

A global review demonstrating the importance of nocturnal pollinators for crop plants

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Abstract

1. Pollinating insects are critical to ecosystem stability and food security. Concerns about the impact of insect declines have therefore seen increased research on the role of wild pollinators in cropping systems. However, this research has predominantly focused on diurnal pollinators such as bees and flies, leaving the role of nocturnal pollinators poorly understood in comparison.
2. Here, we review the literature on nocturnal pollinators of food crops and medicinal plants by undertaking an abstract, title, and keyword literature search in Web of Science Core Collection [v.5.32].
3. We found interactions recorded between plants and nocturnal pollinators for 52 plant families, with Cactaceae, Fabaceae and Asparagaceae being mentioned most frequently in the context of nocturnal pollination. We identified 81 animal families that behave as nocturnal crop pollinators, with Sphingidae and Noctuidae moths and Phyllostomidae bats being mentioned most frequently.
4. The evidence to support claims of pollination by nocturnally active animals varied in strength and mostly involved observations of flower visitation or pollination being inferred based on floral traits. There was a lack of strong experimental evidence. Detailed experimental work, such as pollinator exclusion experiments, is therefore required to corroborate the patterns we have discovered.
5. Our review is biased towards publications in the English language, but despite this our study shows tropical regions such as Brazil appear to be hotspots for nocturnal crop pollination.
6. *Policy implications.* Our findings suggest that nocturnal pollinators visit a large range of crop plants, and may be more important to ecosystem function and food production than currently thought. Current policies in cropping systems implemented to protect bees, such as regulations on pesticide use, are unlikely to also protect nocturnal pollinators. As we develop a better understanding of the importance of nocturnal pollinators for crop plants, many of these regulations may need to be updated to ensure pollination service is not being compromised.

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KEYWORDS

Chiroptera, databases, ecosystem service, experimentation, global patterns, lepidoptera, mutualism, pollination

1 | INTRODUCTION

Globally, animals contribute to the pollination of roughly 85% of angiosperm plant species and 33% of crops produced—insects have the major role in this ecosystem service (Hahn & Bruhl, 2016; Potts et al., 2010). The western honey bee (*Apis mellifera*) is the most well recognised pollinator and the most commonly used managed pollinator for crop pollination (Rader et al., 2009). However, there has been an increased research focus on insects other than honey bees, particularly in crops (Rader et al., 2016). Some examples of these are: bumble bees (*Bombus* spp.; Cutting et al., 2018; McBrydie et al., 2017), solitary bees (Broussard et al., 2011), and non-bee taxa such as butterflies (Rasheed et al., 2015), flies (Cook et al., 2020; Howlett & Gee, 2019; Stavert et al., 2018) and moths (Buxton et al., 2021; Manning & Cutler, 2013; Pattenmore et al., 2018), yet all of these insect groups are still understudied compared with honey bees (Rader et al., 2016). Other understudied pollinators include vertebrates such as birds, lizards and mammals. Some economically and medicinally important crops are known to be dependent on vertebrate pollinators, particularly in the tropics (e.g. durian, Aziz et al., 2017). There are also reports of pollination services being provided to crops by lizards and a range of bird species elsewhere (Ratto et al., 2018). However, the overall role that vertebrates play as crop pollinators may be under-represented in the literature (Bumrungsri et al., 2008; Ratto et al., 2018) and their contribution to crop pollination is largely unknown.

In general, increasing pollinator diversity can enhance pollination services, and encouraging a wider range of pollinators within orchards can result in increased stability and provisioning of pollination services (Rader et al., 2016). Research has found many instances where wild and currently unmanaged pollinators may be better pollinators than honey bees for some crops, such as a study of gold kiwifruit (*Actinidia chinensis* P. 'Haegeum', Actinidiaceae) in Korea where bumble bees (*Bombus terrestris*) were the more efficient pollinators (Lee et al., 2019). Researchers have thus been investigating ways of using and promoting non-honey bee pollinators within orchards; e.g. bumble bee pollination in kiwifruit orchards in the absence of honey bees (Cutting et al., 2018), the provisioning of suitable wildflower habitat within sweet cherry orchards to promote the presence of wild pollinators (Mateos-Fierro et al., 2018), and raising populations of drone flies (*Eristalis tenax*) which behave as co-pollinators for crops such as pak choi and onion (Howlett & Gee, 2019). There are already instances where wild pollinators are encouraged into orchards, such as in some feijoa (*Acca sellowiana*, Myrtaceae) orchards. Feijoa is primarily pollinated by birds so growers can encourage birds by providing habitat and nesting boxes (Patterson, 1989). However, this increased research and use of non-honey bee pollinators has focussed almost entirely on diurnal pollinating species. In general,

nocturnal pollinators receive minimal and often incidental attention in the literature (e.g. Cutler et al., 2012); thus their contribution to the pollination of crop or medicinally important plants remains largely unknown and may be under-represented in the literature (Buxton et al., 2018; Macgregor & Scott-Brown, 2020). There is, however, a growing appreciation that nocturnal insects (particularly moths) may be contributing substantially to the pollination of commercially important crops such as apples (Robertson et al., 2021), avocado (Buxton et al., 2021), and gourds (Lu et al., 2021) making this area of research very timely.

Both diurnal and nocturnal pollination services are likely to be critically affected by declines in insect distribution and abundance. Global insect decline has been labelled 'Ecological Armageddon' (Leather, 2017), however the rate and generality of decline and the driving forces implicated are still poorly understood. For example, Hallmann et al. (2017) reported over 75% decline in flying insect biomass over 27 years in protected areas in Germany, but Macgregor et al. (2019) reported fluctuations, but no substantial decline, in moth biomass over 50 years in Britain, suggesting trends can be temporally and regionally variable. The accuracy surrounding the narrative of the 'Ecological Armageddon' has since come under scrutiny (Saunders et al., 2019).

Vertebrate pollinators such as bats are also increasingly threatened globally. There is evidence to suggest the pollination services of crops and medicinally important plants provided by these vertebrates can become unpredictable and unreliable if bat populations continue to decline (Ratto et al., 2018; Silva-Montellano & Eguarte, 2003), for example, hand pollination of pitaya (*Selenicereus undatus*, Cactaceae) takes place in the absence or reduction of the natural pollinators (Muniz et al., 2019).

Despite some uncertainties on the extent of global pollinator declines whether insect or vertebrate, any declines in both wild and managed pollinators are likely to be correlated with declines in pollination services to plants, which in turn leads to uncertainty around the stability of ecosystems and food production (Hahn & Bruhl, 2016; Ollerton et al., 2011; Potts et al., 2010). Commercial crops are not the only plants under threat if pollinators decline; many wild plant species are significant for medicinal and/or food purposes ("Let food be thy medicine and medicine be thy food"—Hippocrates), and these plant species are typically less studied than their commercially important counterparts. In light of the potential ecological, economic, cultural and social implications associated with the potential decline of pollinators, thoroughly understanding the importance of wild pollinators is a high research priority (Li et al., 2019; Macgregor & Scott-Brown, 2020).

This review will focus on wild nocturnal pollinators and their contribution to the pollination of crop and medicinally important plants, and will address four key questions: (1) what evidence is

there for the importance of nocturnal pollination for crop species? (2) how strong is the evidence and where are the gaps in our understanding? (3) which pollinating taxa and families have been identified as potentially key pollinators? (4) what plant taxa and families have been identified as benefiting from nocturnal pollination to some extent? This review will also address some key inherent biases associated with literature reviews in the context of our own.

2 | MATERIALS AND METHODS

2.1 | Literature search

An abstract, title, and key word search for papers in English, in Web of Science Core Collection (v.5.32) using 'nocturnal', 'pollinat*', and 'crop' as key words was conducted on 16 September 2019 and repeated on 12 March 2020 for literature on nocturnal pollination in cropping systems, and any paper that mentioned a nocturnal plant-pollinator interaction was included. Synonyms of 'crop' ('berry', 'fruit', 'vegetable', 'agri*', 'hort*', 'food', 'fibre', and 'forestry') were also searched. In total, 173 papers were included in the literature review (see Appendix S1).

We did not apply our own criteria for when a plant-pollinator interaction can be deemed 'diurnal' or 'nocturnal' and instead used the information provided in the sources, e.g. the statement "The baobabs comprise of eight species with large, spectacular, nocturnal flowers" in the abstract of Baum (1995) provided enough information to include their paper in our review. We defined a 'crop' plant as one where all or part of the plant is consumed, regardless of whether it was grown on large commercial scales or was harvested in the wild. Plants that are used for medicinal purposes, whether traditionally or commercially, were also included within our definition of a crop plant and were designated as being 'medicinal', regardless of whether there is scientific data to support this status. Many plants are used as both food crops and medicinally and for plants that fit both categories we designate them as crops. For simplicity, the terms 'pollination' and 'pollinator' are used when there is evidence that a floral visitor could act as a pollinator for the given plant, even if this evidence is circumstantial and even when the term 'floral visitor' may be more appropriate where pollination wasn't empirically proven. Despite our thorough search, we acknowledge that there may be additional relevant papers that are not included in the analysis (see the discussion concerning limitations of the literature review).

Plants and pollinating fauna were recorded at the family, genus and species levels, and whether the plant is used for either 'crop' or 'medicinal' purposes. The location of the study was recorded and whether the study identified other diurnal pollinators. Many literature sources provided evidence for nocturnal pollination for more than one plant or animal taxon, so the total number of mentions and evidence types exceeds the number of sources. The size of plant families was obtained from the Angiosperm Phylogeny Website (Stevens, 2001) and the size of the pollinating taxa families was

obtained from 'bugguide.net' and other published sources as required. Ethics approval was not required for this study.

2.2 | The nature of evidence for nocturnal pollination

The different types of evidence used to support the claim of nocturnal pollination in the source literature were recorded, and are ranked by strength in Table 1. For example, evidence types which are suggestive of pollination based on floral syndromes hypotheses (e.g. flower colour; Faegri & van der Pijl, 1979), are less robust than experimental evidence (e.g. pollinator exclusion experiments, which can identify pollinators and their effectiveness); a ranking of the strength of the evidence is thus important to accurately assess current knowledge. Evidence types were grouped into seven ranked categories following Buxton et al. (2018) from less conclusive (inferred) to most conclusive (experimental). Here, we define experimental evidence as any trial that manipulates the natural world to generate a response (e.g. pollinator exclusion experiments, hand cross-pollination), and observational evidence as a trial that records a response or observation in the absence of physical manipulation (e.g. pollen on animal bodies, flower visitation).

2.3 | Data analysis

We used negative binomial generalised linear models to assess whether families were under or over-represented in the literature reviewed, relative to the number of species in each family. The models for plants and pollinators each included the number of mentions in the literature as the response variable, and the number of species within the taxonomic family as the explanatory variable. Modelling was conducted in R (version 4.0.0, R Core Team, 2020).

3 | RESULTS

A total of 22 different evidence types were recorded across the seven evidence categories (Table 1; Figure 1a; Appendix S2). Visitation evidence (422 uses) was the most frequently used type of evidence, followed by contact evidence (218 uses). The presence of pollen on animal bodies had been used 202 times to support nocturnal pollination. Following this, a suite of floral traits (e.g. anthesis, nectar production) had been used at different frequencies to infer nocturnal pollination. When grouped into the seven ranked categories, there was considerably more weak evidence supporting nocturnal pollination than strong evidence (Figure 1b). Inferred evidence (618 mentions) was used most to support nocturnal pollination but trace evidence was used only twice. Visitation, contact, and pollen load evidence was well represented in the literature, but deposition (15 mentions) and experimental (97 mentions) evidence was largely absent from the literature.

TABLE 1 Evidence types, categories of evidence, nature of the evidence and a description of what the evidence encompasses. Evidence is ranked in order from weakest (morphology) to strongest (pollinator exclusion) as described in Buxton et al. (2018)

Evidence type	Category	Definition
Nature of evidence—Observational		
Floral morphology	Inferred	Physical aspects of the flower or animal used to infer pollination
Scent	Inferred	Production of scent from flowers at night
Electroantennography	Inferred	Recording animal response to floral scents
Flower colour	Inferred	Using colours known to be attractive to particular pollinators
Anthesis	Inferred	Flower opening times
Nectar sugar ratios	Inferred	Matching ratio of sucrose, fructose and glucose to certain visitors
Nectar production	Inferred	The availability of nectar to visitor at night
Nectar concentration	Inferred	Matching the amount of sugar in nectar to certain visitors
Stigma receptivity	Inferred	Timing of stigma receptivity to match nocturnal visitors
Anther dehiscing	Inferred	Timing of anthers releasing pollen
Floral heating	Inferred	Flowers being warmer than the surrounding air to attract visitors
Insect trapping	Inferred	Insect trapping to determine which insects are present
Scales on stigma	Trace	Using the presence of moth scales on stigma to infer visitation
Visitation	Visitation	Recording an animal visiting a flower for food or other activity
Contact	Contact	Observing an animal making contact with stigma and/or anthers
Pollen viability	Inferred	Whether pollen is able to germinate at night
Pollen loads	Pollen loads	The presence of pollen on an animal's body
Pollen transfer	Deposition	Measuring how pollen is transferred from one flower to another
Single visit deposition	Deposition	The number of pollen grains on a stigma after one visit to the flower
Nature of evidence—Experimental		
Scent choice test	Experimental	Measuring an animal's response to certain scent profiles in flowers
Hand cross pollination	Experimental	Artificial pollination at night to determine if seeds set
Pollinator exclusion	Experimental	Physically blocking pollinators at particular times of the day

Overall, observational evidence (1363 mentions) dominated the literature, with experimental (97 mentions) evidence only making up a small fraction of the evidence in support of nocturnal pollination (Figure 1).

A total of 52 plant families had been mentioned in the context of nocturnal pollination in the literature surveyed (Figure 2; Appendix S3). The Cactaceae, Fabaceae and Asparagaceae families received the most attention in the literature. A full list of plant families mentioned in the context of nocturnal pollination is available (see Appendix S3). Seventeen of the studies mentioned 11 families containing 26 species where no diurnal pollinators were recorded.

For 11 of the 52 plant families only one type of evidence was reported in the literature. The most frequently used evidence types for the 13 most mentioned plant families were as follows; inference evidence was used most frequently to support nocturnal pollination for Cactaceae (94 mentions), Fabaceae (78 mentions), Bombaceae (39 mentions), Arecaceae (23 mentions), Annonaceae (25 mentions), Convolvulaceae (19 mentions) and Solanaceae (41 mentions). Both inferred and pollen load evidence were used equally in Ericaceae (24 mentions each). Visitation was used the most in Asparagaceae (58 mentions), Cucurbitaceae (58 mentions), Caryophyllaceae (38 mentions), and Myrtaceae (38 mentions). Contact evidence was used most in Campanulaceae (36 mentions).

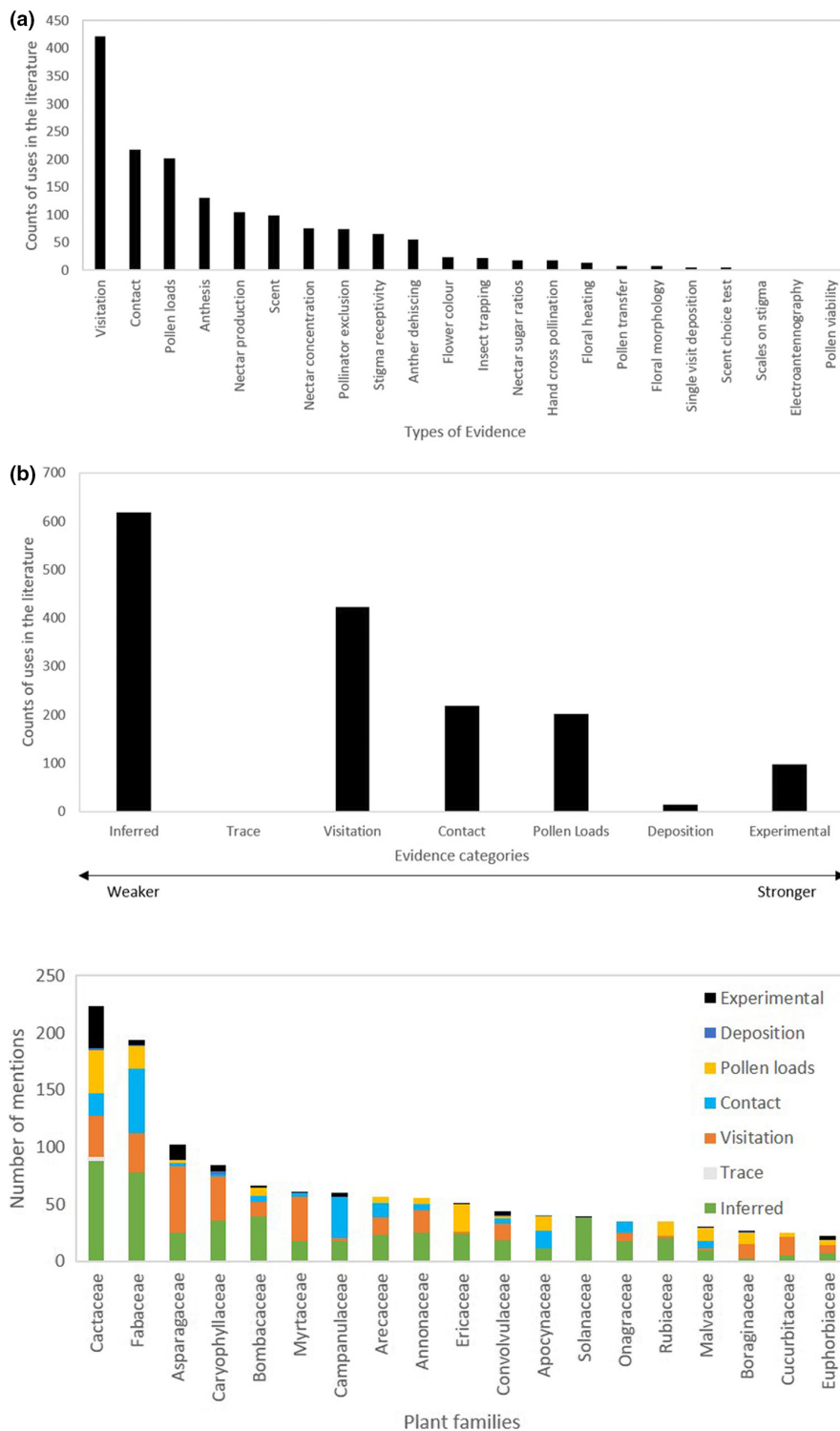


FIGURE 1 The 22 different evidence types (a) and the seven different evidence categories (b) in support of nocturnal pollination. The inferential strength of evidence in the bottom tile is displayed in order of left to right, with the weaker evidence (inferred) on the left and the stronger evidence (experimental) on the right. The y axis refers to the number of times that evidence was used and not the number of papers supporting nocturnal pollination (i.e. most papers included more than one type of evidence).

FIGURE 2 The number of times crop or medicinally important plant families were mentioned as being nocturnally pollinated to some extent and the types of supporting evidence available to support these claims.

Strong evidence types such as deposition and experimental evidence were used infrequently across all plant families, receiving most mentions for plants within Cactaceae (3 and 38 mentions respectively).

A total of 81 animal families had been mentioned as nocturnal pollinators of crop or medicinal plants in the literature surveyed (Figure 3; Appendix S2), with Sphingidae (hawkmoths), Noctuidae (moths), and Phyllostomidae (bats) receiving the most attention. A

diverse range of other pollinating taxa were also identified at lower frequencies (Figure 3; Appendix S2).

Forty-two of the 81 pollinating families were mentioned in association with only one type of evidence. The most common types of evidence associated with the 13 most frequently mentioned pollinating families were as follows; visitation evidence was most frequent for Sphingidae (108 mentions), Noctuidae (63 mentions), Phyllostomidae (46 mentions), Scarabaeidae (15 mentions),

FIGURE 3 The number of times animal families were mentioned as nocturnal pollinators of crop and medicinal plants to some extent and the categories of evidence available to support those claims. Only families with 10 or more mentions are displayed, see Appendix S2 for a full list.

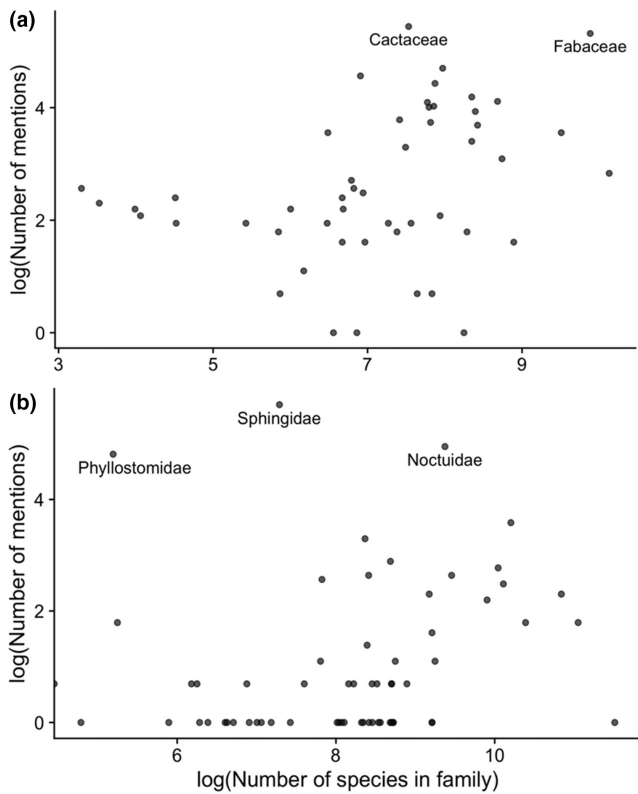
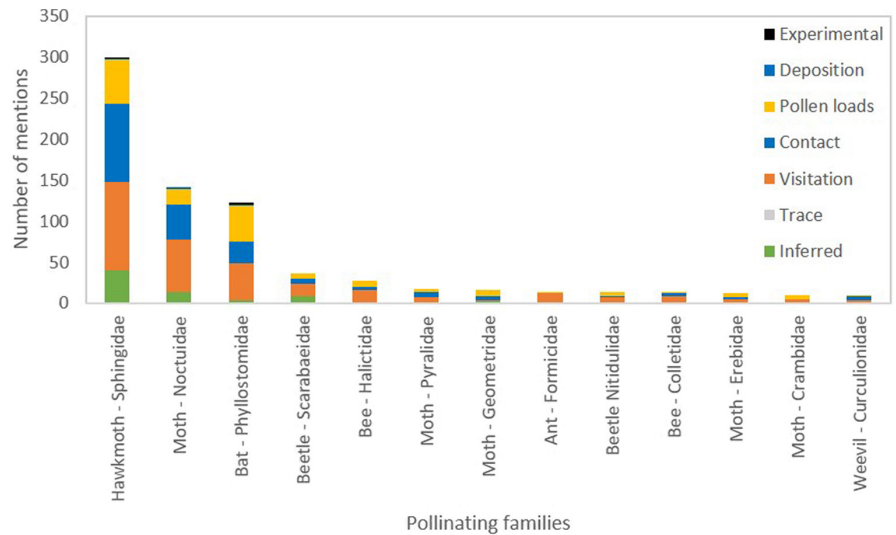


FIGURE 4 The relationship between (log 10) family size and (log 10) number of mentions in the literature for crop and medicinal plant families (a) and pollinator families (b).

Halictidae (16 mentions), Nitidulidae (7 mentions), Formicidae (13 mentions), and Colletidae (9 mentions). Both visitation and pollen loads were used equally for Erebidae and Crambidae (5 mentions each), pollen loads were used most for Geometridae (8 mentions). Strong experimental evidence was poorly represented across all pollinating families, only mentioned at low frequencies for Sphingidae (1 mention) and Phyllostomidae (3 mentions).

Family size (the number of species per family) was a reliable indicator for the number of mentions in the literature for plants ($X^2 = 6.11$, $p = 0.013$; Figure 4a) but family size was not a reliable indicator of mentions in the literature for pollinators ($X^2 = 0.528$, $p = 0.467$; Figure 4b). The plant family Cactaceae was over-represented in the nocturnal pollination literature relative to family size. The pollinating families Phyllostomidae, Sphingidae, and Noctuidae were over-represented in the literature.

We found 173 studies on nocturnal pollination for crop and medicinal plant species from 34 different countries (Figure 5). Mexico, Brazil, the United States of America (USA) and India had conducted the most studies (25, 24, 11, and 10 respectively).

4 | DISCUSSION

4.1 | Evidence for nocturnal pollination

The role of nocturnal pollinators has been largely overlooked on a global scale when compared to studies on diurnal pollinators, and the majority of the evidence available in support of nocturnal pollination generally is based on floral visitation, with more conclusive evidence largely absent (Buxton et al., 2018; MacGregor et al., 2014). This holds true when specifically looking at the role of nocturnal pollinators for crops and medicinally important plants, where visitation is used most frequently, and is likely a reflection of the difficulty of conducting pollinator surveys at night. Documenting the pollen on flower visitors' bodies is a useful solution for overcoming the difficulty of nocturnal surveys; in our review it was the third most commonly used type of evidence. While these data demonstrate plant-animal interactions, a reliance on this quantitative evidence alone is problematic as not all insects that visit a plant pollinate it, and non-pollinating flower visitors can even be detrimental to a plant's overall fitness through the removal of pollen and nectar that would be better used by effective pollinators (Newstrom & Robertson, 2005).

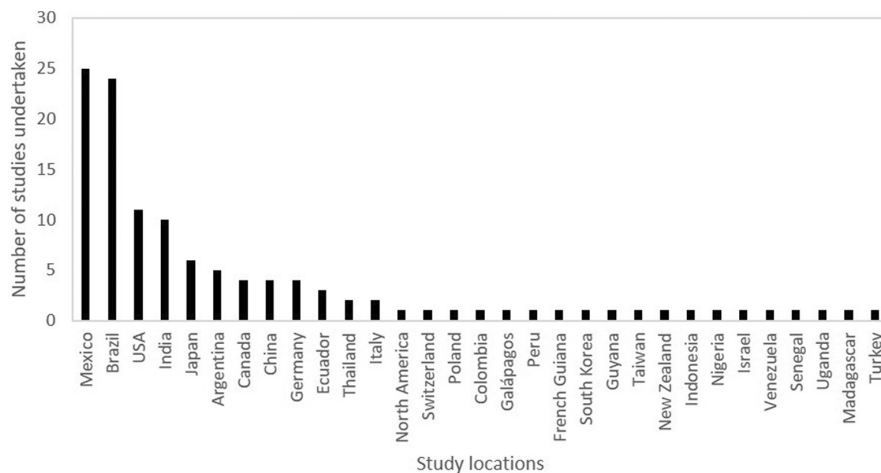


FIGURE 5 Publications on nocturnal pollination for crop plants of economic or medicinal importance by country.

In the literature surveyed, a suite of botanical evidence was also used to suggest that crop plants were at least partially pollinated nocturnally. The most frequently used evidence was anthesis—the timing of flower opening coinciding with the foraging time of nocturnal flower visitors (Macgregor & Scott-Brown, 2020). Flower scent was also used frequently as evidence and in a variety of ways, from the production of scent at night (e.g. Cordeiro et al., 2017) to researchers identifying particular scent compounds known to be attractive to nocturnally active pollinating taxa. For example Raguso et al. (2003) showed two hawkmoth-pollinated *Nicotiana* species emit floral compounds similar to those emitted by other hawkmoth-pollinated plants. Some studies took their research on floral scent significantly further and conducted choice tests where they recorded the response of pollinators to different floral compounds; for example, Vlásáková et al. (2008) measured how *Amazonina platystylata* (the primary pollinator of a *Clusia* species, Clusiaceae) perceived acetoin, which is a floral compound involved in pollinator attraction. Nectar production, the concentration of sugar in the nectar, and the ratio of different sugars in nectar have all been used to identify potential pollinators based on known requirements or preferences of particular flower visitors. Tiedge and Lohaus (2017, 2018) analysed nectar in *Nicotiana* species and found that night flowering species had the greatest nectar sugar concentration in the middle of the night, and suggested that sucrose-rich nectar in tubular flowers may be an adaptation to pollination by long-tongued pollinators such as moths.

Records of floral visitation and botanical evidence are useful for identifying that a plant species may benefit from nocturnal pollinators, however a reliance on these types of evidence alone is problematic as no pollinators are empirically determined and the effectiveness of any flower visitors remains untested. For example, nectar production and sugar concentrations, along with observations of diurnal flower visitation could have led Molina-Freaner and Eguiarte (2003) to conclude that *Agave angustifolium* and *Agave subsimplex* (Asparagaceae) were diurnally pollinated, yet the results of their pollinator exclusion experiments showed that diurnal pollinators contributed very little to overall fruit set and that moths and bats were the main pollinators for these plant

species. Similarly, de Araujo et al. (2020) could have concluded that nocturnal bees contribute to the pollination of *Caryocar brasiliense* (Caryocaraceae) though pollen on bee bodies, bees contacting the sex organs and flowers being receptive at night, but the results of pollinator exclusion experiments determined that nocturnal bees do not contribute to the pollination of this plant which is typically pollinated by bats. These are just two examples of how multiple types of evidence, and particularly conclusive evidence, is required in order to draw reliable conclusions about the reproductive biology of plants.

The more robust categories of evidence for nocturnal pollination, such as pollen deposition and experimental evidence, were present in the crop and medicinal plant literature surveyed, but at low levels. This is consistent with reviews by MacGregor et al. (2014) and Buxton et al. (2018) who found a lack of strong evidence for the role of moths as pollinators generally. This lack of strong evidence is likely due to the difficulty of conducting work at night, and the time and resources required to gather experimental data. Using a range of evidence types, as well as sampling during both the day and the night, are extremely valuable for pollination studies, as exemplified by Cordeiro et al. (2017), even if preliminary nocturnal work is done solely to determine if night sampling is warranted. For example, *Agave angustifolia* produces nectar during the day and is visited by a range of diurnal visitors, but in a comprehensive study, none of these diurnal visits resulted in pollination (Molina-Freaner & Eguiarte, 2003). By using a range of evidence, including more conclusive evidence types such as pollen loads and pollinator exclusion experiments, and including sampling efforts at night, the authors were able to identify the bat *Leptonycteris curasoae* as the primary pollinator for *A. angustifolia*, with moths acting as co-pollinators (Molina-Freaner & Eguiarte, 2003). The existing observation-based literature provides many starting points for further investigation. For example, Gardner-Gee et al. (2014) used visitation data to investigate nocturnal pollination for *Kunzea ericoides* (Myrtaceae) and identified 12 potential nocturnal pollinators. A productive next step would be to experimentally determine the overall contribution of these flower visitors to pollination to better understand their significance to this species.

4.2 | Plant families in nocturnal pollination literature

Nocturnal pollination has been reported for a total of 52 plant families containing crop or medicinal plant species. Cactaceae was found to be considerably over-represented in the literature when compared to families such as Fabaceae, which is a much larger plant family with a similar number of mentions. Rubiaceae and Asteraceae appeared to be particularly under-represented in the literature especially given their very large family sizes. These and other large plant families with few mentions should be further investigated for interactions with nocturnal pollinators. Less commonly mentioned families such as Convolvulaceae, Euphorbiaceae, and Myrtaceae, for which there is some experimental evidence in support of nocturnal pollination, should also be further investigated because of the strong evidence of nocturnal pollinator-plant associations.

For most plant families, there was more than one type of evidence to support claims of nocturnal pollination; only 11 families were associated with only one evidence type, and for these families, the evidence was less conclusive. The majority of the evidence to support nocturnal pollination for all plant families tended to be less conclusive in nature, although nocturnal pollination in the Cactaceae family is supported by substantial experimental evidence. Experimental studies for this family and others in the review tended to be pollinator exclusion experiments, an effective technique that also tends to have a short time investment. These studies offer qualitative data on the contribution of pollinators at various times, but while it is possible to exclude pollinators of different sizes (e.g. bats vs. moths), these experiments typically do not identify the pollinators and discerning this information requires an additional time investment. The use of a wide range of evidence types is again encouraged to discern the identity of pollinators as well as their effectiveness.

No diurnal pollinators were recorded for 11 plant families containing 26 species; these 17 studies stand out as they explicitly state that no diurnal pollinators were recorded despite attempts to do so, as opposed to the remaining studies that either did identify diurnal pollinators, did not look, or simply did not address them. Nocturnal flower visitors can act as primary pollinators (e.g. Scopece et al., 2018), secondary pollinators (e.g. Pelletier et al., 2001), or as co-pollinators with diurnal pollinators (e.g. Cutler et al., 2012). Currently, nocturnal pollinators are not considered to be important pollinators for crops and in particular reference to moths, they are instead considered act as co-pollinators or pollinators for non-crop plants in agricultural spaces (Hahn & Bruhl, 2016). In our review, we do not make comment on the quality or contribution of particular pollinating taxa and instead we report on a taxa pollinating or being pollinated in some capacity at night. However, some of the papers included in this review identified crop plants that are pollinated exclusively at night, for example, *Bauhinia forficata* (Fabaceae) is pollinated primarily by the hawkmoth *Manduca sexta* (Neto, 2013). Bees visited the flowers during the day and removed pollen but did not contact the stigma, making their visits detrimental to the plant's overall fitness (Newstrom & Robertson, 2005). Another example is

Saponaria officinalis (Caryophyllaceae), which is solely pollinated at night by moths and hawkmoths (Wolff et al., 2006), and in apples where both diurnal and nocturnal pollinators contribute equally to fruit set (Robertson et al., 2021). This demonstrates that nocturnal pollination can be important for many plant families, including plants of economic and medicinal importance. However, we suggest that the relative contribution of nocturnal pollinators cannot yet be accurately gauged and further research is necessary and timely.

4.3 | Animal families in nocturnal pollination literature

Nocturnal pollination activities have been reported by species in 81 animal families, however only 19 of these families have been mentioned more than three times in the literature. This suggests there are many opportunities for productive research on these and other taxa and that in general there is very low reporting or investigation of nocturnally active pollinators. We found that pollinating taxa were not mentioned in proportion to the size of the family. The fact that Sphingidae hawkmoths and Phyllostomidae bats received the majority of the attention in the literature despite having fewer species than families such as Scarabaeidae beetles and Geometridae moths may be reflective the charismatic or tractable nature of the study species within these families. Noctuidae, being both a large family and mentioned frequently in the literature supports the observation of Macgregor and Scott-Brown (2020) that large moths may be the best-studied nocturnal taxa.

Not surprisingly, families that have received more research attention also tended to have a greater range of evidence and more conclusive evidence associated with them to support claims of nocturnal crop pollination. Yet, there is very little experimental evidence of pollinator effectiveness, and those few studies typically focused on bats and hawkmoths. Conversely, there is a comparably larger amount of experimental evidence to show plants benefit from nocturnal pollination and this is likely reflective of the experiments conducted, e.g. pollinator exclusion experiments where the pollinators are not typically identified but flower fates can be followed (e.g. Cutler et al., 2012). Records of animals visiting flowers thus offer the most support for plant-pollinator interactions. This wealth of visitation data paired with the diverse range of pollinating families identified, particularly families that have been mentioned a moderate number of times such as Scarabaeidae (scarab beetles), Halictidae (halictid bees), and Formicidae (ants), provides a starting point for more convincing experimental studies of the quality of these flower visitors as pollinators for crops and other plants of significance.

4.4 | Global distribution of the literature and limitations

The global distribution of research on nocturnal pollination of crop and medicinal plant species is patchy, with most work done in Brazil

and Mexico. Studies in Mexico are predominantly on plants in the Cactaceae and Asparagaceae families, particularly *Agave* species. Studies from Brazil were not dominated by any particular plant family, suggesting that Brazil may be a hotspot for the evolution of nocturnal pollination systems or the study of them. There are advantages to both plants and pollinators to interact at night; pollinators can feed in the absence of diurnal predators and avoid direct competition with bees which can dominate the landscape (particularly in agricultural settings), and particularly for plants in tropical regions flowering at night can reduce temperature and water stress (Holland & Fleming, 2002; Macgregor & Scott-Brown, 2020; van Doorn & van Meeteren, 2003). Lower ambient temperatures combined with the higher relative humidity at night may also be favourable for plants that flower at night; high temperatures during the day may inhibit pollen tube growth, as occurs for Durian (*Durio zibethinus*, Malvaceae) in Thailand (Jutamanee & Sirisuntornlak, 2017). We suspect that research into plants that occur in similar climatic conditions experienced in Brazil may reveal additional relationships with nocturnal pollinators.

It is important to note here that our findings reflect only English-language publications, and may not necessarily reflect nocturnal plant-pollinator relationships distributed throughout the world and instead be a reflection of how our literature search was conducted (Nuñez & Amano, 2021). We are aware of at least one example of a publication which is not present in this review and it is our own New Zealand study on the factors inducing nocturnal flowering in Avocado (*Persea americana*, Lauraceae) and the potential for nocturnal pollination (Pattimore et al., 2018). While the words 'nocturnal' and 'pollinat*' occur in the title and key words of this paper, 'crop' and our additional synonyms are missing and may explain the lack of this and other commercially grown crops in our review despite what we believe to be an extensive literature search. To help remedy this, future research and review papers could add a particular focus on plant uses and include a broader definition or range of key words to capture works that would otherwise be missed. There are also large gaps throughout Asia where we would have expected to see at least some literature, particularly on commercial crops such as Durian which are economically important and grown commercially throughout Southeast Asia and pollinated at night (Aziz et al., 2017; Jutamanee & Sirisuntornlak, 2017). In our review, we only came across one paper on Durian pollination, a study by Jutamanee and Sirisuntornlak (2017) where no pollinators were identified but fruit set from nocturnal hand-pollination resulted in more and greater quality fruit than from hand-pollination during the day. There is also likely a lot of information in the form of traditional knowledge as well as unpublished student theses on nocturnal pollinators for culturally and economically important crop plants that has not been published in peer-reviewed scientific literature and thus not included in our review.

Language barriers also influence returns in literature searches when publications are not written in English, especially when taking into account the barriers and biases non-native English speaking authors face (Clavero, 2011; Di Bitetti & Ferreras, 2017; Hanauer

& Englander, 2011). Twelve of the papers found during the search for this review were published with an English title and/or abstract, but the contents of the paper were written in Portuguese (5 papers), Spanish (4 papers), Thai (1 paper), Mandarin (1 paper), and Catalan (1 paper), and our inability to effectively translate these languages excluded their contribution to this review. Many journals are moving to publications exclusively in English (e.g. Brazilian Journal of Botany in 2012 [previously *Revista Brasileira de Botânica*]) but this change does not impact already published literature and can add additional barriers for non-native English speakers. We decided to conduct another literature search using our key words but in Malay, as Malaysia did not appear in our initial results despite our expectations (the one study we located from Malaysia appeared in our second search of the literature [Cho & Ding, 2021]). This search in Malay revealed information on *Dipterocarpus* and *Parashorea* within Dipterocarpaceae, two genera of plants utilised for their timber. Flowers for species in these genera "mostly open in the evening but persist for the next day or two, are visited by both nocturnal and diurnal insects" and particularly for *Dipterocarpus tempehes*, "pollen dispersal by moths and bees is similar" (Ghazoul, 2016). The fact that our study has highlighted tropical regions as hotspots for nocturnal pollination despite the northern temperate bias of the English-language scientific literature strongly suggests that nocturnal crop pollination is even more widespread in the tropics than our review indicates.

In our and many other reviews, grey literature (such as reports commissioned by industries and non-for-profit organisations) may be absent as an artefact of only scientific journals being searched. There is a greater volume of grey literature in tropical regions than peer-reviewed scientific literature on topics such as ecology and conservation where many pollination based studies belong, and this information can be important for research and policymaking (Corlett, 2011; Li et al., 2019). Grey literature can also be the only source of information on particular projects or species, meaning studies on distributions may be misleading (Corlett, 2011). This can be addressed, as exemplified by Li et al. (2019) whose review of pollination in oil palm returned 84 scientific papers on oil palm pollination and a further 200 articles in the grey literature. While it may not always be achievable due to accessibility, searching grey literature and non-English scientific publications could be incorporated into future reviews to get a better and more complete understanding of world-wide trends.

5 | CONCLUSION

In our review, we found 173 papers that dealt with nocturnal pollination for crops and plants of medicinal significance, suggesting that nocturnal pollinators are likely more important than currently considered. Also, our study, though biased by its restriction to largely English-language literature, strongly suggests that nocturnal pollination may be particularly important to crops in tropical regions. However, the majority of the evidence we found that supported nocturnal pollination was incidental and weak

in nature. There were also large biases in plant and pollinating families investigated, with an over-representation of studies on hawkmoths and bats as pollinators and Cactaceae as a family of plants pollinated at night. Future studies need to address these inherent methodological, study system and language biases before we can accurately gauge the global importance of nocturnal pollination for crops and plants of significance. As a first step, crop plants and pollinators in the families identified here, particularly those lesser studied families, need to be investigated using diverse and more conclusive methodological approaches in future pollination studies, such as documenting pollen transfer efficiency and fruit set.

AUTHOR CONTRIBUTIONS

Max N. Buxton, Anne C. Gaskett, Janice M. Lord and David E. Pattemore conceived the ideas and designed methodology; Max N. Buxton collected the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data available via the Figshare Repository <https://doi.org/10.6084/m9.figshare.19149068.v2> (Buxton et al., 2022).

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SUPPORTING INFORMATION

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

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