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A subset of wild bee species boosts the pollination of pigeon pea (*Cajanus cajan*: Fabaceae), an important crop plant of Cameroon

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Abstract

Bee species are thought to vary in their pollination efficiency, but they are rarely compared, particularly in the tropics. Here we determined the role in pollination of 13 native bee species (*Apis mellifera* and 12 other wild bee species) when visiting pigeon pea (*Cajanus cajan*) flowers across two growing seasons in Cameroon. Using observations of floral visits coupled with a field experiment to quantify single-visit pollination efficiency, we found that *Chalicodoma rufipes* was the most efficient pollinator and most abundant flower visitor of pigeon pea. Most other flower visitors, including *Apis mellifera*, detracted from pigeon pea seed set. Our study highlights the importance of quantifying pollination to reveal functionally important bee species.

Keywords: Anthophila, *Apis mellifera*, ecosystem service, efficiency, foraging behaviour, pigeon pea.

Introduction

Human societies derive great benefit from a range of natural ecological functions, referred to as ecosystem services (Costanza et al. 1997). Pollination is known as a crucial step in the reproduction of many wild and crop plants (Kremen et al. 2007; Ollerton et al. 2011; Potts et al. 2016; Rodger et al. 2021), and pollinators thereby provide important benefits to humans through the ecosystem service of pollination by securing a reliable and diverse seed, nut and fruit set (e.g., Frimpong et al. 2011; Klein et al. 2012; Potts et al. 2016; Zou et al. 2017), with more than 75% of the world's most important crops dependent on insect pollination (Klein et al. 2007). Pollinator-dependent crops are also important for balanced human diets by providing many micronutrients such as vitamins A and C (Eilers et al. 2011; Smith et al. 2015).

Agriculture is increasingly dependent on insect pollination (Aizen et al. 2019), and the western honey bee (*Apis mellifera* L.) is often employed by farmers for crop pollination (Breeze et al. 2019; Osterman et al. 2021a). Yet wild pollinators are frequently linked to increased crop production and yield, independent of honey bee abundances (Klein et al. 2012; Garibaldi et al. 2013). The community of potential pollinators in agricultural crops can be diverse, especially across landscapes (Albrecht et al. 2012; Winfree et al. 2018). However, for a pollinating insect to be effective, its behaviour should favour the transport of pollen grains from anthers to stigmas of the same or a different individual of the same plant species (Freitas and Paxton 1998; Singh 2016; Eeraerts et al. 2019).

Bees are considered the most effective pollinators of crops and the most specialized flower visitors because of their morphological adaptations to collect, manipulate, transport, and store pollen efficiently (Klein et al. 2007; Rader et al. 2016). Yet bee species vary in the efficiency with which they achieve pollination when visiting a flower (e.g., Freitas and Paxton 1998; King et al. 2013). To optimise the pollination of crops, it is crucial to investigate the pollination performance of a crop`s flower visitor community (potential pollinators) and, thereby, identify which pollinator species contribute most to its pollination (Garibaldi et al. 2013; Eeraerts et al. 2019). This is all the more important for tropical crops, many of which are understudied.

Pigeon pea, *Cajanus cajan* L. (family Fabaceae), is widely cultivated in tropical and subtropical regions (Saxena et al. 2002). Though originating in the Indian subcontinent (Songok et al. 2010), it is widely grown as a crop across Africa, including Cameroon, where it is grown in bush-grassland and savannah areas (Martins 2008). Pigeon pea beans (seeds) are rich in protein, minerals, fats, and vitamins A and C (Sharma and Green 1980; Gupta et al. 2001; Saxena et al. 2002; Pandey et al. 2015) whilst its leaves are used to treat yellow fever and coughs (Nene and Sheila 1990; Shiying et al. 2001).

Though pigeon pea is self-fertile and can self-pollinate without a flower visitor, many insect species have been reported as visitors (and potential pollinators) of *C. cajan*, with the suggestion that cross-pollination through insect visitation might enhance pollination success (Free 1993; Shiying et al. 2001; Pando et al. 2011; Mazi et al. 2014; Kale et al. 2017; Vogel et al. 2021).

However, in Malawi, neither bee abundance (dominated by honey bees) nor bee richness in the landscape were related to the fruit set of pigeon pea (Vogel et al. 2021). This raises the question of which bee species, and whether honey bees in particular, contribute to pollination of the crop. In Cameroon, pigeon pea often exhibits low pod production, which may be due to a lack of adequate pollination during flowering (Free 1993). We require information on the diversity and abundance of insects visiting pigeon pea flowers and their efficiency in the crop's pollination to evaluate whether crop production in Cameroon may be limited by inadequate pollination.

Here, we investigated the community of visitors of *C. cajan* flowers and assessed their foraging behaviour and pollination efficiency as well as their role in pollination near the city of Ngaoundéré, Northern Cameroon. We integrated flower visitor behaviour together with experimentally determined pollination efficiency to infer the role of 13 native bee species in pigeon pea pollination.

Material and Methods

Study area

The study was conducted in a 437 m^2 plot of *C. cajan* in Dang, near the city of Ngaoundéré, Adamaoua Region, Cameroon, using seeds typically used by local farmers. Data collection was undertaken across two years (1st season: December 2010 to January 2011; 2nd season: December 2011 to January 2012) during the crop's normal flowering period. The Adamaoua region belongs to the high-altitude Guinean Savannah agro-ecological zone (Letouzey 1968; Djoufack et al. 2012) and has a tropical climate characterized by two seasons: a rainy season (April to October) and a dry season (November to March). The annual rainfall varies from 1227.9 mm to 1675.8 mm (Djoufack et al. 2012). The mean annual temperature varies from 22.08°C to

22.93°C while the mean annual relative humidity varies from 64.1% to 67.6% (Djoufack et al. 2012).

Insect visitors to pigeon pea flowers

Observations on pigeon pea flowers were undertaken every day, from 23rd December 2010 to 11th January 2011 and from 20th December 2011 to 12th January 2012, representing the peak of blooming, in four daily observation time frames: 0900 – 1000 h, 1100 – 1200 h, 1300 – 1400 h, and 1500 – 1600 h, on unprotected flowers (treatment Open, 120 flowers, see further description below). Pigeon pea flowers open in the morning and close in the late afternoon (Martins et al. 2008) so we likely sampled those flower visitors contributing most to pigeon pea pollination. During each investigation day, we walked slowly, for each of the above daily time frames, along all labelled flowers of treatment Open and visually identified and counted all insects encountered on them (Delaplane et al. 2013). Results are expressed as the number of visits to determine the relative abundance of each bee species in the community of insects visiting *C. cajan*. A code was given in the field to the unrecognised bee species, which were caught with a sweep net on unlabelled flowers and conserved in 70% ethanol for subsequent identification. Species that we were not able to identify to the species level were grouped into morphological taxa as there is no identification key to the bees of Cameroon.

Bee foraging behaviour

We then quantified the foraging behaviour of flower visitors of pigeon pea flowers, with the focus on bees. We included a bee species if ten individual observations of it were made per year. The relative abundance and behaviour (whether they collected pollen, nectar, or both simultaneously, whether they touched stamens or stigmas) were recorded across the day (20 days in 2010/11 and 24 days in 2011/12): 0900 – 1000 h, 1100 – 1200 h, 1300 – 1400 h, and

1500 – 1600 h (resulting in 80 hours of observations in the 2010/11 flowering period and 96 hours in the 2011/12 flowering period). At the same time, the duration of individual flower visits (time spent by a bee species on one flower to harvest nectar or pollen) was recorded using a stopwatch. Individual bees were followed as long as possible until they were lost from sight. Observers kept reasonable distance to the foraging bees so as to not disturb them but still be able to observe their foraging behaviour on flowers.

Pollination dependency of pigeon pea and single visit efficiency of flower visitors

On both 21st December 2010 and 18th December 2011, 360 *C. cajan* flowers at the bud stage were labelled, of which 120 were left open for insect visitation (treatment Open) and 120 were protected using gauze bags (1 mm mesh) to prevent insect visitors (Roubik 1995; Delaplane et al. 2013) (treatment Bagged). The remaining 120 flowers were labelled at the bud stage and protected from insect visits identical to those of treatment Bagged, then opened at bloom to allow a single visit one of the studied bee species (treatment Single-Visit). After this single visit by one insect, the Single-Visit treatment flowers were re-bagged and were not furthermore handled. For this Singe-Visit treatment, only legitimate flower visitors (i.e., visits in which nectar and/or pollen was removed from the flower) were considered. Thus, if a bee landed on a flower to rest or sunbathe, the flower was not considered to have been legitimately visited and this flower was excluded from further consideration. We hereby aimed to quantify pollination efficiency of each flower visitor using 10 flowers each singly visited by a specific flower visitor species.

The number of flowers that initially set a pod were counted for each treatment. To do so, ten days after shedding of petals of the last labelled flowers, the number of formed pods was counted for each treatment to evaluate the need of pigeon pea for pollination by flower visitors.

When pods (fruits) were ripe, they were harvested for each treatment and the number of fruits and the number of seeds set per fruit were counted. The mean number of seeds per fruit and the percentage of normal seeds (i.e., not shrunken or collapsed seeds) were then calculated for each treatment for formed pods.

Pollination efficiency index

A comparison of yields from treatments with continually bagged flowers (treatment Bagged), unattended flowers (treatment Open), and those from treatments with flowers that were visited by a single bee (treatment Single-Visit) allowed us to evaluate the efficiency of each bee species in pigeon pea pollination. For this, we followed Spears' (1983) method to calculate a pollination efficiency index as:

$$PEi = \frac{(Pi - Z)}{(U - Z)}$$

where P_i, is the mean pod set or number of seeds set per flower receiving a single visit from bee species *i* (treatment Single-Visit), *Z* is the mean pod set or number of seeds set per flower receiving no visitation (treatment Bagged), and *U* is the mean pod set or number of seeds set per flower by a plant population exposed to unrestricted visitation (treatment Open). A *PEi* of 1 indicates that pod set or seed set per formed pod is equal for the singly visited flowers (for that visitor species) and the open flowers; it represents a theoretical upper bound of the service provision of pollination at the field site, summed across all flower visitors (assuming all visitors contribute to pollination). Values between 0 and 1 indicate a lower fruit set of the singly visited flower compared to open pollination. Negative values arise if single visited flowers have a lower fruit set than those that are pollinator excluded (treatment Bagged), which indicates that the visitor detracts from the pollination of this self-fertile plant species that is capable of self-pollination.

Data analysis

We tested the effects of pollination treatment (Open treatment vs. Bagged treatment) and year of sampling on pod set and seed set using a generalized linear model (GLM). For pod set (yes/no) we performed a GLM with a binomial error structure using the package *lme4* (Bates et al., 2015) and for seed set a GLM with a Tweedie distribution to account for the zero-inflation of the data using the R package "statmode" (Giner and Smyth, 2016).

Results

Frequency of insect visits on *Cajanus cajan* flowers

In our investigation, we observed 6,531 (2010/11) and 7,222 (2011/12) insects visiting *C. cajan* flowers (Table 1) for its nectar and pollen. Insects belonged to 18 (in 2010/11) and 24 (in 2011/12) different species, including 17 bee species, 3 wasp species, one species of Hemiptera and three species of Lepidoptera. The most frequent bee species was *Chalicodoma rufipes* with 3,869 visits (28%) across both growing seasons (Table 1). The most abundant families were Megachilidae (66%) and Apidae (19%, Table 1). *Apis mellifera* was seen on flowers only in the second year (2011/12) of the study (Table 1).

Foraging behaviour of bees on pigeon pea flowers

We were able to assess the foraging behaviour of 13 flower visiting bees: *Apis mellifera* (native sub-species), *Ceratina* sp.1, *Chalicodoma cincta cincta*, *Chalicodoma rufipes, Chalicodoma* sp.1, *Chalicodoma* sp.2, *Chalicodoma* sp.3, *Crossisaspidia chandleri*, *Lipotriches notabilis*, *Megachile* sp.1, *Megachile* sp.2, *Xylocopa olivacea* and *Xylocopa* sp.1. All 13 species touched stamen and stigma when they collected nectar and pollen from *C. cajan* flowers (Table S1 and Table S2). Therefore, all were potential pollinators. However, flower visitors differed in the flower visit duration; the shortest was ca. 1 s by *Megachile* sp.2 in 2010/11 and the longest was *Ch*. *rufipes* with 45 s in 2011/12 (Table 2).

Pigeon pea's dependency on insect pollination

Cajanus cajan pod set increased with insect pollination. In the Open treatment, 93% (in the 1st season) and 96% (in the 2nd season) of flowers set pods, whilst in the Bagged treatment only 63% (in the 1st season) and 70% (in the 2nd season) of pods were produced which, compared to the Open treatment, demonstrates benefits to pod set from insect visitation at our field site (GLM, Z = 6.862, P < 0.001). We detected no differences between years in pod set (GLM, Z = 1.355, P = 0.175).

Seed set of *Cajanus cajan* differed between treatments (GLM, t = 10.542, P < 0.001) as well as between years (GLM, t = 3.887, P < 0.001). In the Open treatment on average 4.38 (in the 1st season) and 5.13 (in the 2nd season) seeds per flower (per pod) were produced. In the Bagged treatment, 2.56 (in the 1st season) and 3.19 (in the 2nd season) seeds per flower (per pod) were produced.

Pollination efficiency of bees visiting pigeon pea

The bee species with the highest Spears' pollination efficiency index (calculated as pod set) was *Ch. rufipes* at 0.82 ± 0.71 (2011/12) and 0.89 ± 0.38 (2011/12). Of the 13 bee species assessed, only two in 2010 (*Ch. rufipes* and *Ceratina* sp.1) and one in 2011 (*Ch. rufipes*) had a positive *PEi* pod set value (Figure 1).

The bee species with the highest Spears' pollination efficiency index (calculated as seed set) was also *Ch. rufipes* at 0.90 ± 0.41 in 2010 and 0.99 ± 0.57 in 2011. For many bee species including the honey bee, the *PEi* (seed set) was negative, while only three bee species (*Ch. rufipes, Ceratina* sp.1, and *Chalicodoma* sp.1) had a positive *PEi* (seed set) value for the two years (Figure 1).

Discussion

Here, we show that pigeon pea pod set and seed set can be increased through pollination by a restricted set of bee species. Flower visitor species differed in their foraging behaviour as well as efficiency. Remarkably, only three out of thirteen bee species evaluated contributed to the pollination of *C. cajan* while others, including *A. mellifera,* diminished pod set and seed set compared to non-insect visited flowers. This highlights the importance of protecting a range of wild pollinators to ensure stable food production.

Frequency of bee visits to *Cajanus cajan* flowers

Non-*Apis* wild bees were the main insect visitors of *C. cajan* flowers at our study site. Moreover, members of the family Megachilidae were the most abundant visitors of pigeon pea flowers at 66% followed by Apidae at 19%. Megachilidae are known to be regular visitors of Fabaceae (Martins 2008; Otieno et al. 2016; Singh 2016; Vogel et al. 2021). Martins (2008) also found that carpenter bees (e.g., *Xylocopa inconstance*, Family Apidae) and *Gronocera* sp. (Megachilidae) were predominant visitors of pigeon pea flowers in Tanzania whilst Otieno et al. (2016) found *Megachile* spp., honey bees, *Ceratina* and *Xylocopa* spp. to be frequent visitors at Kenyan pigeon pea fields. Singh (2016) found Megachilidae as the key pollinators in Nagaland State in India, the region of the plant's origin. In another study in India, *Xylocopa* spp., *Apis dorsata*, *Apis florea*, *Trigona* spp., *Apis cerana* and *Ceratina* spp. were all observed visiting pigeon pea flowers. In our study, *Ch. rufipes* (Megachilidae) made 28% of all visits across two years. While flower visitor communities across studies (this study; Martins 2008; Otieno et al. 2016; Singh 2016) were generally similar at the genus level (*Apis*, *Ceratina*, *Megachile*, *Xylocopa*), differences can be seen at the species level. This highlights, the need for further studies investigating the abundance of flower visitors of pigeon pea, an understudied crop of importance for food production, especially in the tropics (Martins 2008), to be able to implement locally relevant conservation measures for its wild bee pollinator species.

Interestingly, *A. melllifera* was absent from pigeon pea flowers in 2010. It has been shown that the western honey bee can be attracted to crops offering a high (nectar or pollen) reward such that, when two crops co-bloom, the honey bees may be drawn away from the crop offering the lowest floral reward, making the honey bee a less reliable crop pollination than other bee species with shorter flight ranges (Osterman et al. 2021b). The absence of honey bees visiting pigeon pea flowers in the first year of our study might be account for by co-blooming crop species.

Pollination efficiency of bees visiting pigeon pea

All 13 bee species observed in our study touched stamens and the stigma of *C. cajan* flowers while harvesting floral products, therefore all were potential pollinators. Insect pollination overall markedly increased the pod set of *C. cajan* compared to pollinator excluded flowers, demonstrating the clear benefit of pollination for pigeon pea seed set. These findings are in line with those of Otieno et al. (2016) and Kale et al. (2017), who found an increase in yield from bagged (self-pollinated) flowers to insect-pollinated flowers in Kenya and India respectively. It is not yet clear, though, which of pigeon pea's flower visitors contribute to its pollination. Correlational data have suggested that *Megachile* spp., honey bees (*A. mellifera*) and carpenter bees (*Ceratina* and *Xylocopa* spp.) all play a role in its pollination (Otieno et al. 2016). We have taken a more direct, experimental approach using singly visited flowers to show that only a subset of the flower visitors enhances pigeon pea's pollination. In this study, we focused on the role of bee species. We acknowledge that non-bees might also contribute to the pollination of pigeon pea, as has been shown in other crops (Rader et al. 2016). Further studies should investigate especially the contribution of wasps, as in our study three species were relatively abundant flower visitors (Table 1).

When measuring individual flower-visitor pollination efficiency (*PEi*), we found that only three bee species: *Ch. rufipes, Ceratina* sp.1, and *Chalicodoma* sp.1, contributed positively to the pollination of pigeon pea. *Chalicodoma rufipes* in particular seemed important for pollination of this Fabaceae crop plant as it had a positive efficiency for pod and seed set across both study years. Also, it accounted for 28% of all observed flower visits. Its high single-visit pollination efficiency and its high abundance lead us to the conclusion that this species is the main pollinator of the crop in this region in Cameroon. Interestingly, all three species with a positive *PEi* also spent more than 10 seconds handling a flower while the other species had comparably lower flower visitation durations.

The pollination efficiency of a flower-visitor species can be explained by the number of pollen grains carried on the bee's body and deposited on a stigma (Singh 2016). Using such data, Singh (2016) suggested that Megachilidae and Apidae were the key pollinators of *C. cajan*. Megachilidae have numerous scopal hairs uniformly covering the abdominal ventral surface (Bzdyk 2012) which provide a suitable structure to collect pollen grains from the anthers of papilionaceous flowers and presumably to deposit pollen on their stigmata. Furthermore, long-tongued insects like members of the Megachilidae are more suitable for pollination of keel-type flowers such as those of the Fabaceae (Wousla et al. 2020). However, here we show that, even within the same genus, pollination efficiency differs greatly between species, indicating that pollination efficiency might be related both to flower-visitor traits as well as to their behaviour.

Our findings show that wild bees play a most important role in the pollination of pigeon pea flower and seem to be the pollinators of this plant species, while the western honey bee is seemingly unimportant in its pollination, as also seen in other studies (Mattu and Thakur 2016; Singh 2016; Wousla et al. 2019; Gail and Jessica 2019). Pollination management in pigeon pea, therefore, needs measures other than employing honey bees or relying on feral honey bee colonies. That the fruit set of pigeon pea was not related to bee abundance or richness in a study in Malawi, where honey bees were the dominant flower visitors (Vogel et al. 2021), could be explained by our observation that only a subset of bees contributes to the pollination of pigeon pea. We identified *Ch. rufipes* as the most important pollinator in our region; measures could be targeted to enhance the abundance of this species to ensure stable pigeon pea crop yields. Future studies should investigate if *Ch. rufipes* is also common in other regions of West Africa and how to support its populations. Also, investigating if farmers are aware of this pollinator species and its importance, and their willingness to preserve pollinators, could highlight possibilities for conservation measures in tropical agricultural landscapes.

Conclusions

Three wild bee species enhance the pollination of *C. cajan* crop yield in Cameroon, especially *Ch. rufipes*, which we show to be the most abundant and most efficient pollinator species. In contrast, most other flower visitor species, including *A. mellifera*, detracted from pod and seed set of *C. cajan*. Bee conservation measures could be targeted towards enhancing *Ch. rufipes* populations near pigeon pea fields to increase the yield of this Fabaceae and, therefore, to enhance food security in Cameroon and likely elsewhere across this bee’s distribution.

Supplementary material

Additional supporting information may be found in the online version of this article:

Table S1. Floral rewards collected by bee species in 2010

Table S2. Floral rewards collected by bee species in 2011

Declaration of Competing Interest

The authors declare that they have no known competing financial interests.

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Contribution

SM conceived the idea, performed the fieldwork, and performed the first data analysis. JO performed the final data analysis. All authors contributed to writing the manuscript.

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Figure captions

Table 1: Number and percentage of visits of different insect species recorded on *Cajanus cajan* flowers in the 2010/11 and 2011/12 growing seasons.

Table 2: Duration of visits of bee species on pigeon pea flowers.

Figure 1. Single-visit pollination efficiency (*PE*i) of bee species in terms of pod set and seed set for two growing seasons. *Apis mellifera* was not present in 2010/11.

Tables

Table 1.

Insects			**2010/2011**		**2011/2012**		**Total 2010.2011 / 2011.2012**	
Order	**Family**	**Species**	$\boldsymbol{n_1}$	**%**	$\boldsymbol{n_2}$	**%**	$\boldsymbol{n_T}$	**%**
Hymenoptera	Apidae	*Apis mellifera*	0	0	112	1.55	112	0.81
		Ceratina sp. 1	670	10.26	1080	14.95	1750	12.73
		Xylocopa olivacea	192	2.94	181	2.51	373	2.71
		Xylocopa sp. 1	200	3.06	134	1.86	334	2.43
		Xylocopa sp. 2	**0**	0	86	1.19	86	0.63
	Total Apidae		**1062**	**16.26**	**1593**	**22.06**	**2655**	**19.31**
	Megachilidae	*Chalicodoma cincta cincta*	407	6.23	552	7.64	959	6.97
		Chalicodoma rufipes	1911	29.26	1958	27.11	3869	28.13
		Chalicodoma sp. 1	955	14.62	1065	14.75	2020	14.69
		Chalicodoma sp. 2	370	5.67	414	5.73	784	5.70
		Chalicodoma sp. 3	334	5.11	224	3.10	558	4.06
		Coelioxys circumscriptus	**0**	0	67	0.93	67	0.49
		Megachile sp. 1	338	5.18	181	2.51	519	3.77
		Megachile sp. 2	82	1.26	93	1.29	175	1.27
		Mégachile sp. 3	0	0	78	1.08	78	0.57
		Megachile sp. 4	0	0	83	1.15	83	0.60
	Total Megachilidae		**4397**	**67.33**	**4715**	**65.29**	**9112**	**66.25**
	Halictidae	*Crossisaspidia chandleri*	263	4.03	151	2.09	414	3.01
		Lipotriches notabilis	197	3.02	46	0.64	243	1.77
	Total Halictidae		**460**	**7.05**	**197**	**2.73**	**657**	**4.78**
	Vespidae	*Belonogaster juncea juncea*	110	1.68	167	2.31	277	2.01
		Belonogaster sp. 1	142	2.17	143	1.98	285	2.07
		Belonogaster sp. 2	72	1.10	47	0.65	119	0.87
	Total Vespidae		**324**	**4.95**	**357**	**4.94**	**681**	**4.95**
Total Hymenoptera			**6243**	**95.59**	**6862**	**95.02**	**13105**	**95.29**
Hemiptera	**Miridae**	*Helopeltis schoutedeni*	**0**	0	95	1.32	95	0.69
Lepidopera	Pieridae	*Catopsilia florella*	111	1.70	65	0.90	176	1.28
		Eurema sp.	136	2.08	165	2.28	301	2.19
	Nymphalidae	*Neptis* sp.	41	0.63	35	0.48	76	0.55
Total Lepidoptera			**288**	**4.41**	**265**	**3.66**	**553**	**4.02**
Grand Total		**18 (2010) / 24 (2011)**	**6531**	**100**	**7222**	**100**	**13753**	**100**

n_1: number of visits to 120 flowers in 17 days; n_2: number of visits to 120 flowers in 20 days p_1 and p_2: percentage of visits; sp.: undetermined species. $p_1 = (n_1/ 6531) \times 100$ and $p_2 = (n_2/ 7222) \times 100$.

Table 2.

Bee species*	**Duration of visit in s (mean ± SE)**	
	2010/2011	**2011/2012**
Apis mellifera adansonii	**	2 ± 1.31
Ceratina sp. 1	10 ± 0.1	16 ± 6.23
Chalicodoma rufipes	45 ± 5.01	35 ± 7.14
Chalicodoma cincta cincta	4 ± 2.51	8 ± 3.12
Chalicodoma sp.1	15 ± 4.15	16 ± 8.01
Chalicodoma sp.2	3 ± 0.56	6 ± 2.21
Chalicodoma sp.3	5 ± 0.25	3 ± 0.51
Crossisaspidia chandleri	4 ± 0.36	2 ± 0.81
Lipotriches notabilis	3 ± 2.54	1 ± 0.87
Megachile sp.1	5 ± 2.58	3 ± 2.09
Megachile sp.2	1 ± 0.15	1 ± 0.11
Xylocopa olivacea	3 ± 2.12	3 ± 0.45
Xylocopa sp.1	3 ± 2.51	2 ± 0.54

*Bee species with at least 10 observations per year
**In 2010/2011, *A. mellifera* was absent

Figures

Figure 1.