Global model		1,149.6	
	Pollinator group	4	1,171.4	21.8
	Time of day surveyed	3	1,151.4	1.8
Feeding on nectar	Global model		1,272.9	
	Pollinator group	4	1,366.2	93.3
	Time of day surveyed	3	1,272.1	-0.8
Feeding on pollen	Global model		899.8	
	Pollinator group	4	1,171.5	271.7
	Time of day surveyed	3	894.0	-5.7
Feeding on both	Global model		1,380.5	
	Pollinator group	4	1,443.9	63.4
	Time of day surveyed	3	1,378.8	-1.7
Stayed on tree	Global model		894.9	
	Pollinator group	4	913.9	19.0
	Time of day surveyed	3	890.4	-4.5
Same tree row	Global model		1,189.8	
	Pollinator group	4	1,260.3	70.5
	Time of day surveyed	3	1,197.8	8.0
Adjacent tree row	Global model		928.5	
	Pollinator group	4	960.9	32.4
	Time of day surveyed	3	929.5	1.0
Flew away	Global model		1,280.5	
	Pollinator group	4	1,311.7	31.2
	Time of day surveyed	3	1,281.3	0.8

Note: Values in bold are significant.

whilst nectar was collected by ~50% of wild bumblebees and honeybees (Figure 2). In contrast, hoverflies behaved markedly different from the bee groups, with most feeding exclusively on pollen (89.0% (± 3.5) of the visits). Time of day did not significantly affect the feeding behaviour of pollinators (Figures S2A–C; Table 1). However, honeybees tended to collect only nectar during late morning (Figure S2A), whilst hoverflies tended to forage on pollen during late morning and early evening compared to early and late afternoon (Figure S2B).

A negative correlation was found between feeding on nectar and stigma contact for all pollinators combined and, particularly, for honeybees, solitary bees and hoverflies (Table S2). However, the correlation between feeding on both nectar and pollen, and stigma

contact was positive for all pollinators combined and, in particular, for honeybees, buff-tailed bumblebees and solitary bees. Buff-tailed bumblebees also showed a negative correlation between feeding on pollen and stigma contact.

3.5 | Flying behaviour for cross-pollination

The location of the tree subsequently visited after the tree being surveyed significantly differed between pollinator groups (Table 1). Around 45% of honeybees tended to forage in the same tree row. Also, trees in the same row were subsequently visited by ~30% of

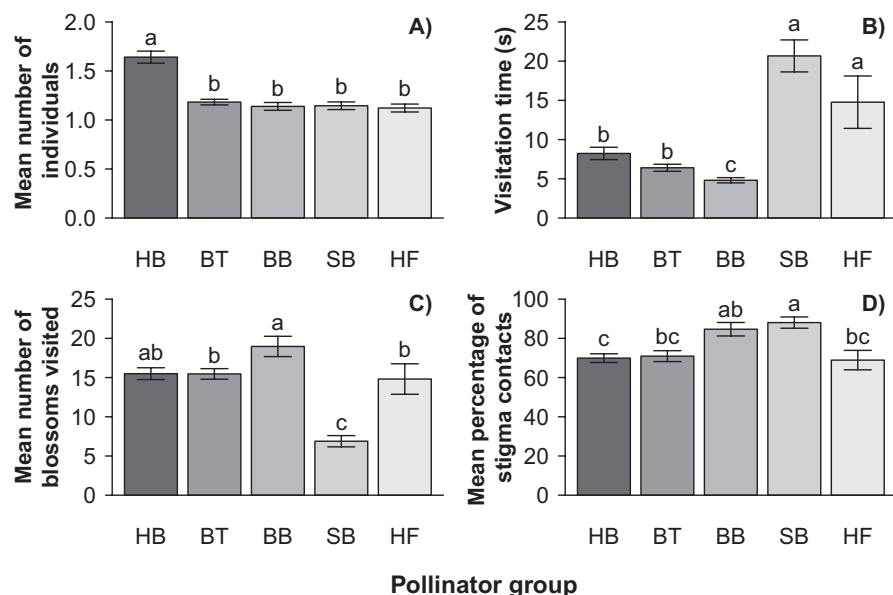


FIGURE 1 (A) Mean number (\pm SE) of pollinator individuals, (B) mean time (\pm SE) spent (s) per individual cherry blossom (visitation time), (C) mean number (\pm SE) of cherry blossoms visited per minute (visitation rate) and (D) mean percentage (\pm SE) of pollinators contacting the stigma of cherry blossoms according to pollinator group. The same superscript letters indicate no significant differences according to the Tukey test ($p > 0.05$). BB, wild bumblebee; BT, buff-tailed bumblebee; HB, honeybee; HF, hoverfly; SB, solitary bee

TABLE 2 Percentage (\pm SE) of three different pollinator body parts that contacted the stigma. Due to the potential for pollinators to contact the stigma with more than one body part during the same visit, total values can exceed 100%

Pollinator group	Head contact %	Leg contact %	Sternum contact %
Honeybee	29.8 (\pm 1.5)	71.7 (\pm 1.6)	71.8 (\pm 1.6)
Buff-tailed bumblebee	35.1 (\pm 1.5)	69.6 (\pm 1.6)	74.9 (\pm 1.6)
Wild bumblebee	51.7 (\pm 1.5)	72.2 (\pm 1.6)	79.0 (\pm 1.6)
Solitary bee	67.1 (\pm 1.5)	91.4 (\pm 1.7)	80.5 (\pm 1.7)
Hoverfly	17.5 (\pm 1.5)	94.4 (\pm 1.6)	15.3 (\pm 1.6)

buff-tailed bumblebees and wild bumblebees, which had similar flying behaviour. However, ~25% of buff-tailed bumblebees, wild bumblebees and solitary bees visited trees in adjacent rows, which were less likely to be visited by honeybees and hoverflies. Solitary bees and hoverflies also showed a similar behaviour, with ~40% flying away within the orchards after leaving the surveyed tree (Figure 3).

Based on all pollinators combined, survey time (Figure S2D–G) influenced whether a tree in the same tree row was visited, but not when pollinators stayed on the surveyed tree, visited a tree in the adjacent tree row or flew away (Table 1). In general, pollinators tended to visit trees in the same tree row during late morning (Tukey test: $Z = -2.62$, $p < 0.05$) and early afternoon (Tukey test: $Z = -3.22$, $p < 0.01$) compared to early evening. In particular, buff-tailed bumblebees frequently visited more trees in the same tree row in late morning compared to early evening (Tukey test: $Z = -3.21$, $p < 0.01$).

4 | DISCUSSION

In this study, pollination behaviour differed between pollinator groups, and due to the behaviour of wild bees, it suggests they are likely to be more effective pollinators of sweet cherry than managed bees. The

greater amount of time solitary bees spent on individual cherry blossoms and the greater number of blossoms visited by wild bumblebees (almost all queens), coupled with more frequent stigma contacts, makes wild bees potentially highly effective pollinators of cherry blossoms. The large size of queen bumblebees facilitated stigma contact, whilst solitary bees spending more time on individual blossoms ensured a greater number of stigma contacts with more of their body parts, consequently increasing the likelihood of pollen being deposited on the stigma (Willmer et al., 2017). Furthermore, pollen grains are more often incidentally attached on solitary bees when collecting pollen or nectar due to the greater time spent on individual flowers (Woodcock et al., 2013). Grains attached on the head or sternum are dry and loose and, as a result, are more likely to be deposited on the stigma (Woodcock et al., 2013). Moreover, pollen collected by solitary bees on scopae and by wild bumblebees on the sternum is also fully available for pollination, rather than being collected, moistened and compacted into the meta-tibial corbiculae (pollen baskets), making it less available for pollination (Parker et al., 2015).

Importantly, solitary bees and wild bumblebees, along with managed buff-tailed bumblebees, were more likely to subsequently visit trees in adjacent rows rather than in the same row, which is essential for cross-pollination of self-incompatible cultivars grown in rows (Koumanov & Long, 2017). In contrast to any other pollinator groups, the greater ability of wild bumblebees to collect and deposit pollen between rows of trees, in combination with visiting a greater number of blossoms, suggests they are likely to be the most effective pollinator group. Consequently, solitary bees and wild bumblebees are believed to have increased effectiveness when pollinating sweet cherry compared to managed pollinators (Eeraerts, Smagghe, et al., 2020), and the behavioural observations made in the current study support this.

The observation that non-Andrenid solitary bees (e.g. *Osmia* L. spp.) were rare in this study on sweet cherry orchards concurs with findings in UK apple (McKerchar et al., 2020) and pear (Fountain et al., 2019) orchards. Consequently, solitary bee visitation in

FIGURE 2 Percentage (\pm SE) of pollinator individuals feeding on nectar, pollen or both (nectar and pollen) according to pollinator group. The same letters above bars for each category (nectar, pollen and both) indicate no significant differences according to the Tukey test ($p > 0.05$)

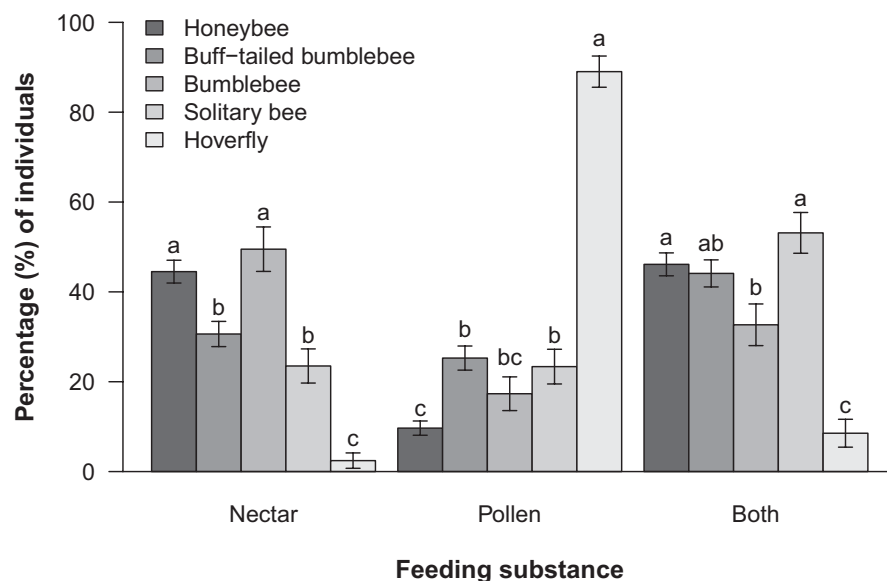
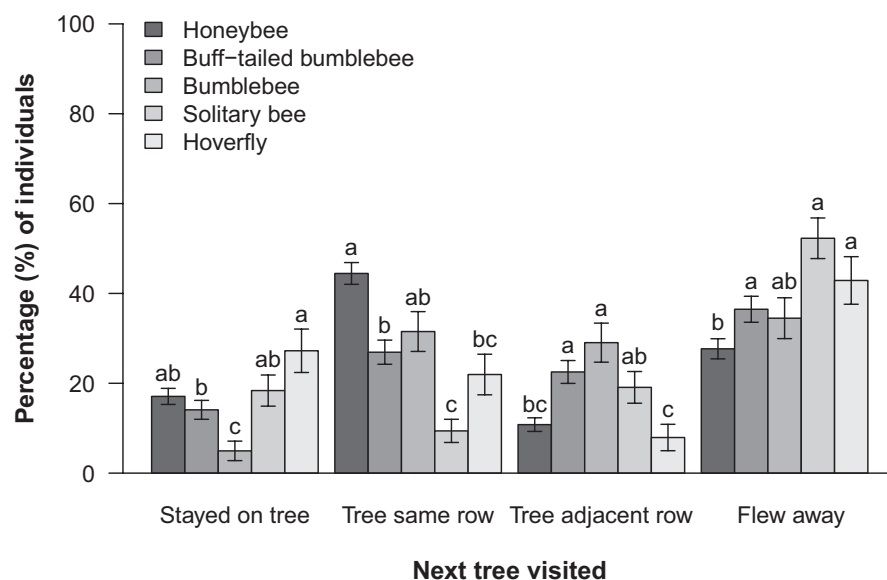


FIGURE 3 Percentage (\pm SE) of pollinator individuals according to pollinator group and location of the cherry tree subsequently visited. The same letters above bars for each category (stayed on tree, same tree row, adjacent tree row and flew away) indicate no significant differences according to the Tukey test ($p > 0.05$)



sweet cherry was dominated by *Andrena* species (96.3% of all solitary bee records). Comparison of solitary bee visitation rates with other studies where managed *Osmia* (Bosch et al., 2006; Eeraerts, Vanderhaegen, et al., 2020) or wild *Lasioglossum* Curtis (Abrol, 2005) were predominant may show a different behaviour for this group. For example, Eeraerts, Vanderhaegen, et al. (2020) recorded an average visitation rate of ~11 flowers per minute for *O. cornuta* and ~5 for other solitary bees, whilst Abrol (2005) recorded ~3 flowers per minute for *Lasioglossum* spp. compared to ~7 flowers per minute recorded for solitary bees in this study. This suggests that variations regarding foraging behaviour occur across multiple bee species, which might have implications on their pollination contribution.

Although, in this study, wild bees were deemed more effective pollinators than hoverflies, based on number of blossoms visited and subsequent visits to trees in adjacent rows, the value of hoverflies as pollinators of sweet cherry may still be significant (Bakshi et al., 2018). In sweet cherry, Bakshi et al. (2018) recorded a visitation

rate of ~4 flowers per minute and a visitation time of ~6 s per flower for hoverflies compared to ~13 flowers per minute and ~14 s per flower in this study, respectively. These differences may also be due to dominance of different species in the hoverfly pool. In Bakshi et al. (2018), only one species was recorded, *Episyrphus balteatus* (De Geer), compared to 14 species in this study, dominated by *E. pertinax*. The fact that hoverflies made stigma contact on nearly 100% of visits suggests that a proportion of fruit set could be due to this group, especially since hoverflies are considered important pollinators for a number of other crops (Rader et al., 2016), and can, along with other wild pollinators, enhance sweet cherry production (Eeraerts et al., 2019). An additional benefit of hoverflies is their role in pest regulation services if their larvae are aphidophagous (e.g. Syrphinae; Doyle et al., 2020; Mateos-Fierro et al., 2021).

In this study, we clearly showed that whilst growers relied on managed pollinators, these groups may not be the most effective pollinators, despite being the most abundant. The tendency for

honeybees to forage on the same row rather than moving between rows suggests their limited value in cross-pollinating self-infertile sweet cherry cultivars. However, honeybee movement between rows might be less significant for self-fertile cultivars, as shown in self-fertile sour cherries (Hansted et al., 2015). Also, due to buff-tailed bumblebee workers not contacting the stigma as often as wild solitary bees or wild bumblebees suggests, again, they are unlikely to be as effective.

Visitation rates for honeybees in this study (~15 flowers per minute) were 2–3 times higher than visits recorded in other studies (Abrol, 2005; Bakshi et al., 2018; Eeraerts, Smagghe, et al., 2020; Eeraerts, Vanderhaegen, et al., 2020; Kwack et al., 2012). This may be a consequence of the pool of species in the pollinator community, which is known to affect honeybee behaviour (Brittain, Williams, et al., 2013; Eeraerts, Smagghe, et al., 2020). Additionally, the use of polytunnels may have also influenced honeybee visitation rates (Hall et al., 2020; Kendall et al., 2021), since hives were deployed at the orchard perimeter and honeybees had to fly into the orchards. However, the time honeybees spent on a single flower was similar to Bakshi et al. (2018) at ~8 s per flower but dissimilar to Kwack et al. (2012) (~15 s per flower). Whilst the managed buff-tailed bumblebee visitation rate and visitation time on a single flower were similar to Kwack et al. (2012) with ~11 flowers per minute and ~6 s per flower compared to ~15 flowers per minute and ~6 s per flower in this study, respectively. This might indicate that reared managed species may behave more similarly than other managed (e.g. honeybees) or wild species, although more research is needed to confirm this.

Landscape attributes might also be important for sweet cherry production due to the influence on wild pollinator abundance and diversity (Kay et al., 2020), and behaviour of managed pollinators may be affected by the wild pollinator community (Brittain, Williams, et al., 2013; Carvalheiro et al., 2011; Eeraerts, Smagghe, et al., 2020). This potentially highlights the role of management and local landscape context on pollinator communities (Eeraerts, Van Den Berge, et al., 2021). However, other factors apart from diversity might also influence pollination behaviour (e.g. polytunnels; Kendall et al., 2021). Thus, further study would be needed to determine which management practices and landscape factors are important to promote species richness and diversity. Within our study sites, only at one site were cherry trees not covered during the blossom period; hence, we had insufficient replication to explore the effect of polytunnels. A different experimental design would therefore be required to investigate this, which could also investigate pollinator composition, landscape context and further study fruit set and yield across sites.

This study also showed differences in behaviour within pollinator groups across the day, which could be related to changes in environmental factors. Nectar is essential in angiosperms for attracting insect pollinators (De la Barrera & Nobel, 2004). However, nectar production varies throughout the day (Fotirić Akšić et al., 2020), and nectar concentration can decrease under increasing temperature and decreasing humidity (Corbet et al., 1979). Consequently, nectar

composition, concentration and secretion may enhance or reduce insect visitors and the duration of their visit (Fotirić Akšić et al., 2020). This may be why some pollinator groups, especially honeybees, tended to focus on collecting nectar during the late morning surveys when values of humidity were greater, and therefore nectar more concentrated, which is consistent with Bakshi et al. (2018) and Sharma et al. (2016), and similar to Abrol (2005), where maximum activity was between 11:00 and 14:00 hr.

In addition, the negative correlation between nectar collection and stigma contact, and positive correlation between both nectar and pollen collection and stigma contact (e.g. honeybees and solitary bees) might affect fruit set. How a pollinator lands on a flower can also predispose their feeding behaviour (Bakshi et al., 2018). The tendency of honeybees to collect nectar alone suggests that visits of this pollinator did not result in stigma contact, contrary to solitary bees, which collected both substances more frequently. Thus, variability in pollinator activity is especially important in sweet cherry as weather conditions during the blossom period can be unfavourable for pollinators and sweet cherry flowering phenology can vary between years.

Hence, a diverse pollinator community with different pollinators active throughout the day reduces the risk of potential yield losses (Williams et al., 2019). It is therefore recommended that growers invest in alternative pollinator management strategies to supplement or replace pollination by managed bees. Focus should be on targeting wild pollinators, for which growers could implement appropriate orchard management strategies, including the incorporation of pollinator habitats (Eeraerts et al., 2019), maintaining wildflowers in orchard alleyways (Eeraerts, Van Den Berge, et al., 2021), or establishing wildflower strips when wildflowers are scarce (Mateos-Fierro et al., 2018). Increasing the abundance and diversity of pollinators is likely to increase the stability of pollination services within and between seasons (Senapathi et al., 2021), underpinning sweet cherry production. We have demonstrated the important role of wild pollinators in sweet cherry pollination and highlighted the need to fully incorporate this pollinator group as part of a sustainable pollination management strategy in sweet cherry.

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CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Z.M.-F. conducted the research, identified the specimens and wrote the manuscript. Z.M.-F., M.P.D.G. and K.A. performed the statistical analysis. All authors conceived the research programme, developed the methodology and contributed to manuscript writing.

DATA AVAILABILITY STATEMENT

Data can be accessed at <https://doi.org/10.5281/zenodo.5607648>.

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