When the day ends: Shedding light on the role of nocturnal moths as pollinators in tropical ecosystems

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Abstract

1. This review synthesises available knowledge on the moth pollination of tropical plants. We reviewed moth adaptations for nectar feeding, floral traits tailored to moth preferences, plant adaptations to moth pollination, the relative proportion of pollination syndromes and the proportion of moth-pollinated plants in tropical communities.
2. Moths are adapted to foraging by advanced vision and olfaction to navigate under low light. Floral traits, including colour, scent, or nectar concentration, adhere to these adaptations, attracting nectarivorous moths or even evolving into phalaenophily and sphingophily pollination syndromes.
3. Moth pollination is crucial for numerous tropical plant species across >25 families. In tropical ecosystems, plants with sphingophilous and phalaenophilous flowers account for 4% to 13% of species diversity, while moth-pollinated plants are represented in 0% to 20% of species. Given the proportion of moth-pollinated plants and that moths are rather infrequent visitors of flowers, we determine moths as crucial pollinators in the tropics.
4. Current research shows biogeographic biases and faces methodological challenges, observational and identification difficulties and limitations by necessary equipment. These constraints result in the limited knowledge of the ecological roles of moths in tropical regions and the need for comprehensive studies on nocturnal pollinators.
5. Future research should integrate community-level surveys and specific pollination system studies. Emphasising modern methods such as camera traps, AI-driven identification, and NGS metabarcoding will be instrumental in addressing current research gaps. Understanding the role of moths in pollination, maintaining biodiversity, and ecosystem services is critical, especially considering the changing climate.

Introduction

Pollination is a key mechanism in the sexual reproduction of flowering plants. Animals, particularly insects, play a major role as pollinators, with about 94% of tropical plant species dependent on animal pollination (Ollerton *et al.*, 2011). Animal-mediated pollination (zoogamy) appears advantageous in diverse species-rich tropical ecosystems where wind transfer of pollen to conspecific plants is less effective (Bawa, 1990; Cox & Grubb, 1991; Ollerton *et al.*, 2011; Ollerton, 2021). However, our understanding of the role of insects as the dominant pollinators of tropical angiosperms remains limited (Vizentin-Bugoni *et al.*, 2018) despite most of their diversity occurring in tropical ecosystems (Basset *et al.*, 2012; Novotny *et al.*, 2006).

Lepidoptera is one of the most diverse insect orders (Stork, 2018), with approximately 160,000 described species (van Nieukerken *et al.*, 2011), mainly composed of moths. Moths form a paraphyletic group with a monophylum of butterflies (Papilionoidea) as an internal clade (Kawahara *et al.*, 2019). They play an exceptional role in most terrestrial ecosystems, serving as important herbivores for nearly all plant groups and as food sources for various vertebrates and invertebrates. While adults of many moth groups are nectarivorous, and some have been proven as efficient pollinators for both wildflowers and crops (Faegri & Pijl, 1979; Rader *et al.*, 2016; Wardhaugh, 2015), and others as nectar thieves (Sakhalkar *et al.*, 2023), their general role as pollinators remains largely unexplored.

This review primarily focuses on Macroheterocera (hereafter referred to as *moths;* Kawahara *et al.*, 2019), a relatively common moth group in pollination studies. Knowledge about other moth groups is sparse, except for the well-studied obligatory mutualism combining active pollination and seed herbivory in yuccas (Asparagaceae), *Pachycereus schottii* (Cactaceae), and a few genera of Phyllantaceae plants whose pollination systems were already reviewed by other authors (e.g. Fleming & Holland, 1998; Kawakita, 2010; Pellmyr, 2003). Nevertheless, this review also touches on *micromoths* when they are undifferentiated from other moths in some pollination studies. We exclude butterflies and diurnally active moths (e.g. zygaenids, sesiids, and diurnal species of other groups; Powell, 2009) due to their differing adaptations to daytime pollination (Willmer, 2011).

We further categorise moths into *hawkmoths* (Sphingiidae) and *settling moths* (e.g. Noctuidae, Geometridae, Erebidae, Pyralidae) based on their adaptations to nectarivory. Hawkmoths, typically large-bodied and big-eyed moths, often have a long proboscis for nectar extraction (Krenn, 2010). They are generally able to hover while feeding (Willmer, 2011), mainly on nectar (Stöckl & Kelber, 2019). They are predominantly crepuscular or nocturnal (de Camargo *et al.*, 2016). Settling moths represent a diverse moth group, with many nectar-feeding species, although adults of many species feed on other sweet liquids, such as fermented fruit and leaking saps (Krenn, 2010). Unlike hawkmoths, they typically do not hover during feeding but settle on flowers for extended periods (Faegri & Pijl, 1979; Ghazoul, 1997). We take the identifications of moths provided in the cited papers as correct without independent corroboration; we only updated the nomenclature whenever necessary.

In this review, we synthesise current scientific knowledge on the role of moths in pollination of tropical plants. We examine the characteristics and adaptations of adult moths related to nectar feeding and pollination and investigate plant adaptations to moth pollination and floral traits that align with moth preferences. This includes a review of moth-related pollination syndromes. We review studies on pollination systems of particular tropical plant species, often providing detailed insights into the behaviour or efficiency of moth pollinators. We assess the importance of moths as pollinators in tropical communities, focusing on the proportion of sphingophilous and phalaenophilous plants and plants primarily pollinated by moths. We also examine the prevalence of moths as flower visitors, focusing on their visitation frequency and proportion relative to other visitors. This review aims to provide a comprehensive synthesis of plant and moth adaptations, research approaches in individual pollination systems and community-level studies, and determine the overall role of moths as pollinators in tropical ecosystems.

Adaptations of moths to pollination

Adult moths possess a tubular proboscis, modified maxillary galeae, and exclusively consume liquid food. As such, foraging moths visit flowers only for nectar (a sugar-rich liquid providing energy), as they cannot feed on pollen and other floral rewards. The fluid intake is facilitated by a sucking pump located inside the head, drawing liquid into the digestive system when the pressure drops (Krenn, 2010). The rate of nectar intake is influenced by its physical properties, such as viscosity, related to its concentration and composition (Nardone *et al.*, 2013). For instance, experiments with hawkmoth *Macroglossum stellatarum* (Linnaeus, 1758) showed that nectar intake rate decreases with increased viscosity (Josens & Farina, 2001). Moth proboscis length varies among groups and species. For instance, hawkmoths can have a notably long proboscis (well over 10 cm), such as in *Agrius convolvuli* (Linnaeus, 1758) and *Coelonia fulvinotata* (Butler, 1875). In contrast, other species like *Hippotion celerio* (Linnaeus, 1758) and *Daphnis nerii* (Linnaeus, 1758) have substantially shorter proboscis (~4 cm or less; Martins & Johnson, 2007). Such variation in the proboscis length can drive the evolution of floral diversity in plant communities, prompting the development of specialised flowers with matching spur or tube lengths to accommodate specific moth pollinators (Whittall & Hodges, 2007).

As pollen vectors, moths lack specialised organs but carry pollen on various body parts, mainly legs, head, and proboscis, depending on their feeding behaviour and morphological match with the visited flowers. Settling moths, typically walking on flowers to access nectar, transfer pollen mainly on their legs and bodies (Faegri & Pijl, 1979). In contrast, hawkmoths, often hovering while consuming nectar, primarily contact flower reproductive organs with their head or proboscis. Consequently, some plants have evolved adaptations, such as sticky or spiky surfaces of pollen grains, to attach pollen to a moth proboscis (Kislev, 1972; Smith *et al.*, 2022). Some plants even target specific sections of the proboscis for pollen attachment, such as observed in hawkmoth-pollinated *Angraecum arachnites* (Orchidaceae) from Madagascar, which attaches pollinaria to the ventral side of a proboscis near the head (Nilsson *et al.*, 1985). Similarly, pollinaria of noctuid-pollinated *Sauroglossum elatum* (Orchidaceae) and pollen of several cacti species (Cactaceae) often attach to a proboscis (Ferreira *et al.*, 2018; Singer, 2002). Interestingly, an unusual attachment of pollinaria to moths' eyes was observed in the tropical *Cynorkis uniflora* (Orchidaceae; Nilsson *et al.*, 1992).

Nocturnal and crepuscular moths possess highly adapted vision and olfactory systems for locating floral resources in dark (Wardhaugh, 2015). Their compound eyes with receptors sensitive to UV, blue and green wavelengths (approximately 350 to 550 nm) allow them to see in colour, even in dim light, as observed in four hawkmoth species (Kelber, 2003). Their limited red sensitivity distinguishes most moths from butterflies (Sondhi *et al.*, 2021). Simultaneously, moths possess olfactory organs located in their antennae and labial palps (Chen *et al.*, 2021; Szyszka *et al.*, 2014), which are essential for locating flowers at night (Balkenius *et al.*, 2006; Klahre *et al.*, 2011). Understanding their visual and olfactory adaptations is crucial for understanding their interactions with flowering plants, particularly regarding pollination syndromes (Willmer, 2011). While distinguishing the relative importance of floral colours and odours for foraging moths is challenging, some moth species perceive colour and odour distinctly (Balkenius & Dacke, 2013). Certain hawkmoths demonstrate remarkable adaptability in learning and responding to new nectar sources based on colour and odour cues, a vital adaptation during migration (Balkenius & Dacke, 2013).

Floral traits and pollination syndromes

Plants adapt their flowers in various features such as colour, scent, size, and shape to attract specific groups of pollinators (Faegri & Pijl, 1979; Willmer, 2011). While these floral traits can attract some pollinators, they may exclude others. For instance, prolonged floral tubes or spurs can restrict short-tongued visitors from consuming nectar (Wang *et al.*, 2020). Similarly, nocturnal anthesis hinders diurnal animals' access to floral rewards designated for nocturnal pollinators (Rocha *et al.*, 2019). Various plants employ distinct strategies, yet certain trait sets have evolved convergently across plant groups (Fig. 1); these trait sets are termed *pollination syndromes* (Faegri & Pijl, 1979; Willmer, 2011). Despite ongoing debates over the general validity of pollination syndromes (Balducci *et al.*, 2019; Queiroz *et al.*, 2021; Santos-Gómez *et al.*, 2021), together with the varying importance of particular traits under differing conditions (Klomberg *et al.*, 2022), they provide a valuable concept for discussing selection pressures and adaptations of floral traits towards particular functional pollinator groups, such as bees, bats, and butterflies. In this context, we will use pollination syndromes to present floral trait adaptations for moth pollination.

For nocturnal moths, two recognised pollination syndromes are *sphingophily* for hawkmoths and *phalaenophily* for settling moths (Faegri & Pijl, 1979; Willmer, 2011). These syndromes share multiple trait adaptations resulting from both moth groups' shared morphological, physiological and behavioural traits. Nocturnal anthesis is essential due to the nocturnal activity of moths. Some plants, *Guettarda speciosa* (Rubiaceae) for example, bloom exclusively at night (Xu *et al.*, 2018), while others, like *Bauhinia forficata* (Fabaceae), open flowers at dusk with stigmas becoming receptive at night (Neto, 2013). Specific orchids, such as *Bonatea polypodantha* and *Bonatea steudneri* (Orchidaceae), remain open for several days but produce scent and nectar only at night (Balducci *et al.*, 2019; Balducci *et al.*, 2020). Both pollination syndromes feature white, cream or pale flowers (Willmer, 2011). White flowers reflect light across all wavelengths, including the short-wavelength light best perceived by moths (van der Kooi, 2021). The contrasting floral colours also enhance visibility in environments with insufficient light (van der Kooi, 2021). Conversely, green or dull-coloured flowers, less noticeable to diurnal visitors, attract nocturnal pollinators with strong scents (Johnson *et al.*, 2020). The scents of moth-pollinated flowers are typically sweet and strong (e.g. Albuquerque-Lima *et al.*, 2020; Neto, 2013; Xiong *et al.*, 2020), although variations exist, like the sour and acrid scent of *Dipcadi brevifolium* (Asparagaceae; Manning *et al.*, 2012). Common scent compounds in both syndromes include, for instance, nitrogen-containing fragrances and linalool (Knudsen & Tollsten, 1993).

Beyond their attractant traits, both moth-related pollination syndromes also share traits linked to floral rewards, aligned with moth physiology (Heinrich, 1975). The nectar concentration in moth-pollinated flowers ranges from 13 to 27% (Hernández-Montero & Sosa, 2016; Maruyama *et al.*, 2010; Nilsson *et al.*, 1987; Potascheff *et al.*, 2020; Rocha *et al.*, 2005; Rocha *et al.*, 2019), although experiments on *Macroglossum stellatarum* under laboratory conditions showed the optimal concentrations as 34% (Josens & Farina, 2001). However, high sugar concentrations can be challenging for moths with long and narrow proboscis to consume (Stöckl & Kelber, 2019).

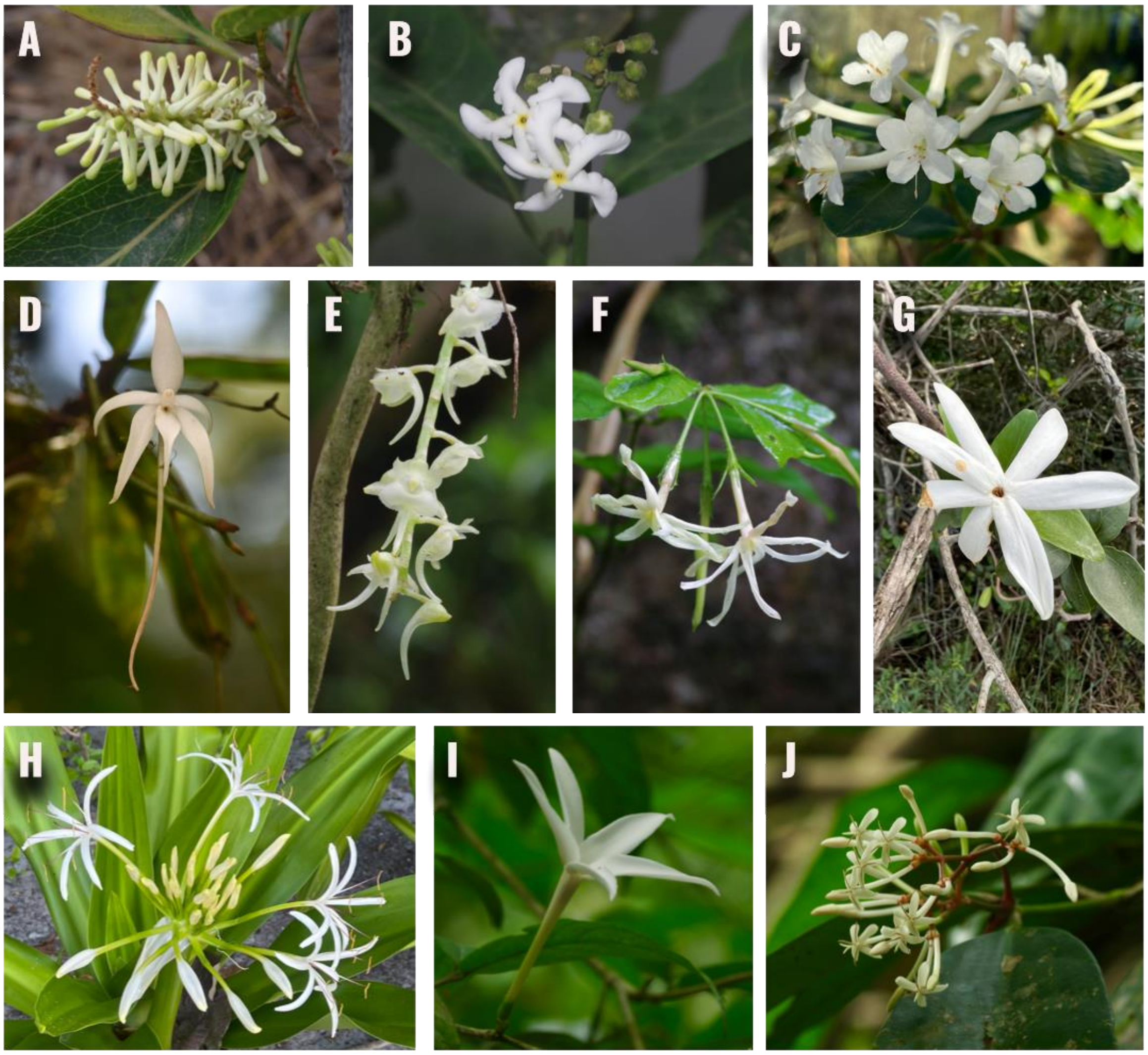

Figure 1: Examples of flowers with co-evolved floral traits for moth attraction and pollination in various plant families. A: *Roupala montana* (Proteaceae), B: *Tabernaemontana ventricosa* (Apocynaceae), C: *Rhododendron* sp. (Ericaceae), D: *Angraecum* sp., E: *Rhipidoglossum* sp. (Orchidaceae), F: *Jasminum preussii*, G: *Jasminum* sp. (Oleaceae), H: *Crinum asiaticum* (Amarylidaceae), I: *Aulacocalyx caudata*, J: *Ixora guineensis* (Rubiaceae). Photo credits: A ©João Medeiros CC BY 2.0; B, D, E, F, I, J ©Štěpán Janeček & Petra Janečková; C, G, H ©Michal Barták.

Regardless of many similarities, the two moth-related pollination syndromes differ in traits, reflecting the distinct foraging behaviour of settling moths and hawkmoths. Phalaenophilous flowers tend to be smaller but bloom in inflorescences large enough for a settling moth to land, whereas hawkmoths often prefer larger flowers (Bawa *et al.*, 1985). Sphingophilous flowers usually bear longer spurs or tubes (Faegri & Pijl, 1979). Additionally, phalaenophilous and sphingophilous flowers may diverge in floral scents' chemical composition, with specific compounds like oxygenated sesquiterpenes found in sphingophilous flowers (Karimi *et al.*, 2021; Knudsen & Tollsten, 1993).

Despite the expectations, the hypothesised pollination syndromes do not always predict the primary pollinator (Fenster *et al.*, 2004). For instance, sphingophilous flowers of the Neotropical tree *Isertia laevis* (Rubiaceae) are predominantly pollinated by hummingbirds (Wolff *et al.*, 2003). However, hawkmoth pollination predicted by the floral traits has been repeatedly validated in several field studies (Balducci *et al.*, 2019; Johnson, 2001; Mertens *et al.*, 2021; Potascheff *et al.*, 2020). Moths also visit flowers lacking specific adaptations for moth pollinations, as seen in Costa Rican rainforests, where hawkmoths visited sphingophilous flowers less frequently than those without moth-related floral traits (Haber & Frankie, 1989). Similarly, hawkmoths did not prefer white flowers on Mount Cameroon (Mertens *et al.*, 2021). Nevertheless, to our knowledge, comprehensive analyses on the validity of moth-related pollination syndromes remain lacking, making it challenging to draw any reasonable conclusions in the near future.

Methodological issues of nocturnal pollination research

The research of nocturnal pollination faces principal methodological challenges, which are responsible for many of the existing knowledge gaps. A primary issue in studying moth pollinators is the difficulty of observation and identification under suboptimal light conditions. This research often requires specialised equipment, including advanced technologies or artificial light sources (e.g. Balducci *et al.*, 2020). Artificial light, whether infrared or visible spectrum, may attract or repel moths or alter their feeding behaviour (Boyes *et al.*, 2021). Furthermore, using artificial light inevitably limits the data sampling efficiency, as observations are confined to the light's range (Baum, 1995). Moreover, the identification of moth species and their specific interactions with plants are compromised and potentially underestimated.

The challenging conditions of nocturnal pollination research also impede our comprehensive understanding of moths' roles in mutualistic interactions, particularly in the generally understudied tropical ecosystems (Fig. 2). Moths exhibit complex behaviour, especially in the timing of their foraging activities during night (e.g. Balkenius & Dacke, 2013; de Camargo *et al.*, 2016). Observing such temporal activity nocturnal patterns becomes almost impossible without advanced technologies. The few existing studies proved the high temporal variability in the nocturnal activity of tropical hawkmoths (de Camargo *et al.*, 2016; Lamarre *et al.*, 2015). Consequently, all-night monitoring is necessary to capture the full extent of moth pollination activities, which is one of the reasons for the lack of studies on pollination systems and plant-pollinator interactions at the community level. Potential solutions include employment of advanced techniques, such as camera traps (Groffen *et al.*, 2016; Karimi *et al.*, 2021), automatised video recording (Balducci *et al.*, 2020; Johnson *et al.*, 2020; Maicher *et al.*, 2020), and pollen identification through light microscopy (Souza *et al.*,

2021) or modern metabarcoding (Ellis *et al.*, 2023). These innovative approaches have not been widely adopted in pollination research, but their broader implementation could significantly enhance our understanding of tropical moth-plant interactions.

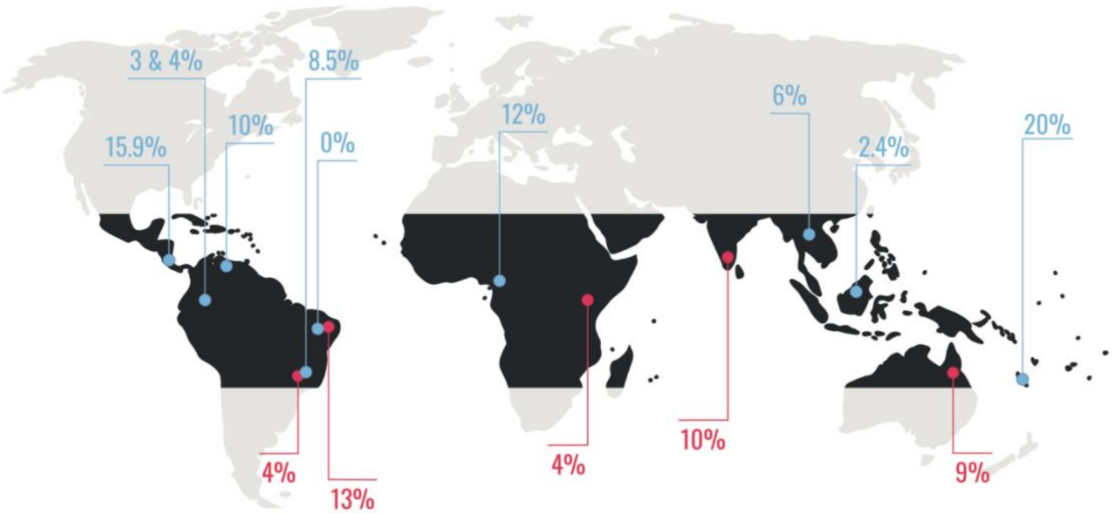

Figure 2: Geographical distribution of the reviewed pollination studies focusing on tropical moth pollination at the community level. Each dot indicates a study site, with accompanying percentages showing the proportion of moth-pollinated plant species (blue) and plant species exhibiting moth-related pollination syndromes, phalaenophily and sphingophily (red). The black background visualises tropical areas. This map highlights the scarcity of comprehensive knowledge in this field.

Tropical moths in plant pollination systems

Clear evidence of pollination efficiency by nocturnal pollinators, especially tropical moths, is scarce. Nonetheless, contact with stigmas and anthers, or pollen attachment/removal, can indicate likely pollinators or estimate the relative importance of particular floral visitors in plant reproduction.

Moths as primary pollinators

Hawkmoths are crucial in pollinating various tropical plants, many exhibiting the floral traits associated with sphingophily (Albuquerque-Lima *et al.*, 2020; Potascheff *et al.*, 2020). Substantial evidence originates from the Afrotropical ecosystems. In their extensive observational study, Johnson & Raguso (2016) confirmed 11 plant species pollinated by two widespread hawkmoths, namely migratory *Agrius convolvuli* and non-migratory *Coelonia fulvinotata*. They suggested that *A. convolvuli* might be the primary pollinator for over 70 savanna plant species with long-tubed flowers across Africa based on similarities in the floral traits with plants where hawkmoth pollination was confirmed (Johnson & Raguso, 2016). In Kenyan savannas, although there were no specific attempts to quantify the hawkmoth pollination effectiveness, predominantly the long-proboscid *Agrius convolvuli*, along with the short-proboscid *Nephele comma* Hopffer, 1857 and *Hippotion celerio*, were frequently recorded visiting 25 sphingophilous plant species from diverse families (Martins & Johnson, 2013). Hawkmoths are also primary pollinators of three out of eight described species of Afrotropical baobabs (*Adansonia*, Malvaceae): *Adansonia rubrostipa*, *A. perrieri*, and *A. za* from Madagascar (Baum, 1995). Among the visitors of their large, bright yellow, strongly-scented flowers, only hawkmoths *Coelonia solanii* (Boisduval, 1833) and *Xanthopan morganii* (Walker, 1856) were repeatedly observed touching the floral reproductive organs while feeding on nectar with 13–22% sugar content (Baum, 1995). Moreover, numerous sphingophilous orchid species in East Africa and Madagascar rely entirely on hawkmoths for pollination, particularly on those with an elongated proboscis, e.g. *C. fulvinotata*, *A. convolvuli, X. morganii*, and *Xanthopan praedicta* Rothschild & Jordan, 1903 (Martins & Johnson, 2007; Martins & Johnson, 2013; Nilsson *et al.*, 1985; Nilsson *et al.*, 1987). As hawkmoths hover during feeding, the specialised orchid pollinaria attach to their long proboscis (Nilsson *et al.*, 1987) or even their eyes (Balducci *et al.*, 2019; Nilsson *et al.*, 1992). Similarly, the matching length of a floral spur and a proboscis was also observed in medium-proboscid hawkmoths. For instance, *Hippotion celerio*, with 37mm proboscis, is the primary pollinator of strongly-scented white flowers of *Delphinium leroyi* (Ranunculaceae) with a 40mm floral spur in East Africa (Johnson, 2001).

While comprehensive studies or syntheses on hawkmoth pollination in other tropical ecosystems are lacking, there is evidence that hawkmoths serve as primary or exclusive pollinators in several studied plant pollination systems. In the Indomalayan realm, hawkmoths were evidenced to pollinate a few sphingophilous plants with large, white, tubular flowers, such as *Chonemorpha macrophylla* (Apocynaceae) and *Jasminum rottlerianum* (Oleaceae) from monsoon forests in Laos (Kato *et al.*, 2008), and *Cerbera manghas* (Apocynaceae), *Morinda citrifolia* (Rubiaceae), and *Oxera inodora* (Lamiaceae) from various vegetation types in New Caledonia in the Australian realm (Kato & Kawakita, 2004). In the Neotropics, several sphingophilous plants were revealed to be pollinated by hawkmoths, including *Bauhinia forficata* (Fabaceae) in the Brazilian Atlantic rainforests (Neto, 2013) or the mass-flowering *Griffinia gardneriana* (Amaryllidaceae) in the Brazilian Caatinga forests (Albuquerque-Lima *et al.*, 2020). Additionally, hawkmoths were documented to pollinate several tree species in the Brazilian Cerrado woodland savanna, including sphingophilous *Qualea grandiflora* (Vochysiaceae) with long-tubed, bright-yellow flowers (Oliveira *et al.*, 2004; Potascheff *et al.*, 2020).

Knowledge about pollination by settling moths, particularly in tropical ecosystems, remains even more insufficient. Nevertheless, several available case studies of particular tropical plants have underscored their potential importance. For instance, noctuid moths were proven to be the only pollinators of the Asian dioecious *Gnetum luofuense* (Gnetaceae; Yang *et al.*, 2021). Despite various insects being attracted to its exposed pollen (Corlett, 2001; Yang *et al.*, 2021), only noctuid moths visit both male and female flowers and efficiently pollinate the plant (Yang *et al.*, 2021). A comprehensive study by Kato & Kawakita (2004) determined several New Caledonian phalaenophilous plants to be pollinated by noctuid, pyralid, or geometrid moths, including *Dracophyllum ramosum* (Ericaceae), *Wikstroemia indica* (Thymelaeaceae), *Nepenthes vieillardii* (Nepenthaceae), *Exocarpos neo-caledonicus and E. phyllanthoides* (Santalaceae), and *Alstonia plumosa* var. *communis* (Apocynaceae). In South Africa, noctuid moths play a major role in the pollination of several plants, including *Dipcadi brevifoliumi* (Asparagaceae) pollinated by *Cornutiplusia circumflexa* (Linnaeus, 1767) noctuid (Manning *et al.*, 2012) or *Struthiola ciliate* (Thymelaeaceae) pollinated by *C. circumflexa* and *Cucullia terensis* Felder & Rogenhofer, 1874 (Makholela & Manning, 2006). In the Neotropics, diverse noctuid and geometrid moths were identified as the exclusive pollinators for certain specialised trees, including *Aspidosperma macrocarpon* (Apocynaceae) and *Roupala montana* (Proteaceae) in the Brazilian Cerrado woodland savanna (Oliveira *et al.*, 2004). In Hawaii, several species of *Schiedea* plants (Caryophyllaceae) are pollinated by the erebid moth *Pseudoschrankia brevipalpis* Medeiros, 2015 (Powers *et al.*, 2020; Weller *et al.*, 2017). Analogous to hawkmoths, settling moths are primary pollinators for numerous tropical phalaenophilous orchids, such as *Sauroglossum elatum*, with small whitish-green, short-spurred flowers pollinated by noctuid moths in Brazilian Atlantic forests (Singer, 2002), and *Habenaria aitchisonii* with greenish-yellow, nights-scented flowers pollinated by three species of noctuid moths (*Autographa gamma* (Linnaeus, 1758), *Thysanoplusia intermixta* (Warren, 1913), and *Heliophobus* sp.) in tropical mountains of southwest China (Xiong *et al.*, 2020).

In conclusion, hawkmoths and settling moths have been confirmed as crucial pollinators for numerous plant species. Yet, we suppose that the full extent of moths' contributions to tropical pollination systems remains significantly underestimated, mainly due to the lack of comprehensive investigations into nocturnal pollination and research focusing only on plants with moth-related pollination syndromes.

Moths in bimodal and mixed pollination systems

Tropical moths also serve as important, though not primary or exclusive, pollinators in plants with bimodal or mixed pollination systems. Bimodal systems involve pollination by two distinct functional pollinator groups (Manning & Goldblatt, 2005). Among potential combinations, the interplay between moths and bats appears most plausible, given their shared attraction to certain floral traits, such as larger, dull or whitish flowers with nocturnal anthesis and nocturnal production of substantial nectar volumes (Willmer, 2011). This interdependency can be illustrated in the Mexican *Agave macroacantha* (Asparagaceae), which is efficiently pollinated by both moths and bats (Arizaga *et al.*, 2000). Some of these bat- and moth-pollinated bimodal flowers resemble sphingophily, such as in Neotropical *Pachira aquatica* (Malvaceae) with long tubular corollas and fragrant odours (Hernández-Montero & Sosa, 2016). Conversely, some resemble chiropterophily, such as in Neotropical *Pilosocereus* spp. (Cactaceae) with large compact flowers with abundant nectar (Miranda-Jácome *et al.*, 2020; Rocha *et al.*, 2019), and Australian *Adansonia digitata* (Malvaceae) with large white flowers with relatively small petals (Groffen *et al.*, 2016). Notwithstanding, a comprehensive study of 155 Venezuelan plant species unveiled only two moth and bat co-pollination instances in the bimodal systems (Ramírez, 2004).

Some tropical bimodal pollination systems combine adaptations for nocturnal moths and diurnal pollinators, primarily observed in flowers that remain open day and night. In Venezuela, six out of 155 studied plant species exhibited bimodal pollination involving nocturnal moths and diurnal pollinators, including two combinations with butterflies, one with bees, and one with beetles (Ramírez, 2004). Additionally, *Dipterocarpus obtusifolius* (Dipterocarpaceae), a tropical Thai tree with large pink flowers opening at dusk and persisting into the following day, is pollinated by moths and butterflies (Ghazoul, 1997). The Brazilian tree *Copaifera coriacea* (Fabaceae), with small whitish flowers clustered in large inflorescences, is pollinated by moths and bees (Souza *et al.*, 2021).

In mixed pollination systems, where multiple functional groups pollinate non-specialised flowers, moths usually play a marginal role. Nonetheless, certain plants with some moth-pollination adaptations (i.e. not the typical generalised flowers) are pollinated by moths together with other functional pollinator groups. For instance, small dull flowers of Asian mangrove trees *Xylocarpus granatum* and *X. mekongensis* (Meliaceae) and white tubular flowers of Brazilian Cerrado tree *Hancornia pubescens* (Apocynaceae) are efficiently pollinated by hawkmoths, butterflies, and bees (Oliveira *et al.*, 2004; Raju, 2019).

Moths as nectar thieves

In many pollination systems, only a small proportion of flower visitors function as efficient pollinators (King *et al.*, 2013; Padyšáková *et al.*, 2013). Among cheaters that consume nectar or other floral rewards without contributing to pollination, we distinguish robbers accessing nectar through perforations in floral structures and thieves extracting nectar through the natural floral opening but mismatching the flower morphology (Inouye, 1980; Irwin *et al.*, 2010). With their usually coilable proboscis, moths are more inclined towards nectar thieving, as they cannot penetrate flowers (Irwin *et al.*, 2001).

Despite moths often being perceived as common nectar thieves due to their lack of specialised pollen-transport structures, reports of their nectar-thieving behaviour in tropical ecosystems are relatively rare. In Cameroonian tropical rainforests, moths are among the least frequent nectar thieves (Sakhalkar *et al.*, 2023). Here, only 1% of hawkmoth visits were documented as having no contact with floral reproductive organs (Mertens *et al.*, 2021). Nevertheless, hawkmoths, particularly the long-tongued ones, can exploit nectar from numerous flowers with short or medium floral tubes or spurs without pollination. Such nectar thieving has been observed in the baobab tree *Adansonia digitata* (Baum, 1995), *Delphinium leroyi* from Malawi (Johnson, 2001), and several African orchid species (Nilsson *et al.*, 1992). Settling moths also occasionally access nectar from large open flowers, such as *Clematis simensis* (Ranunculaceae), or flowers with specialised morphology, such as *Pararistolochia zenkeri* (Aristolochiaceae), without touching their reproductive organs (Karimi *et al.*, 2021; Sakhalkar *et al.*, 2023). Altogether, tropical moths appear to be occasional nectar thieves, and tend to visit flowers they pollinate (Sazatornil *et al.*, 2016).

Pollination by moths in tropical plant-pollinator communities

The confirmed role of moths in pollinating specialised tropical plants represents only a fraction of the overall plant diversity in tropical ecosystems. The quantitative significance of moth pollination in these communities remains largely understudied. To assess their relative importance, we reviewed quantitative studies with three distinct approaches: (1) the proportion of sphingophilous or phalaenophilous plant species within the community, (2) the proportion of documented moth-pollinated plant species, irrespective of their pollination syndromes, and (3) the proportion of moths among visits by all pollinators within the community.

Table 1: Proportions of plant species featuring flowers with moth-related pollination syndrome flowers in tropical plant communities. Sphingophily refers to the pollination syndrome related to hawkmoths, while phalaenophily refers to the pollination syndrome related to settling moths. If both syndromes are listed, the given proportion represents their combined prevalence.

	Country	Ecosystem	Proportion	Pollination syndrome	Reference
Paleotropics	**India**	wet evergreen forest	10%	Sphingophily, phalaenophily	Devy & Davidar (2003)
	Kenya	grassland, bush-savanna, woodland	4%	Sphingophily	Martins & Johnson (2013)
Australasia	**Australia**	deciduous and semi-evergreen vine thicket	9%	Sphingophily, phalaenophily	Hansman (2001)
Neotropics	**Brazil**	Caatinga	13%	Sphingophily, phalaenophily	Quirino & Machado (2014)
		Cerrado	4%	Sphingophily, phalaenophily	Gottsberger & Silberbauer-Gottsberger (2018)

Quantifications of particular pollination syndromes in tropical plant communities are highly limited (Tab. 1, Fig. 2). These assessments indicate that sphingophilous and/or phalaenophilous plants constitute 4% to 13% of plant diversity in tropical ecosystems (Fig. 2). Studies vary across regions, with the proportion of moth-related plants ranging from 4% in Brazilian Cerrado shrublands (Gottsberger & Silberbauer-Gottsberger, 2018) and Kenyan savannas (Martins & Johnson, 2013) to 13% in Brazilian Caatinga forests (Quirino & Machado, 2014). Intriguingly, local variability in the proportion of moth-related syndromes differs across vegetation strata, escalating from 0% in a herbaceous layer to 11% in a canopy layer (Gottsberger & Silberbauer-Gottsberger, 2018). It corresponds with the higher activity of moth pollinators within forest canopies (Schulze *et al.*, 2001). Considering the number of pollination syndromes and the number of generalised flowers, these findings imply that plant species demonstrating moth pollination syndromes may be relatively common in tropical ecosystems.

Table 2: Proportions of plant species pollinated by moths in tropical plant communities. The methods used to determine moth pollinators include morphology match (matching floral and moth traits suggesting potential for pollen transfer), stigma and anther contact (observed contacts of moths to floral reproduction organs), floral traits (presence of moth-attracting floral traits), pollen attachment (monitoring of moths for attached pollen), and visitation frequency (abundance, relative abundance, frequency, or duration of visits).

	Country	Ecosystem	Proportion	Methods	Reference
Paleotropics	**Cameroon**	rainforest, montane forest	12%	stigma and anther contacts	Klomberg *et al.* (2022)
	Laos	monsoon forest	6%	stigma and anther contact, pollen attachment	Kato *et al.* (2008)
	Malaysia	dipterocarp forest	2,4%	morphology match, stigma and anther contact, pollen attachment	Kato (1996)
Australasia	**New Caledonia**	diverse vegetation types	20%	stigma and anther contact, pollen attachment	Kato & Kawakita (2004)
Neotropics	**Brazil**	Caatinga	8,5%	morphology match, stigma and anther contact, floral traits	Machado & Lopes (2004)
	Brazil	high-altitude grassland	0%	stigma and anther contact, pollen attachment	Freitas & Sazima (2006)
	Colombia	seasonally flooded forest	4%	morphology match, stigma and anther contact, visitation frequency	van Dulmen (2001)
	Colombia	upland forest	3%	morphology match, stigma and anther contact, visitation frequency	van Dulmen (2001)
	Costa Rica	lowland rainforest	15,9%	morphology match, stigma and anther contact, floral traits	Bawa *et al.* (1985)
	Venezuela	grassland, savanna	10,2%	morphology match, stigma and anther contact, pollen attachment, visitation frequency	Ramírez (2004)

Empirical studies on moth-pollinated plants in tropical ecosystems are scarce (Tab. 2, Fig. 2). Findings from various regions, such as the Paleotropics, Neotropics, and Australasian realm, demonstrate that the proportion of moth-pollinated plant species ranges widely. Findings from various regions demonstrate that the proportion of moth-pollinated plant species ranges widely, from 3% in Colombian upland forests (van Dulmen, 2001) to 20% in diverse ecosystems of New Caledonia (Kato & Kawakita, 2004). Surprisingly, moths were not observed as primary pollinators for any of the 124 studied plant species in Brazilian high-altitude grasslands (Freitas & Sazima, 2006). Nevertheless, the methodological constraints of night pollination research have yet to be considered in these quantitative studies (as listed in Tab. 2), so any solid conclusions are problematic.

Quantitative data on the proportion of flower visitation by moths compared with other pollinators on the community level are rare in tropical ecosystems, with highly varying results among the studied ecosystems. On western African Mount Cameroon, hawkmoths are extremely rare among pollinators, accounting for only about 0.06% (106 out of the 18,439) of all flower visits (Mertens *et al.*, 2021). In tropical monsoon forests in Laos, moths constituted approximately ~2% (23 out of 1073) of recorded flower visits, confirming their infrequency (Kato *et al.*, 2008). In contrast, in New Caledonia, moths were recorded in 89 (~8.5%) out of 1038 visits made by all visitors of 99 plant species (Kato & Kawakita, 2004). In a few non-quantitative community-wide studies, moths were reported verbally as occasional flower visitors in Hong Kong (Corlett, 2001) and rare flower visitors in the Cerrados of Central Brazil (Oliveira *et al.*, 2004).

Conclusions

Despite the relative rarity of their visits to flowers, nocturnal moths have an essential role as pollinators in tropical ecosystems. Their nectar feeding and pollination adaptations include well-developed vision and olfaction, which helps them effectively navigate and utilise nectar resources in low-light conditions. Key floral traits such as colour, scent, and nectar concentration, i.e. the main indicators of phalaenophily and sphingophily pollination syndromes, are crucial in attracting settling moths and hawkmoths by matching their preferences.

The review of the case studies on plant pollination systems proved moths are important pollinators for a wide array of plant species across more than 25 families. The detailed studies allowed us to delve into more or less specialised relationships where some plants, such as baobab trees, orchids, and various tropical trees and shrubs, rely heavily, sometimes exclusively, on moths for effective pollination. In tropical plant communities, moth-adapted plants constitute a minority, ranging from 4% to 13%. The proportion of plants pollinated by moths varies across tropical ecosystems, ranging from 0% to 20%. Nevertheless, given the low visitation rates and number of distinct pollination syndromes, the proportions of moth-adapted or moth-pollinated plants in these communities are relatively high. Therefore, we highlight nocturnal moths as belonging among keystone pollinators in tropical ecosystems.

A significant insight from this review is the uneven geographic distribution of studies on moth pollination systems. Research is predominantly concentrated in East Africa and parts of Brazil, particularly in savanna and forest ecosystems. In contrast, vast areas such as Central and West Africa, Southeast Asia, the Amazon basin, the tropical Andean regions, and the Pacific Islands remain markedly underexplored. This disparity in research attention can lead to a skewed understanding of moth pollination, potentially overlooking moths' unique interactions and ecological roles in these diverse tropical regions.

The review also illuminates methodological challenges in studying moth pollination. The nocturnal nature of moths poses substantial observational and identification challenges, requiring specialised equipment that can influence moth behaviour and limit data collection efficiency. The complex behaviour of moths, coupled with their mobility and varied feeding strategies, necessitates detailed field observations, which are logistically demanding in tropical ecosystems. The scarcity of comprehensive data on nocturnal pollination at the community level limits our understanding of the full spectrum of plant-moth interactions. These methodological constraints underscore the need for more innovative and integrated research approaches.

Based on this review, future research on moth pollination in tropical ecosystems should combine community-level studies with detailed investigations of particular pollination systems. Community-wide surveys quantifying moth pollination importance and in-depth studies of moth feeding behaviour and pollen transfer are crucial for understanding these mutualistic relationships, their ecological impact, and their importance in tropical communities. Although most plants flower during the day, comparative analysis of diurnal and nocturnal pollinators is required for a more balanced view of their roles in tropical ecosystems. Large research gaps still exist in understanding the ecological significance of moth pollination in maintaining biodiversity and ecosystem services, particularly under the impacts of habitat fragmentation and climate change. Modern research methodologies, such as camera traps and continuous video recording supported by AI-driven pollinator identification and next-generation sequencing (NGS) metabarcoding of pollen carried by moths, are poised to revolutionise studies in these areas. Adopting these advanced techniques will be instrumental in filling the current research gaps and enhancing our understanding of the critical role moths play in maintaining the health and diversity of tropical ecosystems.

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Author contributions

Both authors conceived the idea and reviewed the literature; MB wrote the first draft, which was finalised by both authors.

Data availability statement

Data sharing does not apply to this article as no datasets were generated or analysed during the current study.

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