

Review

# Nocturnal Bees as Crop Pollinators

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**Abstract:** Bees are typically diurnal but around 1% of described species have nocturnal activity. Nocturnal bees are still poorly studied due to bias towards studying diurnal insects. However, knowledge concerning their biology and role as crop pollinators has increased. We review the literature on nocturnal bees' traits and their host plants, and assess the crop pollination effectiveness of this neglected group. Nocturnal bees have visual adaptations to cope with low light intensities, and floral scents are a key sensory cue used to find their host flowers. Nocturnal bees generally show high flower constancy, the ability to vibrate flowers, and high transfer rates of pollen grains to stigmas. The flowers visited by nocturnal bees range from small radial and zygomorphic flowers to large brush blossoms; moreover, they visit plants with different flowering strategies. Nocturnal bees are effective pollinators of regional fruit crops in Brazil, such as cambuci (*Campomanesia phaea*), guaraná (*Paullinia cupana*), cajá (*Spondias mombin*), and in North America of cultivated pumpkins (*Cucurbita* species). However, they most likely are pollinators of several other crops. Strategies to host high numbers of nocturnal bees around cropping areas should be taken, such as preserving adjacent native forests, restricting soil management, providing food resources beyond crop flowers, and avoiding light pollution.

**Keywords:** biodiversity; crepuscular bees; crop production; floral scent; food security; nocturnal pollination; nocturnal vision; *Megalopta*; *Ptiloglossa*

## 1. Introduction

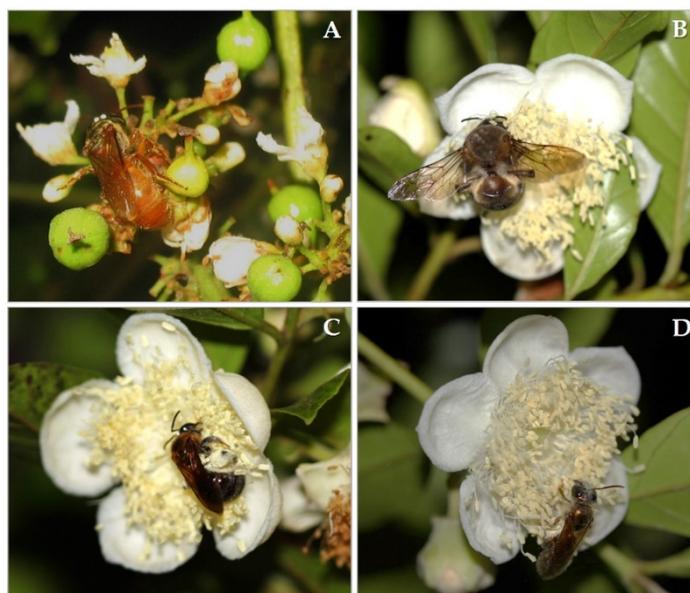
Pollination is an essential ecosystem service and is crucial for guaranteeing global food security [1], with its economic importance estimated at USD 235–577 billion annually [2].

Bees are the most important crop pollinators worldwide [3], with *Apis mellifera* being the main managed pollinator species for crops around the world [4]. However, several crops demand specific solitary bees to guarantee efficient pollination and fruit set [5–7], and indeed, an overall high diversity of native bee pollinators enhances crop yield [8,9].

Bees are typically diurnal but approximately 1% of described species (*ca.* 250) have crepuscular and/or nocturnal activity. Crepuscular bees fly pre-sunrise and post-sunset, and truly nocturnal bees fly all night or for most of the night [10–14]. This behavior has arisen independently in four of the seven bee families: Andrenidae, Apidae, Colletidae, and Halictidae [13,15]. It is hypothesized that these bees developed nocturnal habits to escape diurnal competition for floral resources and to avoid enemies such as kleptoparasites, which are less active at night [11,15–17].

Foraging at night and during twilight is thus likely to be beneficial, as flowers are often rich in pollen and nectar early in the morning before being exploited by diurnal flower visitors [18], as well as late into the evening before nocturnal visitors arrive, providing a “competitor free space” [12,16]. In addition, by mainly visiting plant species with abundant floral rewards available, they would spend little time searching for host plants [19,20].

Most crepuscular/nocturnal bees (hereafter referred to as nocturnal bees) occur in Neotropical regions and are widespread, mainly in South America [21]. The biology of nocturnal bees is poorly studied due to a preferential bias towards studying diurnal insects. One of the most studied and common nocturnal bee genera is *Megalopta* (Halictidae), which currently accounts for 32 species distributed from South Mexico to Argentina [22,23]. *Megalopta* bees build their nests in cavities within dead wood, and in some species more than one female per nest was recorded, suggesting a facultative social behavior [24–26]. The other abundant nocturnal bee genus, *Ptiloglossa* (Colletidae), has 55 described species occurring from the Southern United States to Argentina [21,27]. These bees dig tunnels in the ground to build their nests [28–30]. The genus *Xylocopa* has some records related to its nocturnal representatives, as *X. tranquebarica* from Asia [31]. Besides these, there are other genera of nocturnal bees, such as *Megommation*, *Zikanapis*, and *Xenoglossa* [15,32] (Figure 1). There are species with facultative nocturnal behavior that forage during the day but occasionally have also been reported at night, among them *Apis dorsata*, *A. mellifera adansonii*, and other *Xylocopa* species [12,33].



**Figure 1.** Nocturnal bees: (A) *Megalopta aeneicollis*, (B) *Ptiloglossa latecalcarata*, (C) *Megommation insigne*, (D) *Megalopta sodalis*.

These bees visit a high number of plant species, among them crops [34]. The pollination efficiency of nocturnal bees was recently shown for Brazilian crops of different families, such as Anacardiaceae (*Spondias mombin*), Myrtaceae (*Campomanesia phaea*), and Sapindaceae (*Paullinia cupana*) [18,35–37], but they are potential pollinators of other crops as well [38,39]. Here, we review the literature on nocturnal bees: how they find flowers, their pollinator traits and host plants, and assess the crop pollination effectiveness of this neglected group. We then address perspectives on how to provide appropriate habitats to improve the presence of nocturnal bees around cropping areas to facilitate pollination.

## 2. How Do Nocturnal Bees Find Flowers in the Darkness?

Bees use visual (shape, brightness, and color) as well as chemical (scent) floral cues to find flowers and to obtain food resources such as nectar and pollen [40–42]. As nocturnal bees have a very restricted period of activity to collect their food resources (*ca.* 1–2 h), one might expect that these bees need to be very efficient at finding flowers. Compared to diurnal bees, nocturnal bees have several visual adaptations to cope with low light intensities. They typically have larger apposition compound eyes and ocelli [10,43–45], optical mechanisms for increasing light capture in dim light [10,13,44,46–49], and specialized neural mechanisms that enhance visual performance by boosting retinal signal reliability [50] and by summing photons in space and time [13,47,51,52]. Light intensity thresholds determine flower search behavior more than other abiotic environmental factors [11,53]. Moreover, nocturnal bees tend to visit flowers with a broad reflection spectrum that likely creates a high contrast white target against the dark backgrounds of the sky and vegetation [53–56].

In addition to visual adaptations for dim light, nocturnal pollinators often heavily depend on floral odors to find their host flowers [55]. Indeed, nocturnal bees tend to visit and are attracted by flowers releasing a strong perfume at night [20,39,56], with volatiles from various biosynthetic routes. For example, nocturnal bees are attracted to the strong scent of *Campomanesia phaea* (Myrtaceae) flowers, which is mainly composed of aromatic (2-phenylethanol and benzyl alcohol) and aliphatic (1-octanol and 1-hexanol) compounds [18]. The floral scents emitted by *Paullinia cupana* (Sapindaceae) and attractive as a mixture to nocturnal bee pollinators are, among others, the terpenoids linalool and (*E*)- $\beta$ -ocimene, and the nitrogen-bearing compound phenylacetonitrile [36]. These available data demonstrate that strong floral scents composed of compounds widespread among flower scents [57] are a key sensory cue used by nocturnal bees to find their host flowers.

## 3. Traits of Nocturnal Bees and Their Host Plants

As diurnal bees, nocturnal bees depend on floral resources to survive and feed their offspring, and actively seek flowers from which to take up nectar and collect pollen. Some of the pollen grains thereby adhere to the pilosity of their body surface. These grains can subsequently be passively deposited on the stigma of conspecific flowers, completing the pollination process [58]. Nocturnal bees generally show high flower constancy since individual bees preferentially visit flowers of the conspecific species during a foraging flight, as observed in Myrtaceae [18,38,39,59] and Caryocaraceae [20]. Furthermore, nocturnal bees are able to vibrate flowers (Supplementary Material), which is a quite efficient mechanism for collecting pollen [33,60,61]. This behavior was even observed in plant species with non-poricidal anthers [18,39,59]. In one case, nocturnal bees have been shown to transfer higher quantities of pollen grains to the stigma of flowers than diurnal bees [18], and are sometimes more abundant floral visitors than diurnal bees [18,62].

Nocturnal bees explore different types of flowers. Some floral features certainly favor pollination or visitation by nocturnal bees, such as nocturnal anthesis, high light reflectance, and a strong perfume. However, the forms and sizes of flowers visited by nocturnal bees are quite variable. Among such flowers are large brush blossoms (e.g., *Caryocar brasiliense*) [20], small zygomorphic flowers (e.g., *Paullinia cupana*) [36,37], keel flowers (e.g., *Machaerium opacum*) [56], and disk flowers (e.g., Myrtaceae species) [18,39]. Nocturnal bees also visit plants with different flowering strategies, like those with mass

(e.g., *Plinia cauliflora*, *Machaerium opacum*) or steady-state flowering (e.g., *Campomanesia phaea*, *Eugenia pyriformis*) [18,39,56,63].

#### 4. Host Plants of Nocturnal Bees

Nocturnal bees visit a wide spectrum of wild and crop plants and they can efficiently pollinate some of them, such as *Cambessedesia wurdackii* (Melastomataceae) [62], *Campomanesia phaea* (Myrtaceae) [18], *Paullinia cupana* (Sapindaceae) [36,37], *Machaerium opacum* (Fabaceae) [56], *Passiflora pohlii* (Passifloraceae) [64], *Trembleya laniflora* (Melastomataceae) [33], and *Cucurbita* species (Cucurbitaceae) [65,66]. Several other species are visited by nocturnal bees, but there is still little information about their pollination efficiency. Among such species are *Calathea insignis* (Marantaceae) [67], *Gustavia augusta* (Lecythidaceae) [68], *Parkia velutina* (Fabaceae) [69], *Ipomea* species (Convolvulaceae) [70,71], *Solanum* species (Solanaceae) [30,67,72,73], and *Eugenia*, *Syzygium*, and *Plinia* species (Myrtaceae) [39].

Pollen analysis from brood cells of nocturnal bees, or from pollen attached to their bodies, has shown that these bees also visit several chiropterophilous (bat-pollinated) and sphingophilous (moth-pollinated) species [16,19,34,74]. However, in only a few cases has the role of nocturnal bees as pollinators of these plants been studied. In the bat-pollinated *Cayaponia cabocla* (Cucurbitaceae), they are potential pollinators [75], but in the bat-pollinated tree *Caryocar brasiliense*, they efficiently remove floral resources without contributing to fruit set [20]. In chiropterophilous and sphingophilous flowers that provide easily accessible flowers with abundant pollen and nectar, nocturnal bees seem to generally be poor pollinators due to their morphological mismatch [20].

Moreover, nocturnal bees are generalists with regard to their food resources, and highly opportunistic. For instance, *Megalopta* bees captured on field bioassays in guaraná crops carried only pollen grains of this crop on their body, but other individuals of the same species also carried pollen of other species, mainly *Arecaceae* and *Euphorbiaceae* species [36]. Analysis of brood cell provisions of two *Megalopta* species has revealed pollen of 64 plant species from 19 families [34]. Bees of *Ptiloglossa* also visit different night-flowering plants, but in one single brood cell a monofloral pollen load was found [20]. The Paleotropical bee species *X. tranquebarica*, which visits flowers throughout the night, seems to be a generalist, as it was found to feed on diurnal leftovers from 71 plant species [76].

#### 5. Nocturnal Bees as Crop Pollinators

Our knowledge concerning crop pollination by nocturnal bees has increased recently (Table 1). Nocturnal bees have been recorded to be effective pollinators of regional crops in Brazil, such as cambuci (*Campomanesia phaea*-Myrtaceae), which are native to the Atlantic Forest, and guaraná (*Paullinia cupana*-Sapindaceae), native to the Amazon region. Both species are cultivated in their original habitat and both have regional economic importance [18,36,37,77]. Nocturnal bees most likely are pollinators of other Myrtaceae crops in the neotropics, for example of species in the genera *Eugenia*, *Campomanesia*, *Myrcia*, and *Pisidium*, which produce fleshy fruits. Flower opening before sunrise and an intense floral scent is common to all these species [18,38,39,59].

Nocturnal bees also pollinate flowers of cajá (yellow mombin, *Spondias mombin*-Anacardiaceae [35], which is an economically important and common fruit crop native to and cultivated in Northeast and Northern Brazil, and Central America. The genus *Spondias* includes other frequently used fruit crop species (e.g., *S. purpurea*, *S. tuberosa*) with similar blossoms, nocturnal anthesis periods, and floral resources [78,79], that also might be pollinated by nocturnal bees.

In North America, squash bees of the genera *Peponapis* and *Xenoglossa* display crepuscular flight activity that begins before sunrise. *Xenoglossa* is only active during twilight, whereas *Peponapis* also forages throughout the day [65,66,80,81]. Both species are oligolectic on species of *Cucurbita* (Cucurbitaceae) and effective pollinators of cultivated pumpkins (*Cucurbita foetidissima*, *C. maxima*, *C. pepo*).

Nocturnal bees visit flowers of a broad spectrum of families (at least 40 families) [82], such as Fabaceae, an important group of cultivated plants, where they show the ability to open the keel, typical for flowers of this family [56]. Their capacity to vibrate flowers to collect pollen makes nocturnal bees potential pollinators of a range of cultivated plants with poricidal anthers, such as *Solanum* species (eggplant, peppers, tomato) [30,56,72,73].

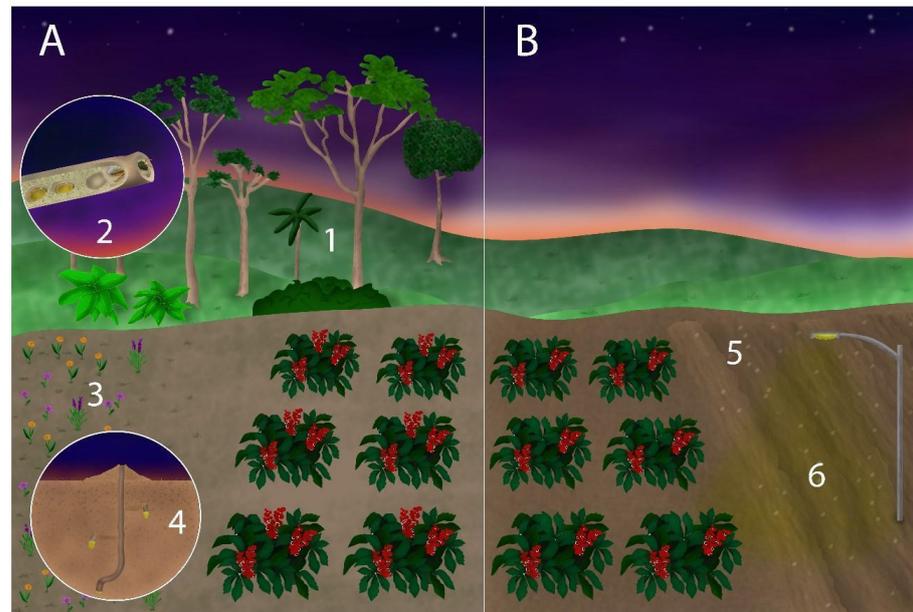
**Table 1.** List of crop plant families and species known to be pollinated (E = effective, P = potential pollination) by nocturnal bees; nocturnal bee genera that visit them; geographical occurrence; references (Ref.).

Plant Family	Plant Species (Popular Name)	Nocturnal Bee Genera	Role as Pollinators	Occurrence	Ref.
Anacardiaceae	<i>Spondias mombin</i> (cajá, yellow mombin)	<i>Megalopta</i> , <i>Ptiloglossa</i>	E	Caatinga-Brazil	[35]
	<i>Spondias pinnata</i> (wild mango)	<i>Xylocopa</i>	P	Tropical Forest-Southeast Asia	[83]
Cucurbitaceae	<i>Cucurbita foetidissima</i> (pumpkin)	<i>Peponapis</i> , <i>Xenoglossa</i>	E	Dry environments-Mexico/USA	[81]
	<i>Cucurbita maxima</i> (pumpkin)	<i>Peponapis</i> , <i>Xenoglossa</i>	E	Dry environments-Mexico/USA	[80]
	<i>Cucurbita pepo</i> (pumpkin)	<i>Peponapis</i> , <i>Xenoglossa</i>	E	Dry environments-Mexico/USA	[65,66,80]
Myrtaceae	<i>Campomanesia phaea</i> (cambuci)	<i>Megalopta</i> , <i>Ptiloglossa</i> , <i>Megommation</i> , <i>Zikanapis</i>	E	Atlantic Forest-Brazil	[18]
	<i>Campomanesia pubescens</i> (gabirola)	<i>Megalopta</i> , <i>Ptiloglossa</i>	E	Atlantic Forest, Cerrado-Brazil	[84]
	<i>Eugenia brasiliensis</i> (grumixama)	<i>Megommation</i>	P	Atlantic Forest-Brazil	[39]
	<i>Eugenia dysenterica</i> (cagaita)	<i>Ptiloglossa</i>	P	Cerrado-Brazil	[39]
	<i>Eugenia florida</i> (guamirim)	<i>Megalopta</i>	E	Amazon, Atlantic Forest, Caatinga, Cerrado-Brazil	[59]
	<i>Eugenia involucrata</i> (cereja-do-Rio-Grande)	<i>Megalopta</i> , <i>Megommation</i>	P	Atlantic Forest-Brazil	[39]
	<i>Eugenia neonitida</i> (pitangatuba)	<i>Ptiloglossa</i>	P	Atlantic Forest-Brazil	[38]
	<i>Eugenia punicifolia</i> (cereja-do-cerrado)	<i>Ptiloglossa</i>	P	Amazon, Atlantic Forest, Caatinga, Cerrado-Brazil	[38]
	<i>Eugenia pyriformis</i> (uvaia)	<i>Ptiloglossa</i>	P	Atlantic Forest-Brazil	[39]
	<i>Eugenia rotundifolia</i> (abajurú)	<i>Ptiloglossa</i>	P	Atlantic Forest-Brazil	[38]
	<i>Eugenia stipitata</i> (araçá-boi)	<i>Megalopta</i> , <i>Megommation</i>	P	Amazon, Atlantic Forest-Brazil	[39,85]
	<i>Eugenia uniflora</i> (pitanga)	<i>Ptiloglossa</i>	P	Atlantic Forest-Brazil	[38,39]
	<i>Myrciaria floribunda</i> (cambuí)	<i>Megalopta</i>	E	Amazon, Atlantic Forest, Caatinga, Cerrado-Brazil	[59]
	<i>Myrciaria dubia</i> (camu-camu)	<i>Megalopta</i>	P	Amazon-Brazil	[86]
	<i>Plinia cauliflora</i> (jabuticaba)	<i>Ptiloglossa</i>	P	Atlantic Forest, Cerrado-Brazil	[39]
<i>Psidium acutangulum</i> (araçá-pera)	<i>Megalopta</i>	P	Amazon-Brazil	[87]	
<i>Syzygium malaccense</i> (jambo-rosa)	<i>Ptiloglossa</i>	P	Atlantic Forest-Brazil	[39]	
Sapindaceae	<i>Paullinia cupana</i> (guaraná)	<i>Megalopta</i> , <i>Ptiloglossa</i>	E	Amazon-Brazil	[36,37]

This demonstrates not only the great potential of nocturnal bees as pollinators but also the necessity of extending observations in crops with nocturnal anthesis to analyze their contribution to pollination and food production in species of economic interest.

## 6. Requirements on Crop Areas to Host High Numbers of Nocturnal Bees

The biology of nocturnal bees is still poorly understood, and there is no possibility of acquiring nests commercially, as is possible for diurnal bees (e.g., *Osmia*, *Megachile*, bumblebees, stingless bees or honeybees), but some strategies to provide appropriate habitats to improve their presence around cropping areas will now be suggested (Box 1, Figure 2).



**Figure 2.** Comparing a more (A) and a less (B) sustainable crop area for hosting high numbers of nocturnal bee pollinators. Adjacent natural areas to provide food (1) and nest (2) resources; a range of cultivated, native flowering species offer food beyond the crop flowering season (3); potential nesting sites of ground-nesting species (e.g., *Ptiloglossa*) should be identified and protected (4); soil disturbance, such as that caused by deep tillage, fire, and superficial movements in the area by agricultural machines should be minimized, at least during the flowering season (5); artificial light pollution at night (ALAN) near crop areas should be avoided (6).

**Box 1.** Summary of nocturnal bee traits and needs in crop areas.

### Traits that make nocturnal bees efficient pollinators

- First floral visitors of resource-rich flowers
- Abundant floral visitors
- Generalists in terms of preferences for floral signals
- Generalists that visit different kinds of flowers
- Generalists in obtaining food resources
- Transfer of high amounts of pollen to stigmas
- Efficient buzzing of anthers
- Visit plants with different flowering strategies (mass-flowering or steady-state)

### Requirements for crop areas to host high numbers of nocturnal bees

- Large patches of natural vegetation
- Availability of several flower resources
- Conspicuous floral advertisement (e.g., floral scent)
- Appropriate nesting sites
- Reduced light pollution
- No pesticide application

Nocturnal bees typically nest around or within forest patches in the ground (e.g., *Ptiloglossa*, *Zikanapis*, *Megommation*) or in tree wood (*Megalopta*). Most crops known to be pollinated by nocturnal bees are surrounded by patches of native forest [18,36,37,59]. This indicates nocturnal bees' affinity to diverse native habitats with available flowers

and nesting sites nearby. In the context of fluctuating, or even disappearing resource environments, any sustainable practices that ensure a local diversity of flowers and nesting sites are essential, such as agroforestry management strategies. Moreover, if a crop can only offer pollen as a resource (e.g., Myrtaceae species) to nocturnal bees, it would be beneficial to provide other plants that also provide nectar, and vice versa. Furthermore, if the crop has a short blooming period, such as cambuci and guaraná, it is necessary to preserve further food sources beyond the crop flowering seasons [88]. Thus, future studies are needed to determine which wild plants are also able support nocturnal bees.

Based on these characteristics, crop producers should preserve native forest reserves adjacent to the cropping area as much as possible and restrict management of the soil, especially during the flowering season. For instance, nest aggregations of *Peponapis* and *Xenoglossa* are found near or even at the edge of pumpkin patches, and tilled soil disturbs their population and renders them less frequent in *Cucurbita* flowers [66,89]. Therefore, it is crucial to identify potential nests of nocturnal bees that build aggregations and to isolate the nesting site, to avoid movements by agricultural machines that could damage the nests. Moreover, the practice of applying pesticides should be avoided if the crop can potentially be pollinated with nocturnal bees.

Another factor to consider is light pollution. Nocturnal bees are traditionally captured by a range of different light-based traps, indicating that they are easily attracted by artificial white light and dark (UV) light [90]. Moreover, light is the most important factor controlling the activity of nocturnal bees at nests and flowers [53,54]. Thus, changes in natural light intensities, as might be caused by local light pollution, could affect their flight and pollination services. This so-called artificial light pollution at night (ALAN) is estimated to interfere with the nocturnal visits of pollinators to their host plants, reducing nocturnal visitation by up to 62% [91]. Moreover, light pollution can affect pollinator behavior, as seen in moths spending more time at artificial light sources than at flowers [92]. However, LED lamps have fewer negative effects, and tree cover can mitigate the effect of ALAN on nocturnal moth pollinators [93]. Therefore, even though more studies are necessary that investigate the effect of light pollution on nocturnal bee pollination, it is advised that local farmers should maintain artificial light sources as far as possible from orchards and crop areas, and keep their intensity at low levels, especially during twilight, since outdoor lighting can certainly disturb bees and deviate them from flowers.

## 7. Conclusions

As pollination is an essential service for world food security, we must understand and protect its agents, and this includes pollinators that have, to date, been relatively neglected, such as nocturnal bees. The role of nocturnal bees was, until recently, largely overlooked, since these bees were rarely seen or collected. However, as soon as nocturnal bees were studied in more detail, their importance as pollinators was determined to be much greater than previously reported. Long before the visits of diurnal bees, nocturnal bees are already in the flowers and have already contributed to plant reproduction. Thus, night-blooming crop species need to be reevaluated to determine whether nocturnal bees visit their flowers and if so, which species are visiting, and during which months and at which times during the night visits occur. It will also be necessary to investigate how these bees participate in the pollination of their hosts. Most plants mentioned visited by nocturnal bees also have diurnal anthesis and are also visited by diurnal bee species. Therefore, it is important to determine whether the pollination roles for nocturnal and diurnal species are complementary.

In this review, nocturnal bees were identified as effective pollinators of some crop species and potential pollinators of others. When attempting to take advantage of nocturnal bees as pollinators of crops, some precautions should be taken by farmers, such as soil management, provision of other food resources to local bees, and control of light pollution. In a world facing the challenges of climate change, habitat destruction, and biodiversity

loss, there is an urgent need to rescue as many crop pollinators as possible around the globe, including nocturnal bees.

### 8. Outstanding Questions for Future Studies

Are there other crops, apart from those we currently know, that are pollinated by nocturnal bees?

During which months (or seasons) of the year are nocturnal bees active in crop pollination?

What is the contribution of nocturnal bees, both biologically and economically, to the pollination of crop plants?

Are the crop pollination roles of nocturnal and diurnal bees complementary?

How do scent, brightness, and color of flowers interact to attract nocturnal bees?

How does light pollution affect nocturnal bee pollination in crop areas?

Is there any level of artificial light that can actually increase/decrease flower visitation by nocturnal bees and perhaps influence yields?

How does the wavelength composition of artificial light (i.e., different colors) affect the foraging activity of nocturnal bees?

Apart from crops, which wild plants support nocturnal bees?

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/article/10.3390/agronomy11051014/s1>, Video S1: *Ptiloglossa latecalcarata* (Colletidae) vibrating flowers of *Campomanesia phaea* (Myrtaceae) before sunrise.

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