

Charles University

Faculty of Science

Study program: Biology

Branch of study: Ecological and Evolutionary Biology



Michal Barták

Moths as nocturnal pollinators in the tropics
Noční motýli jako noční opylovači v tropech

Bachelor thesis

Supervisor: RNDr. Robert Tropek, Ph.D.

Prague, 2022

Acknowledgments

I would like to thank my supervisor, RNDr. Robert Tropek, Ph.D., for his valuable advice and help during the writing of this thesis and the opportunities and motivation during my studies. I would also like to thank my loved ones for their omnipresent support.

Čestné prohlášení

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Mnichovicích, 31. 3. 2022

Michal Barták

Abstract in English

In this thesis, I reviewed the available knowledge on the role of moths in the pollination of flowering plants in tropical ecosystems. Moths appeared as relatively frequent visitors of flowers with moth-attracting adaptations. Moths were proved to be essential pollinators of some specialized plant species. An obligatory mutualism with micromoths was found in more than 550 highly specialized plant species. Macromoths appeared as effective pollinators of numerous tropical shrubs, trees, and herbs from numerous plant families. Moths were the only recorded visitors and/or pollinators in several cases. In communities, plant species with moth pollination syndromes were relatively uncommon, and moths were generally infrequent visitors of their flowers, which could also be affected by abiotic factors. The proportion of actually moth-pollinated plant species in communities was even slightly lower than the proportion of plants with moth pollination syndromes in other areas. Some moths (e.g., hawkmoths) can steal nectar from virtually any shorter-spurred/tubed flowers with their long proboscis. Other moths were reported as nectar thieves in some too accessible flowers. However, moths were reported to be rare nectar thieves and prefer visiting the flowers they also pollinate. This thesis should summarize the published knowledge on moth pollination, review the importance of moths as pollinators, mention gaps in the current knowledge, and point out a possible way for further research.

Keywords: plant-insect interactions, moths, hawkmoths, nocturnal pollination, flowering plants, pollination syndromes, pollination networks, communities

Abstrakt v češtině

Tato práce je rešerší dostupných znalostí o roli nočních motýlů v opylování kvetoucích rostlin v tropických ekosystémech. Noční motýli se ukázali jako relativně častí návštěvníci květů s adaptacemi na jejich přilákání. Noční motýli jsou esenciální opylovači některých rostlin. Obligátní mutualismus rostlin s Microlepidoptera (drobní motýli) byl nalezen u 550 druhů rostlin. Makro noční motýli (Macroheterocera) jsou zase efektivními opylovači řady tropických stromů, keřů a bylin. V několika případech byli noční motýli dokonce jedinými návštěvníky a/nebo efektivními opylovači. Druhy rostlin s phalaenofilii a sphingofilii nejsou ve společenstvech příliš početnými. Také noční motýli jsou málo častými návštěvníky jejich květů, to může být ovlivněno ale některými abiotickými faktory. Proporce druhů rostlin skutečně opylovaných nočními motýly byla o trochu nižší než četnost rostlinných druhů s polinačnými syndromy spojenými s opylením nočními motýly v některých oblastech. Někteří noční motýli (například lišajové) mohou krást nektar prakticky ze všech květů s kratší květní ostruhou nebo trubkou, protože mají dostatečně dlouhý sosák. Jiní noční motýli zase byli zaznamenáni jako zloději nektaru z některých příliš otevřených (přístupných) květů. Nicméně, noční motýli byli zaznamenáni jako vzácní zloději nektaru a v určitých oblastech více preferovali květy, které zároveň opylovali. Tato práce by měla shrnout dostupné poznatky o opylování nočními motýly, posoudit, jak jsou noční motýli důležitými opylovači, zmínit některé nedostatky současného vědění a ukázat možný směr dalšího výzkumu.

Klíčová slova: interakce rostlin a hmyzu, noční motýli, lišajové, noční opylení, kvetoucí rostliny, polinační syndromy, polinační sítě, společenstva

Contents

1. Introduction	1
1.1. Aims	2
2. Characteristics and importance of moths	3
3. Moths as pollinators	5
4. Flower traits and pollination syndromes	9
5. The role of moths in pollination of plant species	12
5.1. Micromoths as pollinators in obligatory mutualisms	13
5.2. Plants relying on pollination by hawkmoths	16
5.3. Plants relying on pollination by settling moths	18
5.4. Moths as significant but not the only pollinators	19
5.5. Moths as nectar thieves	21
6. Moth pollination in communities	22
6.1. Proportion of pollination syndromes in plant communities	22
6.2. Proportion of moth-pollinated plants in communities	24
6.3. Flower visitation rates of moths	25
7. Conclusions	28
References	30

1. Introduction

Pollination is one of the key interspecific interactions in nature and an important mechanism in the sexual reproduction of angiosperms (flowering plants; Crow, 1994). Pollination is the transfer of pollen to stigma (i.e., the part of female reproductive organs where the pollen is received and germinates). It can be either abiotic by wind or water (anemogamy and hydrogamy, respectively) or biotic (zoogamy), where the pollen vector is an animal, most commonly searching for flower rewards. Besides the importance of pollination for the pollinated plant, many animals (e.g., frugivorous birds and mammals, including humans) thrive on the “product” of zoogamy – the fruits or seeds (Oliveira et al., 2019; Porto et al., 2021).

Animal pollination occurs worldwide. However, the highest relative proportion of zoogamous plants is in the tropics – about 94%, compared to about 78% of animal-pollinated plants in the temperate (Ollerton et al., 2011). The tropics – defined as an area between the Tropics of Cancer and Capricorn – also have the highest species diversity. Although wind can disperse pollen for long distances in open landscapes, such dispersibility strongly declines in environments with high humidity or a lot of rainfall (Regal, 1982), and mild or no wind, like in a tropical rainforest (Corlett, 2004). Also, it unlikely “finds” a stigma of a conspecific plant among the high amount of species in rainforests (Cox & Grubb, 1991). Therefore, in the species-rich tropics, zoogamy can be advantageous (Ollerton et al., 2011).

Insects are the major pollinators of zoogamous flowering plants (Bawa, 1990), but some pollinator groups receive less attention than other groups. In this aspect, Lepidoptera (butterflies and moths) are understudied, even though they are somewhat popular among the general public. Despite adult lepidopterans foraging for nectar in flowers (Wardhaugh, 2015), there has not been much summarized on their importance in particular ecosystems or their pollination effectiveness, especially for moths. In some plants, we can find some adaptations to pollination by moths and moth pollination syndromes – sets of adaptive flower traits for attracting a particular functional pollinator group (moths and hawkmoths, in this case). Altogether, pollination by moths certainly deserves more attention.

1.1. Aims

I aim to review the published knowledge on the role of moths as pollinators in tropical ecosystems. I ask how frequent visitors of flowers and how important pollinators moths are in particular plant species – if they are effective pollinators or just nectar thieves. I also review the importance of moths as pollinators by the proportion of plants with moth pollination syndromes in communities and the proportion of plants in communities pollinated by moths. Another goal is to find out what flower traits are the best to attract moths.

2. Characteristics and importance of moths

Moths are a diverse group of insects with an extraordinary value as a part of many terrestrial ecosystems. Their adults and larvae are often a part of the diet of birds, bats, or even humans, in many parts of the world. Moths can be used as bioindicators of the ecosystem state (Correa-Carmona et al., 2021). As important pests or pollinators of crops, they are important for humans as well (Buxton et al., 2021; Lu et al., 2021; Robertson et al., 2021).

Moths share some apomorphies (e.g., body plan, six legs) with other insects; however, they stand out with unique properties. They are holometabolous insects (immature wingless stages differ from adults and undergo a metamorphosis into a non-feeding stage, the pupa, before emerging as winged adults), with primarily herbivorous larvae (caterpillars). Although moths have several developmental stages, only the adults can be pollinators of flowers. Together with butterflies, moths are a part of the order Lepidoptera (Fig. 1a; Kawahara et al., 2019). An autapomorphy of lepidopterans is their wings covered with scales (modified “hairs”). An autapomorphy of the monophylum Glossata (containing more than 99% of lepidopterans) is a proboscis – maxillary galeae (mouthparts) modified into a tubular feeding organ for sucking fluids (its first appearance in the evolution of Lepidoptera is marked at Fig. 1a; Kawahara et al., 2019).

There are approximately 160,000 described species of Lepidoptera (van Nieukerken et al., 2011), making them one of the most diverse insect orders (Grimaldi & Engel, 2005). Most (ca. 88%) of this order are moths, a paraphyletic group, with a monophylum of butterflies (Papilionoidea, Fig. 1a) as an internal clade (van Nieukerken et al., 2011; Kawahara et al., 2019). Representatives of Macroheterocera (Fig. 1a), so-called macromoths (often larger moths) were included in numerous studies on pollination, unlike a rarely studied paraphyletic group of so-called micromoths (Microlepidoptera). However, the size of the moth is not very relevant, some macromoths can be very small and, conversely, some micromoths can be large. More importantly, Macroheterocera is a monophyletic clade of phylogenetically more “advanced” moths (Kawahara et al., 2019).

Moths are very diverse ecologically, and various life histories can be encountered among them. Although the common ancestor of all lepidopterans had probably nocturnal activity (Kawahara et al., 2019) and moths are usually nocturnal animals, some groups of Lepidoptera are diurnal. Diurnal activity has evolved mainly in butterflies. However,

representatives of diurnal moths can be found in several families, for example, in Zygaenidae and Sesiidae with primarily diurnal moths (Powell, 2009). The adaptations of plants to diurnal pollinators can often significantly differ (psychophily is the pollination syndrome adapted to pollination by diurnal butterflies; Willmer, 2011). The literature on pollination by diurnal moths is limited, almost none from the tropics. Thus, this thesis will focus only on macromoths with nocturnal and crepuscular activity, with mentioning a few important examples of highly specialized micromoths. While butterflies and diurnal moths will be ignored due to their diurnal activity, most of the micromoths will be overlooked entirely here, because there are scarce or even no data on their pollination.

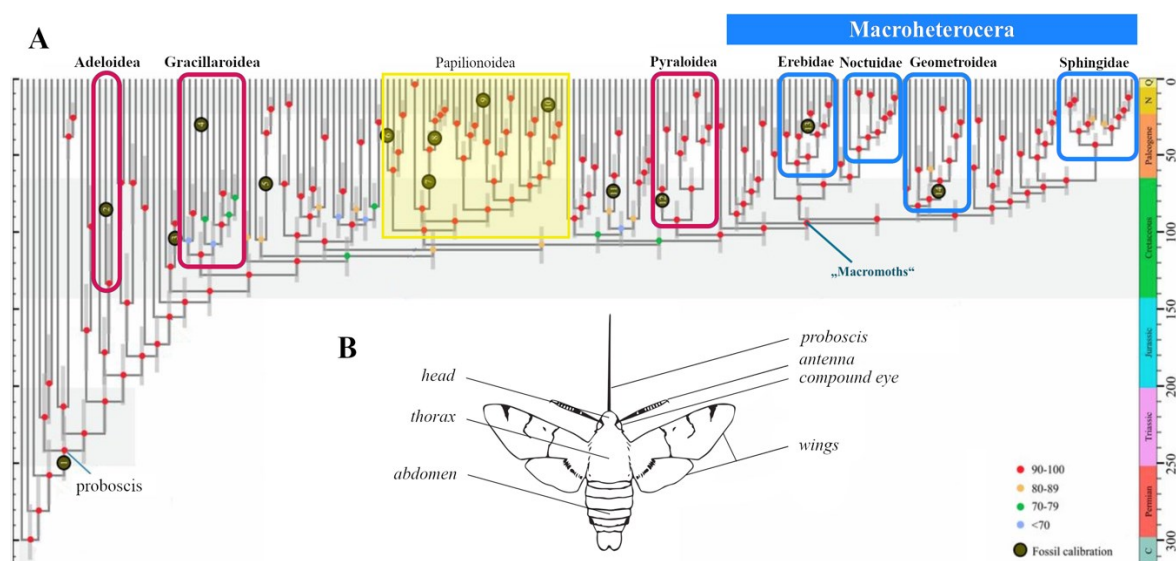


Fig. 1 A Phylogeny of the order Lepidoptera (adapted from Kawahara et al., 2019), with indications of groups studied in the reviewed literature. Blue squares are macromoths (Macroheterocera), the group of moths focused on in this thesis. Red squares are groups of important micromoths mentioned in this thesis. The large yellow square is the monophylum of butterflies (Papilionoidea). The first appearance of the proboscis is marked in the down, left corner. **B** Morphology of a hummingbird hawkmoth (silhouette obtained from www.divulgare.net).

Sphingidae, hawkmoths (Fig. 1a, b), are large-bodied, big-eyed moths with a long proboscis, typically able to hover while feeding (similar to hummingbirds). Their wingspan can be large, but it varies among species. For instance, in *Callionima falcifera*, it spans around 7 cm (Haber & Frankie, 1989), in *Xanthopan morgani* over 13.8 cm (Arditti et al., 2012). Most hawkmoths are crepuscular or nocturnal (with a few well-known day-flying species, such as *Macroglossum stellatarum*; de Camargo et al., 2016a), and most of them feed on nectar (Stöckl & Kelber, 2019). Noctuidae, Geometridae, and Erebidae (Fig. 1a) are among the most diverse moth families, with many nectar-feeding species. They share some characteristics: they typically do not hover when foraging but land on the flower and spend more time feeding (with some exceptions, such as some fluttering noctuids; Ghazoul, 1997).

Thus, they are often referred to as “settling moths” (otherwise unidentified in many pollination studies). Prodoxidae (Adeloidea), Gracillariidae, and Pyralidae (Fig. 1a) are the most studied representatives of pollinating micromoths, however, the knowledge about their pollination is still highly limited.

3. Moths as pollinators

Pollinators generally do not visit flowers with the intention of pollination. Therefore, plants attract pollinators by offering rewards (e.g., pollen or nectar) that pollinators can consume. That is the reason why they visit flowers. Adult moths can hardly feed on pollen because they lack chewing mouthparts (with very rare exceptions in basal lineages). Their mouthparts are modified into a tubular proboscis (Fig. 1b). The fluid intake is secured by a sucking pump located inside the head – when the pressure inside the pump drops, the liquid flows into the digestive system (Krenn, 2010). Therefore, moths visit flowers only for nectar (sugar-rich liquid providing energy). The nectar has some physical properties that can affect the intake rate by moths, such as viscosity. For example, experiments on *Macroglossum stellatarum* (Sphingidae) showed the intake rate decreases with the growing viscosity of the solution (Josens & Farina, 2001).

The length of a proboscis can differ between functional pollinator groups and species and can greatly affect the morphology of flowers (longer or shorter spur/tube). Hawkmoths can have a notably long proboscis (> 10 cm), such as *Agrius convolvuli* or *Coelonia fulvinotata*, however, hawkmoths with a shorter proboscis (~ 4 cm), for instance, *Hippotion celerio* or *Daphnis nerii* are also common (Martins & Johnson, 2007). Darwin’s coevolutionary race model (Fig. 2) assumed that elongating a flower spur is connected to the gradual elongating of a proboscis of the pollinator (Darwin, 1862, as cited in Whittall & Hodges, 2007). However, the speciation of a longer spur also (and more likely) can be driven by pollinator shifting (change of the primary pollinator). Pollinator shifting occurs when a long-tongued visitor becomes predominant in some part of the plant’s range. In this case, the plant does not prolongate the spur gradually with the gradually prolonged proboscis of its pollinator, but it rapidly evolves a longer spur to match the length of a different pollinator’s proboscis (Whittall & Hodges, 2007).

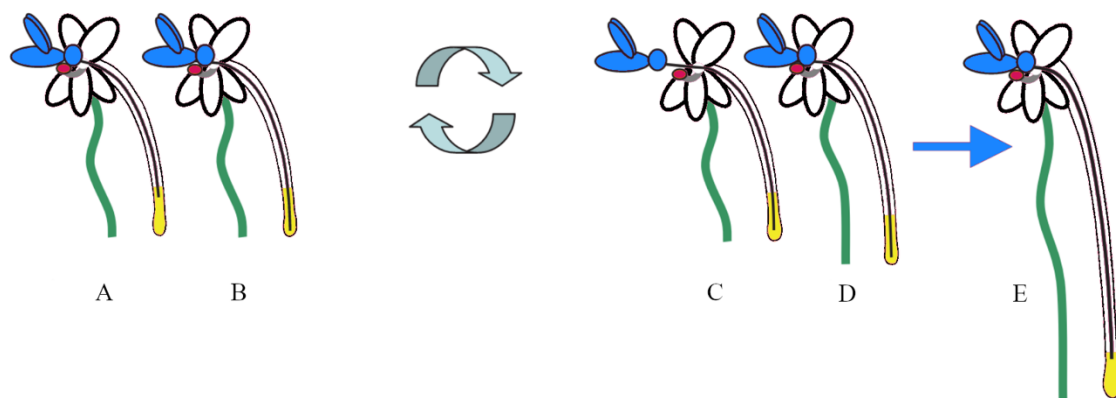


Fig. 2 Darwin's coevolutionary race model, adapted from Whittall & Hodges (2007). White flowers with long spurs with yellow nectar inside. Red = reproductive organ, blue silhouette = a moth with a long proboscis. **A** – pollinator touches reproductive organs and reaches for nectar. **B** – pollinator elongates its proboscis. **C** – pollinator has too long proboscis and does not touch the flower's reproductive organs. **D** – flower elongates its spur making the visitor go deeper to reach the nectar, and the pollinator touches the reproductive organs again. This selection for a longer proboscis and spur can repeat several times and evolve to **E** – extremely long proboscis and spur (known from, for example, *Angraecum sesquipedale* and *Xanthopan praedicta*; Darwin, 1862, as cited in Whittall & Hodges, 2007).

However, not all moths consume nectar, some have adapted to different food resources. There are exceptions even in hawkmoths; for example, *Acherontia atropos* feeds on honey and has a very short proboscis (Stöckl & Kelber, 2019). Many other moths, such as numerous species of erebid moths, feed on fruits or different nutrient-rich liquids (Zaspel et al., 2014). Some adult moths, such as saturniids, do not feed at all; many of these have reduced mouthparts and live from the energy accumulated in the larval stage (de Camargo et al., 2016b).

Moths with nocturnal and crepuscular activity have a well-adapted vision and an olfactory system, which they use to locate nectar resources in the dark (Wardhaugh, 2015). Moths have two compound eyes, which consist of ommatidia. They have color vision, and possess color constancy (recognize colors even in dim light; Kelber, 2003). The ommatidia of moths have receptors for UV, blue and green color; this was confirmed in four species of hawkmoths, one nocturnal (*Deilephila elpenor*), one diurnal (*Macroglossum stellatarum*), and two species with both diurnal and nocturnal activity (*Hyles galii* and *H. lineata*; Kelber, 2003). These photoreceptors cover the spectrum from the wavelengths of about 350 nm to about 550 nm (Kelber, 2003), meaning these hawkmoths are less sensitive to yellow and do not see red color. Conversely, butterflies are known to react to red color in flowers, and the red color is also one of the values of flower traits in the psychophily (Willmer, 2011).

The ancestor of lepidopterans probably did not see the red color (Briscoe, 2008), and the perceiving of the color red is possible, among other things, probably thanks to the duplication of a long-wavelength opsin (Sondhi et al., 2021). It seems that the light of the environment likely drives selection for the duplication in the diurnal lepidopterans (Sondhi et al., 2021). Such duplication was recorded only in eight families and eleven genera of lepidopterans (mainly butterflies), from which only two genera are nocturnal (*Spodoptera* sp., Noctuidae and *Tischeria* sp., Tischeriidae; Sondhi et al., 2021). In general, most of the moths are probably unable to see red color, which is important to keep in mind when discussing flower colors.

Besides the visual perception of flowers, moths also have two olfactory organs located in the antennae and labial palps to perceive odor molecules from the air (Szyszka et al., 2014; Chen et al., 2021). The olfactory reaction to a stimulus, tested on hawkmoth *Manduca sexta*, can be swift (Szyszka et al., 2014). Hawkmoths can also smell flowers from greater distances than they would see them, especially when flying upwind, making it an essential cue to locate flowers (Balkenius et al., 2006; Klahre et al., 2011). Experiments on hawkmoths have shown that they usually use both color vision and olfactory sense to localize the nectar source (Raguso & Willis, 2002; Balkenius & Dacke, 2013), but no such studies were performed on settling moths. This perception by both senses separately and not fusing the target into one stimulus of particular color and odor makes some hawkmoths able to learn and adapt to resources with different traits when migrating to new locations (tested on *Manduca sexta*; Balkenius & Dacke, 2013). Overall, color vision and a sensitive olfactory system are two essential senses for locating flower resources and starting the foraging successfully.

Animal pollinators carry the pollen on themselves; thus, flowers have adapted to attach pollen to them when they visit the flower for resources. Moths, as they approach flowers, insert the proboscis into the spur or tube with nectar, and do not necessarily touch the reproductive organs by other body parts (Fig. 2). When the contact is made, pollen grains or pollinaria (in orchids) are attached to them. Plants expose pollen in flowers in different ways (brush-like anthers, pollinaria near the nectar spur, etc.) and the pollen is attached to different parts of the moth. Some moths then transfer the pollen on, for instance, legs, especially settling moths, as they typically walk on flowers (Faegri & Pijl, 1979). Numerous plant species expose the pollen the way it attaches to the moth's proboscis (Fig. 3; Kisle, 1972). Plants can even target several different sections of the proboscis; several hawkmoth-

pollinated orchid species from Madagascar, attach their pollinaria on the ventral side of the proboscis or a place closer to moth's head (Nilsson et al., 1985). Pollinaria of noctuid-pollinated *Sauroglossum elatum* (Orchidaceae) and pollen of several cacti species (Cactaceae) are often attached to the proboscis as well (Singer, 2002; Ferreira et al., 2018). A bit strange attachment of pollinaria is to eyes (Fig. 3). It is recorded from tropical orchid *Cynorkis uniflora* (Nilsson et al., 1992), and this way of attachment was recorded in a species from the temperate zone as well (*Platanthera chlorantha*; Orchidaceae; Steen, 2012).

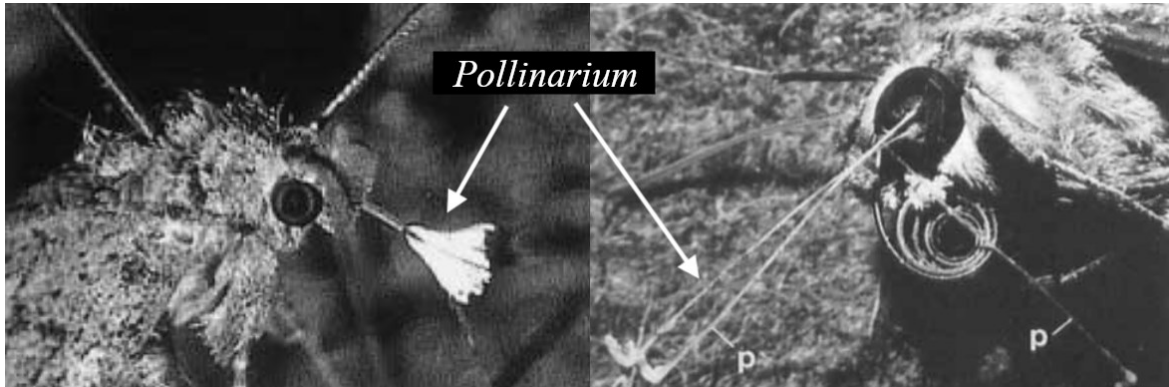


Fig. 3 Pollinarium attached to moths; the image on the left: pollinaria fixed to the proboscis of an owlet moth (Noctuidae; source: Singer, 2002); picture on the right: long pollinaria (p) attached to an eye of a hawkmoth (*Nephele densoi*, Sphingidae; source: Nilsson et al., 1992); under the eye, there is a long curled-up proboscis visible.

Another adaptation for increasing chances of receiving pollen from an unrelated conspecific individual is, for example, distyly – a type of heterostyly. Distyly means having two morphs of flowers that differ in the length of styles. This was recorded, for instance, in hawkmoth-pollinated *Psychotria faxlucens* (Pérez-Nasser et al., 1993), *Faramea cyanea* (Maruyama et al., 2010), and *Palicouorea tetragona* (Martén-Rodríguez et al., 2013), from the Rubiaceae family. Some plants may also minimize self-pollination by having dichogamous flowers – in hermaphroditic flowers, either anthers or stigma mature sooner. For instance, protandric flowers (male organs mature before female) of *Sauroglossum elatum* (Orchidaceae) are reported to be pollinated by settling moths (Singer, 2002). This way, moths collect pollen on fresh flowers with mature anthers and pollinate stigmas of older flowers with mature female organs. Overall, moths can carry pollen in several placements, and moth-pollinated plants are adapted to outcrossing and the pollination technique of the particular pollinator by, for example, exposing pollen in different places of the flower or temporally differencing the maturity or reproductive organs in flowers.

4. Flower traits and pollination syndromes

Zoogamous flowers have adapted to attract pollinators to assure their pollen will be transferred (Willmer, 2011). The properties of flowers that can be measured or defined are called flower traits (Willmer, 2011). Some of the traits can be perceived visually by the pollinator, such as the color, size, and shape of flowers. A trait perceived by the olfactory system is the scent flowers emits. Particular pollinators are adapted to perceive particular stimuli differently and are attracted by different traits, such as different scents (some prefer a strong sweet scent, some an unpleasant smell) or different colors and sizes of flowers (Faegri & Pijl, 1979). Thus, with a particular set of traits, flowers can attract particular visitors. I have mentioned moths' adapted vision and olfactory; in plants, color and scent proved to be the essential flower traits to attract moths (Klahre et al., 2011). However, on Mount Cameroon, only the color was an important flower trait, and the preferred colors (values) can change with the elevation (Klomberg et al., 2022). In some cases, also the spur/tube length can play a role in attracting moths (Klomberg et al., 2022). Apart from attractive flower traits, some traits can be restrictive; for example, when flowers open only at night, they are unlikely visited or utilized as a nectar resource by diurnal pollinators (e.g., Rocha et al., 2019). Some flower shapes or long flower spurs prevent particular visitors from getting resources (Wang et al., 2020) as they may be too big or do not have the tongue long enough to reach the nectar.

To better understand the pollination ecology of moths, the specialization of plants to moth pollination, and the importance of moths as pollinators in general, it is essential to look at the so-called pollination syndromes. Pollination syndromes are complex sets of adapted flower traits that have evolved among different plant families convergently to attract a particular group of pollinators (Faegri & Pijl, 1979; Willmer, 2011). Particular pollinator groups differ in many characteristics – morphology, activity time, vision and olfactory, foraging behavior, resource utilization, or the length of a proboscis. And particular pollinators prefer different traits, such as nectar concentration, color, or scent. Plants followed these preferences and evolved pollination syndromes to attract them (Willmer, 2011). Phalaenophily and sphingophily were defined as a set of adapted traits for pollination by settling moths and hawkmoths, respectively (Tab. 1; Faegri & Pijl, 1979; Willmer, 2011).

The characteristics of moths as pollinators can help derive some values of various flower traits, and I will now synthesize the above-mentioned characteristics of moths as

pollinators with different values of flower traits. Nocturnal anthesis of flowers, for example, is widely preferred because moths are usually nocturnal animals. As moths usually do not see red color, moth-pollinated plants usually have white- or pale-colored flowers. White-colored flowers reflect the light of all lengths of the (human) visible spectrum, thus, even the short-wavelength light that moths see the best, unlike, for example, red-colored flowers that reflect mainly long-wavelength light (Fig. 4; van der Kooi, 2021). The composition, volume, and concentration of the nectar in flowers often differ among plant species. It depends, among other things, on the pollinator group (e.g., birds vs. insects) targeted by the plant (Janeček et al., 2021), and their ability to consume nectar. In nature, the concentration of sugars in the nectar of the moth-pollinated flowers usually ranges from 13 to 27% (Nilsson et al., 1987; Rocha et al., 2005, 2019; Maruyama et al., 2010; Hernández-Montero & Sosa, 2016; Potascheff et al., 2020) to meet the requirements of the metabolism of moths (Heinrich, 1975) and physical properties of the proboscis (Stöckl & Kelber, 2019). The above-mentioned flower traits are usually shared among both moth pollination syndromes (Faegri & Pijl, 1979; Willmer, 2011).

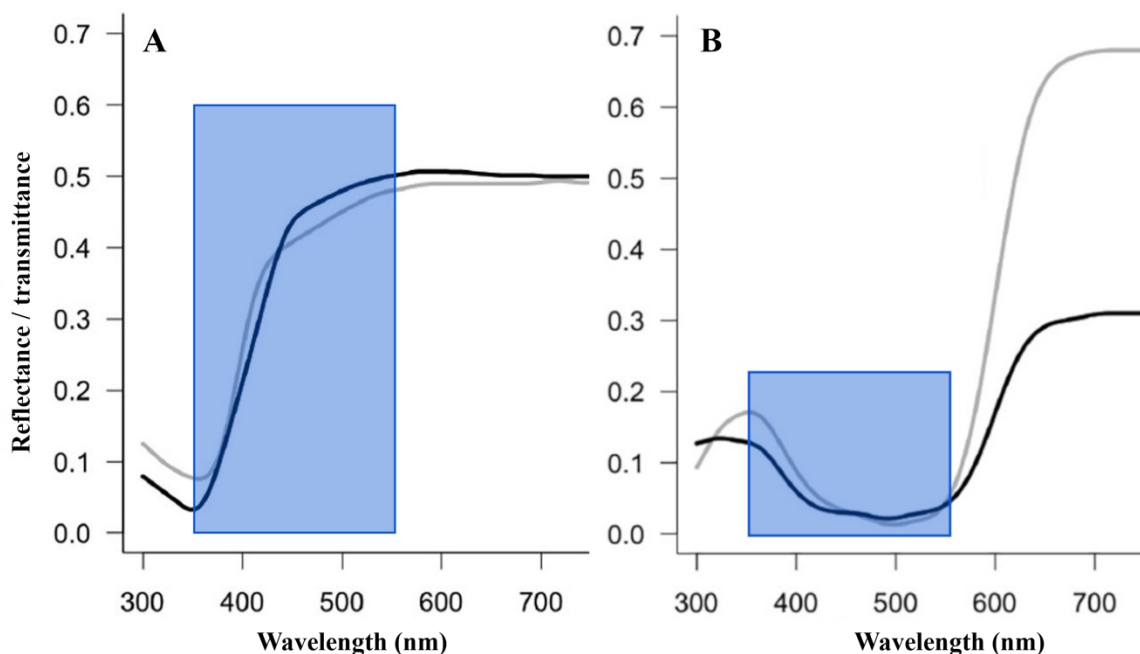


Fig. 4 The reflectance (black curve) and transmittance (grey curve) spectra (adapted from van der Kooi, 2021). **A** white flower of *Silene latifolia*; **B** red flowers of *Papaver rhoeas*. The blue area indicates the approximate vision spectrum of a moth (350 – 550 nm; Kelber, 2003). Apparently, more of the light within the spectrum visible to moths is reflected from the white flowers.

Phalaenophily is a general moth pollination syndrome, a set of adaptations to pollination by settling moths (noctuids, geometrids, erebids, etc.). The uniqueness of hawkmoths resulted in a separate set of adaptations to pollination by hawkmoths, the sphingophily. As the foraging behavior of settling moths is different from hawkmoths, phalaenophilous flowers are usually smaller and have a landing site or an inflorescence of flowers for a settling moth to land– they usually do not hover (some may flutter). Hawkmoths, on the other hand, prefer much larger flowers than settling moths (Bawa et al., 1985). They can also have much longer proboscides than settling moths, and sphingophilous flowers usually have a longer flower spur/tube (Faegri & Pijl, 1979). The scent, which also proved an important flower trait of moth-pollinated flowers (Klahre et al., 2011), can differ in some compounds among the pollination syndromes. In both moth pollination syndromes, the scent contains, e.g., nitrogen compounds and linalool. However, some compounds, such as oxygenated sesquiterpenes, were found only in sphingophilous flowers (Knudsen & Tollsten, 1993).

Tab. 1 Pollination syndromes – sphingophily and phalaenophily, comparison of some flower traits according to Willmer (2011), Faegri & Pijl (1979), and Knudsen & Tollsten (1993).

	Sphingophily	Phalaenophily
color	cream, white, pale	pastel shades, cream, white, green, rarely pale pink, yellow
size	large	small
shape		tubular
length	40–100+ mm	5–15 mm
odor	higher amounts of 1,8-cineole, linalool and nitrogen-containing compounds, geraniolic compounds and oxygenated sesquiterpenes	lower amounts of 1,8-cineole, linalool and nitrogen-containing compounds
anthesis		dusk, night
blooming length		1–3 days
nectar		dilute (15–25 %), low to moderate volume
landing site	usually not – mainly hovering	yes – settle, may flutter

The hypothesis of pollination syndromes does not necessarily predict the actual pollinator (Fenster et al., 2004); pollination syndromes (based on the flower traits) and direct

observations of pollinators can be different. Although the sphingophily, for example, has been often supported by direct observations of hawkmoth pollinators (Johnson, 2001; Balducci et al., 2019; Potascheff et al., 2020; Mertens et al., 2021), in some cases, the pollination syndrome has only partly predicted even the hawkmoth visitation. For example, in a study on oceanic islands in Asia (Wang et al., 2020), five flower traits from the pollination syndromes were tested, and visitors were, afterward, directly observed. These five traits explained only 22.5% of the variability of the visitors, as the flowers were visited by many other groups that the pollination syndromes would predict (Wang et al., 2020). Another example, *Isertia laevis* (Rubiaceae), typically has sphingophilous flowers, but the direct observations showed that hummingbirds are frequent visitors and pollinators (Wolff et al., 2003). Sometimes even the flower traits of moth-pollinated flowers in nature can have different values; for example, on Mount Cameroon, hawkmoths did not prefer white flowers, which opposed the sphingophily definition (Mertens et al., 2021), and the color preference changed with altitude (Klomberg et al., 2022). In a community level example, in Costa Rican rainforest, the flowers without adaptations to moth pollination were visited by hawkmoths more frequently than sphingophilous plants (Haber & Frankie, 1989). Above all this, pollination syndromes seem to be a very useful cue to prepare plant species for further observations of visitors and confirming its pollinators, eventually.

5. The role of moths in pollination of plant species

The role of moths in pollination systems can vary among species and the applied scale. In this chapter, I reviewed the available knowledge on the importance of moths for particular plant species, their pollination ecology systems, and reproductive strategies of plants. Some plants fully depend on moth pollination in an obligatory mutualism. In some other highly specialized plants, moths were recorded as the exclusive pollinators. However, many plants are pollinated by more functional groups of pollinators, and I reviewed the cases where moths are effective but not the only pollinators in bimodal and mixed pollination systems.

The important thing to say is that it is quite challenging to study nocturnal pollination, and in many plant species, only the diurnal pollinators are known. In nocturnal pollination, plants with some clear flower traits typical for nocturnal pollination and flowers with moth pollination syndromes are usually studied. Also, the observations are missing in some

bimodal, and almost all mixed pollination systems in the tropics, and the role of moths in such pollination systems is still unknown.

5.1. Micromoths as pollinators in obligatory mutualisms

As discussed, zoogamous pollination is *usually* an unintentional process from the visitor's perspective. Nevertheless, in some plant-pollinator relationships, animals can pollinate flowers on purpose. Although these relationships were considered infrequent (Baker, 1961), they can be found in numerous taxa of moths. An obligatory mutualism was found in some Phyllanthaceae plants with moths from the genus *Epicephala* (Gracillariidae), in Yuccas (*Yucca* spp. and *Hesperoyucca* spp., Asparagaceae) with Yucca moths (*Tegticula* spp. and *Parategticula* spp., Prodoxidae), and in senita cactus (*Lophocereus schottii*, Cactaceae) with senita moth (*Upiga virescens*; Pyralidae). In all these cases of obligatory mutualisms, the plants and the moths depend on each other and virtually do not reproduce without the other. The adult moths actively pollinate the flowers, for which they have special adaptations to collect pollen and transfer it to stigma. The moth larvae are specialized predators of the plant seeds. Nevertheless, there are some differences between particular relationships (Tab. 2).

The most important relationship, as found in over 500 plant species, is the relationship of some Phyllanthaceae plants with *Epicephala* moths (Kawakita, 2010). In this diverse plant family, many species are pollinated by ants, bees, or flies; however, the pollination by gracillariid moths is important as well. The first record of such a relationship was encountered in *Glochidion acuminatum* (Kawakita, 2010). *Glochidion* is one of the most diverse genera from this family and has Indo-Australian distribution (Fig. 5).

After further research the same basic pollination strategy was encountered in other species of this genus, and the pollination by *Epicephala* moths is probably shared among all > 300 *Glochidion* species (Kato et al., 2003, 2008; Kawakita, 2010; Kawakita et al., 2019). In this plant genus, female moths damage the flowers when laying eggs with the ovipositor, and larvae consume 25 – 50% of developing seeds (Kawakita, 2010). *Breynia* is another genus with Indo-Australian distribution (Fig. 5), with 35 described species, mostly pollinated by *Epicephala* moths as well (Kawakita, 2010). The moth larvae destroy most of the seeds in the infested fruit. In particular *Breynia* species, female moths place eggs in particular

places of the flower, and in some cases, they do not damage the flowers with the ovipositor (Kawakita, 2010).

Phyllanthus is the last genus with species associated with pollination by gracillariid moths to mention. In this case, larvae consume all the seeds in the developing fruit during larval development (Kawakita, 2010). The *Gomphidium* subgenus has two main areas of distribution with distinct species. Approximately 150 species occur across tropical Australia and Melanesia; seven species are endemic to Madagascar (Fig. 5; Kawakita, 2010; Kawakita et al., 2019). The Australia-Melanesian *Gomphidium* is pollinated by gracillariid moths, but the placement of eggs is different from other groups of the *Phyllanthaceae* plants as the female moth does not necessarily have to damage the flowers to lay eggs (Kawakita, 2010). In the Malagasy *Gomphidium*, the pollination by *Epicephala* moths was not directly observed but was hypothesized based on the larvae-infested fruits and captured adult females carrying pollen (Kawakita, 2010). Finally, the subgenus *Anisonema* (30 species) is distributed in tropical Asia and Africa (Fig. 5), with most species in Madagascar. In this case, female moths damage the flowers by laying eggs into the plant's ovary (Kawakita, 2010). Although the larvae destroy all the seeds in some cases, not all larvae survive to maturity. Thus, some pollinated flowers produce vital seeds and can reproduce; the factors responsible for the survival of larvae in individual infested fruits remain unknown (Kawakita, 2010).

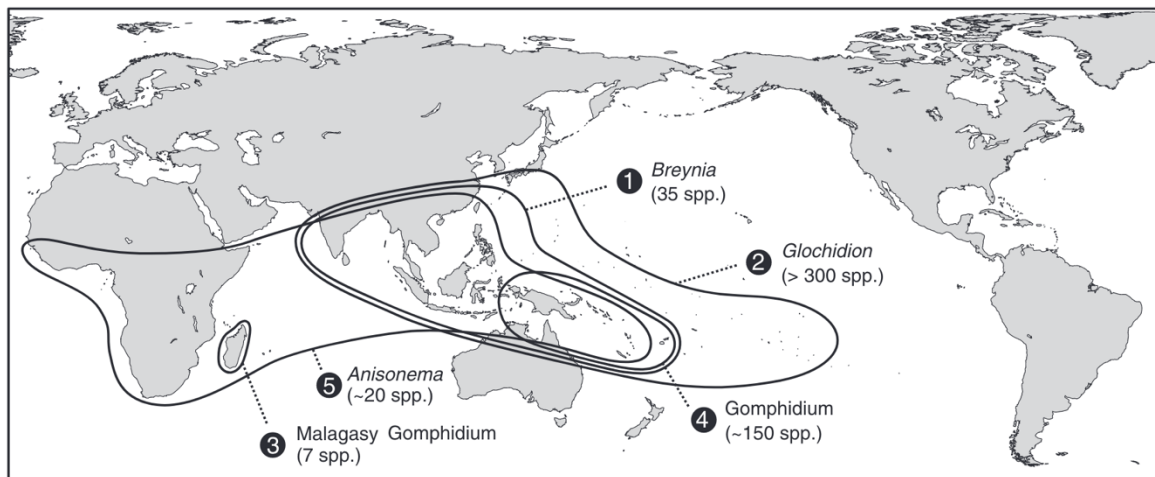


Fig. 5 Distribution of the clades in the Phyllanthaceae family with the obligatory mutualism with the pollinating Gracillariidae moths. Adapted from Kawakita (2010).

A complete dependency on micromoths can also be found in yuccas, genera *Yucca* and *Hesperoyucca* (Pellmyr, 2003). Yuccas are perennial plants, ranked as shrubs or trees, with usually white flowers, distributed in the Northern and Central America (Pellmyr, 2003).

Self-pollination is practically impossible due to the morphology of flowers, as anthers and stigma are distant (Baker, 1961). *Yucca* plants are self-incompatible, and flowers are pollinated exclusively by *Yucca* moths (*Tegeticula* spp. and *Parategeticula* spp.; Powell, 1992). Female moths purposefully collect pollen from anthers by maxillary tentacles (special adaptation), then lay eggs into the pistils of another flower and pollinate its stigma. The larvae then feed on seeds but never destroy all seeds in the fruit and the plant can reproduce as well (Powell, 1992). This obligatory mutualism established already approx. 40 million years ago (Pellmyr & Leebens-Mack, 1999).

Another case of such mutualism has been studied in senita cacti. Senita cactus (*Lophocereus schottii*) is distributed only in the Sonoran Desert in North America and has pale pink flowers. It has evolved a mutualism with the senita moth *Upiga virescens* (Fleming & Holland, 1998). The pollination process is similar to the previous cases; senita moths are the primary pollinators, carry pollen on adapted hairs on the abdomen, and their larvae predate cactus seeds. In previous cases of mutualisms, secondary pollinators were not recorded. Senita cacti, on the other hand, might be occasionally pollinated by halictid bees (Hymenoptera) as secondary pollinators (Fleming & Holland, 1998).

Tab. 2 Comparison of three obligatory mutualisms. Sources: Baker (1961); Fleming & Holland (1998); Pellmyr & Leebens-Mack (1999); Kato et al. (2003; 2008); Pellmyr (2003); Kawakita (2010); Kawakita et al. (2019).

	Phyllanthaceae	Yuccas (Asparagaceae)	<i>Lophocereus schottii</i> (Cactaceae)
Distribution	Paleotropics	Americas	The Sonoran Desert
Plant species	> 518	ca. 40	1
Flower anthesis	nocturnal	nocturnal	nocturnal
Moth species	<i>Epicephala</i> spp.	<i>Tegeticula</i> spp., <i>Parategeticula</i> spp.	<i>Upiga virescens</i>
Family of moth	Gracillariidae	Prodoxidae	Pyralidae
Pollen transfer	hairs on proboscis	maxillary tentacles (near proboscis)	pollen brush on abdomen
Other pollinators	no	no	halictid bees

5.2. Plants relying on pollination by hawkmoths

The known relationships between macromoths (hawkmoths and settling moths) and plants are not as close as in the above-mentioned obligatory mutualisms. Macromoths are less selected in the visited flowers, and they do not lay eggs in flowers they pollinate. Adult Macroheterocera moths usually utilize the resources by themselves, and their caterpillars feed on leaves of often a different plant species (Xu et al., 2018). Flowers adapted to moth pollination are relatively frequently visited by moths that make up about one-third of the visitors (Raju, 2019; Potascheff et al., 2020). In some highly specialized sphingophilous plants, hawkmoths can even be exclusive visitors (Albuquerque-Lima et al., 2020). Such flowers are then often pollinated by them.

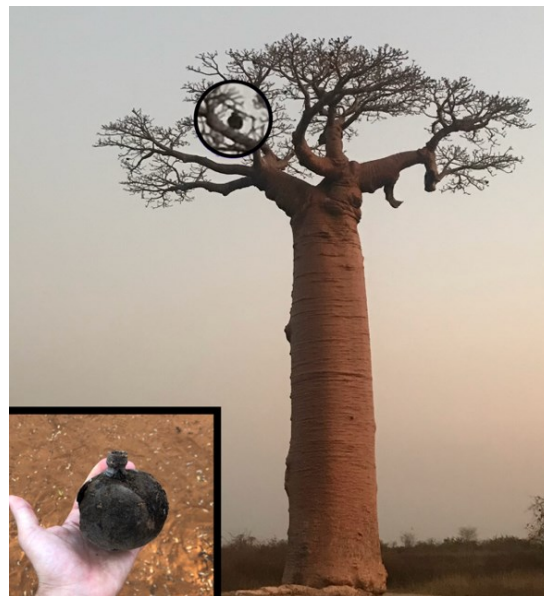


Fig. 6 – Baobab *Adansonia grandidieri* (Malvaceae), during the dry season; in the magnifying glass (in the tree crown) and in the bottom corner is the fruit.

Baobabs (Fig. 6) are majestic trees with wide trunks used as water reservoirs in the dry season and large flowers. The genus *Adansonia* (Malvaceae) has eight species; one is native to Australia, one in tropical Africa, and six in Madagascar. Half of the Malagasy (Madagascan) baobab species, *Adansonia rubrostipa*, *A. perrieri*, and *A. za*, are pollinated by hawkmoths (Baum, 1995). All these species have yellow flowers that the moths probably may not see very well; however, the scent is sweet, and hawkmoths may locate the nectar, containing 13 – 22% of sugars, by olfactory system (Baum, 1995). Mentioned baobab species bloom in different “sections” (early, middle) of the wet season. Flowers of *A. rubrostipa* were the only flowering sphingophilous plants during the time of the study. Flowers of *A. rubrostipa* and *A. za* were visited by various visitors, but only *Coelonia solanii*

(Sphingidae) was observed to make legit contact with the reproductive organs, and it was considered a major pollinator (Baum, 1995). In this study, *Xanthopan morganii* (Sphingidae) was observed to visit only flowers of *Adansonia perrieri*, and was the main pollinator of this baobab species, together with hawkmoth *Coelonia solanii* (Baum, 1995).

Hawkmoths are reported as important pollinators of several species of orchids, one of the most diverse families of angiosperms. In the Paleotropics, pollination and reproductive biology were studied in sphingophilous Angraecoid orchids with long flower spurs from East Africa and Madagascar. These orchids are highly specialized, and hawkmoths (*Coelonia fulvinotata*, *Xanthopan morganii*, and *Agrius convolvuli*) were their exclusive pollinators (Nilsson et al., 1985, 1987; Martins & Johnson, 2007, 2013). In Madagascar, an orchid *Cynorkis uniflora* attaches pollinaria to hawkmoth's eyes (pictured in Fig. 3), which ensures the pollen is transferred correctly to a conspecific flower (Nilsson et al., 1992). *Xanthopan morganii* was already mentioned as a pollinator of *Adansonia perrieri* and some *Angraecum* spp. orchids. It also was observed as an important pollinator of *Bonatea steudneri* (Orchidaceae), together with *Coelonia fulvinotata*; both moth species visited the long-spurred linalool-emitting white flowers and carried the orchid's pollinaria on their eyes (Balducci et al., 2019). Some orchids are known for the highly specialized flowers (long spurs, nocturnal anthesis, pollinaria attachment) to hawkmoth pollination, and hawkmoths were observed as very important pollinators, sometimes even the exclusive pollinators, and the reproduction of some orchids fully depends on them.

Hawkmoths have also been observed visiting more than 25 other plant species from 13 different families (such as Verbenaceae, Solanaceae, Oleaceae) in Kenya (Martins & Johnson, 2013). In some cases, the length of a flower tube slightly exceeded the length of the hawkmoth's proboscis, and pollen was visibly collected on the proboscis. However, the effectiveness of hawkmoths as pollinators was not quantified in this study, so their role in the pollination of these plants remains unclear (Martins & Johnson, 2013). Although tropical Africa is still understudied, hawkmoths are suggested to be the most important pollinators of long-tubed flowers in the Africa (Johnson & Raguso, 2016). The study took place in South Africa, and the plant species with the flower tubes longer than 80 mm were studied, for example, *Crinum* spp. (Amaryllidaceae), *Gladiolus longicollis* (Iridaceae), *Gardenia* spp. and *Oxyanthus pyriformis* (Rubiaceae), *Harveya speciosa* and *Cycnium adonense* (Orobanchaceae), and several representatives of Orchidaceae.

In different parts of the world, a similar synthesis of the importance of hawkmoths is missing. Still, numerous examples of hawkmoth-pollinated plant species (apart from the already-mentioned species) are recorded. For instance, *Delphinium leroyi* (Ranunculaceae) from East Africa has medium-spurred (40 mm) white flowers emitting a strong scent in the evening (Johnson, 2001). Various hawkmoths frequently visited its flowers, but the main pollinator was *Hippotion Celerio* (Sphingidae), of which proboscis is around 37 mm long, matching the flower spur length (Johnson, 2001). In the Neotropics, hawkmoths were also observed as pollinators of some plants; for example, a tree *Bauhinia forficata* (Fabaceae), distributed in the Atlantic rainforest of Brazil, is sphingophilous (white to cream corolla, emitting sweet scent, late evening anthesis) and exclusively pollinated by hawkmoths (Neto, 2013). Also, in a mass-flowering plant from Brazil, *Griffinia gardneriana* (Amaryllidaceae), hawkmoth pollination leads to a great reproductive success (Albuquerque-Lima et al., 2020).

5.3. Plants relying on pollination by settling moths

The literature on settling moth pollination is generally very limited, especially from the tropics; however, in some areas, settling moths can be even exclusive pollinators of some species. In the Paleotropics, an example of an ancient Asian species, *Gnetum luofuense* (Gnetaceae), has dull inflorescences (strobili) and starts producing flower scents in the evening. Many insects visited its flowers, but the only pollinators were noctuid moths (Corlett, 2001; Yang et al., 2021). The reproduction success of *G. luofuense* can even be decreased by bees that collect pollen (that they utilize) from male flowers and, unlike moths, do not visit female flowers (that only produce nectar) to pollinate them (Yang et al., 2021).

The Neotropical *Sauroglossum elatum* (Orchidaceae), of which flowers are phalaenophilous (small, white-green, short-spurred), are pollinated by noctuids (Singer, 2002). Noctuids, together with geometrids, were reported as exclusive visitors and pollinators of some neotropical trees, e.g., *Aspidosperma macrocarpon* (Apocynaceae) and *Roupala montana* (Proteaceae; Oliveira et al., 2004). The erebid moths can also play a role in the pollination of some plant species. For example, flowers of the Hawaiian genus *Schiedea* (Caryophyllaceae) are exclusively pollinated by an erebid *Pseudoschrankia brevipalpis* (Weller et al., 2017; Powers et al., 2020).

Settling moths are also reported to pollinate *Habenaria aitchisonii* (Orchidaceae) in the south-eastern China (Xiong et al., 2020). Noctuids were reported as pollinators of some plant species of southern Africa as well, for example, of *Dipcadi brevifoliumi* (Asparagaceae; Manning et al., 2012) and *Struthiola ciliata* (Thymelaeaceae; Makholela & Manning, 2006). Although southern Africa and China are already in subtropical zones, moth pollinators (e.g., *Cornutiplusia circumflexa*, Noctuidae; pollinator in South Africa) are widespread also throughout the tropics, and I decided to mention them as well. Settling moths are sometimes vital pollinators of particular plant species. They are certainly less studied than hawkmoths, but they deserve more attention, especially in the tropics. Their importance in pollination can be higher than we currently know, based on some studies performed in other areas (e.g., the mentioned subtropics).

Numerous mentioned plant species from various areas of the tropics were observed to be pollinated primarily by hawkmoths and settling moths. That may indicate that many plants in the tropics are specialized. However, this higher specialization in the tropics (compared to the temperate) could be just a bias of sampling (Ollerton & Cranmer, 2002). Many published studies focused on the reproduction success of plants adapted to moth pollination to some degree, and there are still numerous unstudied areas in the tropics (Ollerton & Cranmer, 2002).

5.4. Moths as significant but not the only pollinators

Moths are not the only pollinators in ecosystems, and sometimes moths are one of many effective pollinators of some plant species in bimodal or mixed pollination systems. Bimodal pollination system is encountered in plants, of which flower morphology allows (or is adapted to) being pollinated by two different functional pollinator groups (Manning & Goldblatt, 2005). In such cases, moths are one of the two main functional pollinator groups. The other functional pollinator group in the bimodal system, pollinating flowers together with moths, can be various. The combination of moths and bats is probably the most logical. Hawkmoths and bats share some flower trait preferences. Both groups usually prefer nocturnal anthesis of large (dull or whitish) flowers and nocturnal production of ample amount of somewhat hidden nectar (Willmer, 2011). In Venezuela plains, such a bimodal moth-bat system occurred in 1.3% of studied plant species (Ramírez, 2004).

Ideal flowers, having both hawkmoth and bat floral traits, are quite rare – I only found a single example, *Agave macroacantha* (Agavaceae). It is a succulent distributed in a tropical desert of Tehuacán-Cuicatlán, effectively pollinated equally by both bats and moths (Arizaga et al., 2000). Flowers fitting morphologically more into the sphingophily are rare in bimodal pollination systems as well. For example, in *Pachira aquatica* (Malvaceae), a Neotropical tree of wetlands, the sphingophilous morphology of flowers is supplemented with chiropterophilous scents, resulting in an effective pollination by both groups equally (Hernández-Montero & Sosa, 2016). On the other hand, flowers fitting more into the bat pollination syndrome can also be pollinated by hawkmoths, which is more common (based on the found examples) than vice versa. Chiropterophilous flowers that both bats and hawkmoths effectively pollinate are recorded in, for example, several cacti species (*Pilosocereus* spp., Cactaceae), or *Adansonia digitata* (Malvaceae); they show various levels of dependence on bats as main pollinators, while also being pollinated by sphingids (Groffen et al., 2016; Rocha et al., 2019; Miranda-Jácome et al., 2020). In a few cases, despite flowers having chiropterophily, hawkmoths were the main pollinators, and bats as secondary pollinators. For example, the pollination of *Adansonia digitata* by bats (Baum, 1995) was recently challenged by citizen science observations (Taylor et al., 2020), and hawkmoths were later confirmed as the main pollinators, while bats only play a minor role in its pollination (Karimi et al., 2021). In rare cases, one group may replace the other. For example, bats may be replaced by hawkmoths when bats disappear from the area, and the originally chiropterophilous flowers are then pollinated by hawkmoths alone (Haber & Frankie, 1982; Karimi et al., 2021). This is known from, for instance, *Pilosocereus gounellei* (chiropterophilous pollination syndrome; Rocha et al., 2019).

Although sharing the mainly nocturnal pollinators seems more logical, some bimodal pollination systems involve moths and diurnal pollinators. For instance, in *Dipterocarpus obtusifolius* (Dipterocarpaceae) from Thailand, the whole order Lepidoptera contributes to the pollination – both diurnal butterflies and nocturnal moths (Ghazoul, 1997). Such moth-butterfly bimodal system was recorded in 2.6% of plants studied in Venezuela (Ramírez, 2004), which is two times more than in the moth-bat bimodal system. Another example is *Copaifera coriacea* (Fabaceae), a tree species from Brazil, which is pollinated mainly by settling moths and bees (Souza et al., 2021); such bimodal system also occurred only in 1 species (0.6%) in Venezuela (Ramírez, 2004).

Moths also play a marginal role in the pollination of more generalist flowers – in a “mixed” pollination system – where moths are one of many pollinators. In Venezuela, for example, moths were part of a mixed system (> 2 main pollinator functional groups) in 1.3% of studied plant species (Ramírez, 2004). I have mentioned that the knowledge on mixed systems is really scarce; however, flowers of a few plant species with some adaptations to moth-pollination (not typically generalist flowers) have a mixed pollination system. Flowers of, for example, *Xylocarpus* spp. (Meliaceae), mangrove trees found in the tropical tidal forests of the Old World, and a tree *Hancornia pubescens* (Apocynaceae), are pollinated by bees, butterflies, and moths (Oliveira et al., 2004; Raju, 2019).

5.5. Moths as nectar thieves

Not all flower visitors are efficient pollinators; some visitors getting nectar without providing pollination of the flower are called nectar thieves or robbers (Inouye, 1980). Nectar robbers usually make a hole into the flower to get the nectar. Conversely, nectar thieves do not usually damage flowers (Inouye, 1980). Moths do not have chewing mouthparts; thus, they only can be considered nectar thieves or secondary nectar robbers (getting nectar from the hole the primary robber made; Irwin et al., 2010). Nectar thieving can negatively affect the reproductive strategy as the plants need to spend additional energy to produce more nectar to replace the losses and, eventually, attract pollinators again. It also may affect the population dynamics as plants have fewer resources to invest in offspring (Irwin et al., 2001). As far as I know, the direct influence of nectar thieving has not yet been studied in moths so the effect may differ.

Chiropterous flowers of baobab *Adansonia digitata*, for example, were reported to be pollinated by bats, while *Nephele* spp. hawkmoths were classified as nectar thieves (Baum, 1995). Later, it was found that hawkmoths actually pollinated the flowers as well, and this time, small settling moths (with access to big open flowers) were marked as nectar thieves (Karimi et al., 2021). Hawkmoths with long proboscides, such as *Agrius convolvuli* or *Hippotion osiris*, may thief nectar from plants that target short- or medium-tongued pollinators – for example, of some (already-mentioned) African orchids (Nilsson et al., 1992; Martins & Johnson, 2013; Balducci et al., 2020) or *Delphinium leroyi* (Ranunculaceae) from Asia (Johnson, 2001).

Some moths have a great potential as nectar thieves; however, the nectar thievery in moths may be very rare in nature. Long-tongued hawkmoths have access to numerous flowers with short- or medium-sized tubes. Small settling moths can sometimes easily reach the nectar of large flowers without touching the reproductive organs. However, it seems that moths may prefer visiting flowers with a similar-sized tube as is their proboscis (Sazatornil et al., 2016). For example, on Mount Cameroon, only 1% of hawkmoths did not touch the flowers' reproductive organs during the visit were consumed nectar without pollinating (Mertens et al., 2021). To conclude, settling moths are generally rarely studied as pollinators, even less as nectar thieves. Despite having a great potential to steal, hawkmoths were rarely recorded as nectar thieves and in some areas, seem to prefer flowers with a spur of a just-right length, which they also pollinate.

6. Moth pollination in communities

The importance of moths as pollinators in plant communities may differ from the importance of moths as pollinators of particular plant species (plants) in the ecosystem. Most of the studies I have mentioned in previous chapters focused mainly on reproductive strategies of flowering plants and their pollination ecology. Studying pollination in communities in the tropics is not easy in general. But especially the nocturnal pollination, which requires special equipment and methods is often overlooked completely in such pollination studies. Based on the available knowledge, I will assess a few important aspects of moth pollination in plant communities to better understand the importance of moths as pollinators.

6.1. Proportion of pollination syndromes in plant communities

The proportion of pollination syndromes in plant communities may somewhat reflect the significance of the particular functional pollinator group. The hypothesis of pollination syndromes has been well-defined for more than 40 years (Faegri & Pijl, 1979). Yet, only few studies focused on the proportion of plants with particular pollination syndromes in plant communities. Here, I reviewed how often can be sphingophilous and phalaenophilous flowers (species) encountered in the tropics. Indeed, more studies are needed to determine the general proportion of phalaenophilous and sphingophilous plants in tropical communities and the factors influencing the proportion in particular ecosystems.

Only a single such study has been performed in the Afrotropics; it reported the sphingophily in only 4% of plant species in the plant diversity of Kenya (Martins & Johnson, 2013). In the Indo-Australian tropics, the moth pollination syndromes were reported in about 10% of plant species in a forest vegetation (Hansman, 2001; Devy & Davidar, 2003).

In the Neotropics, the proportion of phalaenophilous or sphingophilous plant species ranges from 4% in Brazilian Cerrado, dominated by trees and shrubs (301 plant species in a one-hectare plot; Gottsberger & Silberbauer-Gottsberger, 2018) to 13% species in the arboreal and shrub Caatinga in Brazil. (Quirino & Machado, 2014). In Cerrado, a pattern of vertical stratification of vegetation was recorded; the proportion of plant species with moth pollination syndrome flowers increased from 0% at the ground layer to 11% in the tree layer (Gottsberger & Silberbauer-Gottsberger, 2018). Maybe because some moths are more likely canopy animals and do not spend much time in the lowest vegetation strata (Schulze et al., 2001).

Tab. 3 Proportions of the moth pollination syndromes (sphingophily and phalaenophily) in particular areas; both = phalaenophily and sphingophily.

Area	Ecosystem	Pollination syndrome	Proportion	Reference
South America, Brazil	Caatinga (shrubland, thorn forest; other plants overlooked)	both	13%	Quirino & Machado, 2014
South America, Brazil	Cerrado (lower trees and shrubs)	both	4%	Gottsberger & Silberbauer-Gottsberger, 2018
Africa, Kenya	grassland, bush-savanna, woodland	sphingophily	4%	Martins & Johnson, 2013
Asia, India, Western Ghats	wet evergreen forest	both	10%	Devy & Davidar, 2003
Australia, Queensland	dry rainforest	both	9%	Hansman, 2001

The proportions of plant species with moth pollination syndromes in particular areas are summarized in a table (Tab. 3). Plants species with moth pollination syndrome flowers seem relatively rare. From the available literature, it seems that plant species with sphingophily and phalaenophily are more common in forests and less common in relatively

open landscapes, such as savannas. The proportions may also increase with higher vegetation in some areas.

6.2. Proportion of moth-pollinated plants in communities

To summarize how often are plants in communities pollinated by moths, studies focused on larger-scale pollination with pollinator observations are needed. I summarized the proportion of plants pollinated by moths in several areas (Tab. 4). The relative importance of moths as pollinators in flowering plant communities can be read from the proportion of moth-pollinated plants alone. Additionally, the proportion of moth-pollinated plants may also be compared to the proportion of plant species with moth pollination syndromes (chapter 6.1). However, the limitations of published literature did not allow much interpretation of the differences. Only in a single area were the data available for both proportions in the plant communities.

In the Paleotropics, two studies with observations of pollinators were performed. In the Malaysian dipterocarp forest, moths pollinated only 2.4% of trees (Kato, 1996); however, in lower layers of the forest, the percentage was higher (not quantified; Momose et al., 1998). Interestingly, the proportion of plants pollinated by moths opposed (decreased) the trend of an increasing proportion of plant species with moth pollination syndromes in Cerrado (mentioned in the previous chapter). In Africa, moths were the primary pollinators of about 12% of plant species studied on Mount Cameroon (based on the observations of moth visits with contacting the reproductive organs; Klomberg et al., 2022).

In the Neotropics, the proportion of plant species pollinated by moths ranged from 3 – 4% in Colombian seasonally flooded and upland forest (trees and lianas; van Dulmen, 2001) to 15.9% of tree species in Costa Rican lowland rainforest (Bawa et al., 1985). Here the difference is quite striking and may be caused by the vegetation structure, or the species diversity of the forest, for example. The only case where the proportion of moth-pollinated plants can be somewhat compared to the proportion of plants with moth pollination syndromes (chapter 6.1.) is the Brazilian Caatinga. In the pollinator observation study, representatives of numerous species from the whole plant community were studied, and moths pollinated 8.5% of these species (Machado & Lopes, 2004). The limitation in comparing the proportion of plants with moth pollination syndromes from Caatinga (13%) is in the methods – only trees and shrubs were included in Quirino & Machado (2014). In neotropical grasslands, the proportion of plants pollinated by moths may depend on

elevation; for example, on Venezuela plains, moths were effective pollinators of 10.2% of plants (Ramírez, 2004). However, in Brazilian high-altitude grasslands, moths were completely missing in the studied pollination network (Freitas & Sazima, 2006). Overall, moths certainly do play a part in the pollination systems; however, the interpretation of the exact importance can be difficult as the tropics are still very understudied, and further knowledge is needed.

Tab. 4 Proportion of plants pollinated by all moths (settling moths and hawkmoths together) in flowering plant communities in particular areas and ecosystems. Vegetation = type of plant species focused in the study, of which moth-pollinated proportion is mentioned in the next column.

Area	Ecosystem	Vegetation	Proportion	Reference
Asia, Malaysia	Dipterocarp forest	understory	2.4%	Kato (1996)
Africa, Mount Cameroon	rainforest, montane forest	all plants	12%	Klomberg et al. (2022)
Central America, Costa Rica	lowland rainforest	trees	15.9%	Bawa et al. (1985)
South America, Colombia	seasonally flooded forest	canopy	4%	van Dulmen (2001)
South America, Colombia	upland (<i>tierra firme</i>) forest	canopy	3%	van Dulmen (2001)
South America, Brazil	Caatinga (shrubland, thorn forest)	all plants	8.5%	Machado & Lopes (2004)
South America, Venezuela	grassland, savanna	all plants	10.2%	Ramírez (2004)
South America, Brazil	high-altitude grassland	all plants	0%	Freitas & Sazima (2006)

6.3. Flower visitation rates of moths

Although moths may be the most frequent flower visitors of particular specialized plant species, their frequency in the entire community can be significantly lower. The limitations in this chapter are similar to the ones in the previous chapters and chapter 5 (pollination on the species level). Generally, nocturnal visitors/pollinators of flowers in communities are not systematically studied and are often overlooked in pollination studies. On the species level, particular visitors' frequency is easier to track than on a community level. However, the frequency of moths as flower visitors is important to include because it depends (among

other things) on the abundance of pollinators, which can be influenced by many factors, and the abundance of pollen vectors can, eventually, affect the pollination itself.

The absolute flower visitation rate in moths was recorded, for example, in baobab flowers, where around five individuals per flower appeared in the first hour of observations (Baum, 1995). On Mount Cameroon, the rate was 0.056 moth visits per hour (counted as all recorded moth visits divided by all recorded observational hours; Klomberg et al., 2022). To compare the visitation rate of moths to the rate of other flower visitors, in the two most common flower visitors on Mount Cameroon, it was 0.339 visits per hour in bees and 0.19 visits per hour in flies (counted the same way as in moths; Klomberg et al., 2022). The proportion of moths in visitor communities can also be very low; on Mount Cameroon, for example, moths accounted for only about 0.6% of all flower visits (14.4% of moth visits from the 4% of all Lepidoptera visits in the plant community; Mertens et al., 2021).

In the studies I encountered, the visitation rate or the proportion of moths in visitor communities was often not quantified and only expressed verbally. It was “measured” by the observer: “it was not uncommon for hours of nocturnal observation to pass without a single visitor,” in the Brazilian Cerrado (Oliveira et al., 2004). Also, Corlett (2001) stated that moths are occasional visitors (on a scale of occasional < regular < numerous) in a degraded tropical landscape in Hong Kong. In this case, it was based on the ratio of visitors, but without any numerical values again (Corlett, 2001). A similar abstract frequency statement was encountered in studies of Kato et al. (2008) and Maruyama et al. (2010), where moths were generally less frequent visitors than, for example, bees. The exact data of flower visitation rates of moths are missing from almost all areas. Additionally, in flower visitation rates can be temporal (seasonal) and spatial differences, affected by many factors.

The abundance of moths can influence the visitation rate of flowers. The pollen vectors need to be available to visit the flowers in the first place – low abundances can leave many flowers unvisited (Baker, 1961) and the gene flows between plants can be limited (Amorim et al., 2014). However, the abundance does not necessarily predict the particular importance of moths in pollination (Devoto et al., 2011). In the tropics, hawkmoths are most abundant during the wet season in some areas (Duarte-Júnior & Schlindwein, 2005; Primo et al., 2013). The moth species richness correlates with the wet season in some areas, such as in the Brazilian Caatinga (Duarte-Júnior & Schlindwein, 2005). However, it did not correlate in the rainforests of Northeastern Brazil or the rainforests of Mount Cameroon

(Primo et al., 2013; Mertens et al., 2021). In the short term, the weather can affect the abundance of pollen vectors as well. The temperature can affect the activity of moths. They do not usually fly if the temperature drops under a certain level (Baker, 1961; Corlett, 2001; de Camargo et al., 2016a); thus, the flower visitation rate can decrease. High precipitation can affect the quality of pollination abilities of moths and decrease pollen-dispersal distances (Linhart & Mendenhall, 1977).

In some cases, the flowering is synchronized with the pollinator availability. It seems logical; both nectar resources and pollen vectors can be utilized when synchronized. This appears to be true in some plants. The flowering of some phalaenophilous flowers is somewhat concentrated in the rainy season in Caatinga (Quirino & Machado, 2014). In Costa Rica, the flowering of sphingophilous plants peaks during the wet season; however, some plants in the community flower during the dry season and altogether provide nectar all year long (Haber & Frankie, 1989). Mass-flowering of some plants is also concentrated in the rainy season when moth pollinators are most abundant in some areas. During mass-flowering, many flowers open simultaneously, emit a strong odor and attract pollinators. This ensures a successful reproduction (as not all seeds will be predated if there are too many). Some of the mass-flowering plants rely on the olfactory of sphingids as pollinators. Such plant from Brazil, *Griffinia gardneriana* (Amaryllidaceae), blooms during the rainy season and is pollinated by hawkmoths (Albuquerque-Lima et al., 2020). Another example of a plant mass-flowering during the wet season is *Inga sessilis* (Fabaceae). It has white, brush-type (not typical for phalaenophily) flowers. Hummingbirds, bats, and hawkmoths visit its flowers, but only the latter two pollinator groups proved as legitimate pollinators, and both bats and hawkmoths contribute to the reproductive success of the plant (Amorim et al., 2013). On the other hand, in baobab *Adansonia gregorii* (Malvaceae), the flowering does not sync with the hawkmoth pollinator. One of its effective pollinators, *Agrius convolvuli* (Sphingidae), becomes active and visits flowers when only a few trees remain flowering (Baum, 1995). In this case, hawkmoths are secondary pollinators of mainly bat-pollinated species, so the hawkmoth-asynchronous flowering should not lower the plant's reproductive success.

7. Conclusions

Moths are a diverse group of insects with many values in terrestrial ecosystems. The role (mainly importance) of nocturnal and crepuscular moths in pollination has been reviewed in this thesis. Numerous moths visit flowers where they consume nectar. To find nectar at night, moths have adapted vision and olfactory systems. Flower traits are properties of flowers that can be measured or defined (color, scent, nectar composition, etc.). Particular pollinators prefer particular values of flower traits (white color, sweet scent, etc.). Therefore, plants from numerous families matched those preferences and convergently evolved pollination syndromes – sets of adaptations specialized to attract a particular functional pollinator group (from definition). Moth pollination syndromes are phalaenophily and sphingophily, adaptations to pollination by settling moths and hawkmoths, respectively. Some values of flower traits are shared among both moth pollination syndromes because some flower traits are preferred by both settling moths and hawkmoths (e.g., nocturnal anthesis, whitish color).

Moths have proven important pollinators of many plant species. An obligatory mutualism with some micromoths is found in more than 550 plant species (mainly Phyllanthaceae). Moths are vital pollinators of these species and both moths and plants depend on each other in order to reproduce. Flowers (somewhat adapted to moth pollination) of other plants from more than 25 families are frequently visited by macromoths (in some cases, moths are the only visitors). For some plant species, such as orchids, baobabs, or various tropical trees and shrubs, macromoths are important effective pollinators, often the only pollinators and in such cases, plants rely on moth pollination. Moths are sometimes one of many pollinators of the plant species in bimodal or more generalist pollination systems, where they serve as effective pollinators together with some other functional pollinator group, such as bats, butterflies, or bees. Moths visit numerous plant species for nectar (generalists, for example, *Agrius convolvuli*, Sphingidae) as hawkmoths can reach the nectar in numerous plant species with their proboscis and settling moths can steal nectar from large open flowers. However, the nectar thievery (getting nectar without providing pollination services) showed as very rare in some tropical communities. In some areas, moths even preferred to feed from flowers with a spur of a length corresponding to the length of their proboscis – the flowers moths also pollinate.

Plants adapted to moth pollination seem uncommon in communities; however, the proportion of flowers with moth pollination syndromes varies among different tropical areas.

Proportion of plants pollinated by moths (pollinator observations) in plant communities was very low in some areas. It varied among different ecosystems and the methods of the study was also important to mention. On the community level, moths are generally infrequent visitors of flowers and their abundance and pollination can be influenced by many factors.

The determination of the role of moths in pollination is somewhat complicated. Moths proved as essential pollinators of numerous plant species across the tropics. However, the proportion of moth-pollinated plant species is low. There could be several interpretations of the role of moths in pollination; some of them may be even limited by the methods. (1) Moths may be essential pollinators of plants that are rare in the given area, so the individuals of such plants were not included in the study due to the lack of collected data from the studied plot. Also, moths are also very mobile animals, which may allow such plant species have lower population densities, and possibly, such plants did not occur in the particular studied area. (2) The statement can also simply mean that moths are less important pollinators in communities, as there are functional pollinator groups that pollinate flowers of more plant species. (3) However, not only the quantity, the quality of pollination is important as well. In orchids, for example, a single moth visit with successful pollinaria attachment to a particular place on the moth can result in a great reproductive success of the plant. Such plant species then do not need to be frequently visited and (as already mentioned) do not need high population densities. (4) In some cases, moths may even replace some pollinators (e.g., bats) when they disappear and pollinate such species instead of the original main pollinator. Also, it has been shown (in some places) that moths do not intend to steal nectar.

In the end, this thesis suggests that moths are rare visitors and pollinators of plants in communities, however, they are high quality pollinators of particular plant species, that may often depend on their pollination. Moths generally contribute to the heterogeneity and diversity of tropical ecosystems with their pollination services and are important pollinators.

Future research should aim to study the tropical pollination networks more (in general) and make a higher effort to comprehensively study the pollination, for example, by also including nocturnal pollinators. In this thesis, I have mentioned several limitations in the nocturnal pollination research. Although the conditions of field research in the tropics are challenging, with new approaches and technology (cameras, computing technology, cooperation with the locals), the research may be expanded. That is also what I would like to build on my bachelor thesis in the future.

References

- ALBUQUERQUE-LIMA S., DOMINGOS-MELO A., NADIA T.C.L., BEZERRA E.L.S., NAVARRO D.M.A.F., MILET-PINHEIRO P. & MACHADO I.C. 2020: An explosion of perfume: Mass flowering and sphingophily in the Caatinga dry region in Brazil. — *Plant Species Biol.* **35**: 243–255.
- AMORIM F.W., GALETTO L. & SAZIMA M. 2013: Beyond the pollination syndrome: Nectar ecology and the role of diurnal and nocturnal pollinators in the reproductive success of *Inga sessilis* (Fabaceae). — *Plant Biol.* **15**: 317–327.
- AMORIM F.W., WYATT G.E. & SAZIMA M. 2014: Low abundance of long-tongued pollinators leads to pollen limitation in four specialized hawkmoth-pollinated plants in the Atlantic Rain forest, Brazil. — *Naturwissenschaften* **101**: 893–905.
- ARDITTI J., ELLIOTT J., KITCHING I.J. & WASSERTHAL L.T. 2012: ‘Good Heavens what insect can suck it’ – Charles Darwin, *Angraecum sesquipedale* and *Xanthopan morganii praedicta*. — *Bot. J. Linn. Soc.* **169**: 403–432.
- ARIZAGA S., EZCURRA E., PETERS E., DE ARELLANO F.R. & VEGA E. 2000: Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. — *Am. J. Bot.* **87**: 1004–1010.
- BAKER H.G. 1961: The adaptation of flowering plants to nocturnal and crepuscular pollinators. — *Q. Rev. Biol.* **36**: 64–73.
- BALDUCCI M.G., MARTINS D.J. & JOHNSON S.D. 2019: Pollination of the long-spurred African terrestrial orchid *Bonatea steudneri* by long-tongued hawkmoths, notably *Xanthopan morganii*. — *Plant Syst. Evol.* **305**: 765–775.
- BALDUCCI M.G., VAN DER NIET T. & JOHNSON S.D. 2020: Diel scent and nectar rhythms of an African orchid in relation to bimodal activity patterns of hawkmoth pollinators. — *Ann. Bot.* **126**: 1155–1164.
- BALKENIUS A. & DACKE M. 2013: Learning of multi-modal stimuli in hawkmoths. — *PLoS ONE* **8**: e71137.
- BALKENIUS A., ROSÉN W. & KELBER A. 2006: The relative importance of olfaction and vision in a diurnal and a nocturnal hawkmoth. — *J. Comp. Physiol. A* **192**: 431–437.
- BAUM D.A. 1995: The comparative pollination and floral biology of baobabs (*Adansonia* — Bombacaceae). — *Ann. Mo. Bot. Gard.* **82**: 322–348.
- BAWA K.S. 1990: Plant-pollinator interactions in tropical rain forests. — *Annu. Rev. Ecol. Syst.* **21**: 399–422.
- BAWA K.S., BULLOCK S.H., PERRY D.R., COVILLE R.E. & GRAYUM M.H. 1985: Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. — *Am. J. Bot.* **72**: 346–356.

- BRISCOE A.D. 2008: Reconstructing the ancestral butterfly eye: Focus on the opsins. — J. Exp. Biol. **211**: 1805–1813.
- BUXTON M.N., HOARE R.J.B., BROUSSARD M.A., VAN NOORT T., FALE G.R.T., NATHAN T. & PATTEMORE D.E. 2021: Moths as potential pollinators in avocado (*Persea americana*) orchards in temperate regions. — N. Z. J. Crop Hortic. Sci. **AHEAD-OF-PRINT**: 1–12.
- DE CAMARGO A.J.A., DE CAMARGO N.F., CORRÊA D.C.V., DE CAMARGO W.R.F., VIEIRA E.M., MARINI-FILHO O. & AMORIM F.W. 2016a: Diversity patterns and chronobiology of hawkmoths (Lepidoptera, Sphingidae) in the Brazilian Amazon rainforest. — J. Insect Conserv. **20**: 629–641.
- DE CAMARGO N.F., DE CAMARGO W.R.F., CORRÊA D. DO C.V., DE CAMARGO A.J.A. & VIEIRA E.M. 2016b: Adult feeding moths (Sphingidae) differ from non-adult feeding ones (Saturniidae) in activity-timing overlap and temporal niche width. — Oecologia **180**: 313–324.
- CHEN Q., LIU X., CAO S., MA B., GUO M., SHEN J. & WANG G. 2021: Fine structure and olfactory reception of the labial palps of *Spodoptera frugiperda*. — Front. Physiol. **12**: 680697.
- CORLETT R.T. 2001: Pollination in a degraded tropical landscape: A Hong Kong case study. — J. Trop. Ecol. **17**: 155–161.
- CORLETT R.T. 2004: Flower visitors and pollination in the Oriental (Indomalayan) region. — Biol. Rev. **79**: 497–532.
- CORREA-CARMONA Y., ROUGERIE R., ARNAL P., BALLESTEROS-MEJIA L., BECK J., DOLÉDEC S., HO C., KITCHING I.J., LAVELLE P., LE CLEC'H S., ET AL. 2021: Functional and taxonomic responses of tropical moth communities to deforestation. — Insect Conserv. Divers. **15**: 236–247.
- COX P.A. & GRUBB P.J. 1991: Abiotic pollination: An evolutionary escape for animal-pollinated angiosperms [and discussion]. — Philos. Trans. Biol. Sci. **333**: 217–224.
- CROW J.F. 1994: Advantages of sexual reproduction. — Dev. Genet. **15**: 205–213.
- DARWIN C. 1862: The various contrivances by which orchids are fertilized by insects. John Murray, UK, London, 365 pp.
- DEVOTO M., BAILEY S. & MEMMOTT J. 2011: The ‘night shift’: Nocturnal pollen-transport networks in a boreal pine forest. — Ecol. Entomol. **36**: 25–35.
- DEVY M.S. & DAVIDAR P. 2003: Pollination systems of trees in Kakachi, a mid-elevation wet evergreen forest in Western Ghats, India. — Am. J. Bot. **90**: 650–657.
- DUARTE-JÚNIOR J.A. & SCHLINDWEIN C. 2005: The highly seasonal hawkmoth fauna (Lepidoptera, Sphingidae): Of the Caatinga of Northeast Brazil: A case study in the state of Rio Grande do Norte. — **59**: 212–218.

- VAN DULMEN A. 2001: Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. — *Plant Ecol.* **153**: 73–85.
- FAEGRI K. & PIJL L. VAN DER. 1979: The principles of pollination ecology. Pergamon Press, Oxford; New York, 244 pp.
- FENSTER C.B., ARMBRUSTER W.S., WILSON P., DUDASH M.R. & THOMSON J.D. 2004: Pollination syndromes and floral specialization. — *Annu. Rev. Ecol. Evol. Syst.* **35**: 375–403.
- FERREIRA B.H.S., GOMES A.C., SOUZA C.S., FABRI J.R. & SIGRIST M.R. 2018: Pollination and reproductive system of synchronopatric species of Cactaceae (Cactoideae) subject to interspecific flow of pollen: An example of ecological adaptation in the Brazilian Chaco. — *Plant Biol.* **20**: 101–112.
- FLEMING T.H. & HOLLAND J.N. 1998: The evolution of obligate pollination mutualisms: *Senita cactus* and *senita moth*. — *Oecologia* **114**: 368–375.
- FREITAS L. & SAZIMA M. 2006: Pollination biology in a tropical high-altitude grassland in Brazil: Interactions at the community level. — *Ann. Mo. Bot. Gard.* **93**: 465–516.
- GHAZOUL J. 1997: The pollination and breeding system of *Dipterocarpus obtusifolius* (Dipterocarpaceae) in dry deciduous forests of Thailand. — *J. Nat. Hist.* **31**: 901–916.
- GOTTSBERGER G. & SILBERBAUER-GOTTSBERGER I. 2018: How are pollination and seed dispersal modes in Cerrado related to stratification? Trends in a Cerrado *sensu stricto* woodland in southeastern Brazil, and a comparison with Neotropical forests. — *Acta Bot. Bras.* **32**: 434–445.
- GRIMALDI D.A. & ENGEL M.S. 2005: Evolution of the insects. Cambridge University Press, Cambridge UK, 755 pp.
- GROFFEN J., RETHUS G. & PETTIGREW J. 2016: Promiscuous pollination of Australia's baobab, the boab, *Adansonia gregorii*. — *Aust. J. Bot.* **64**: 678–686.
- HABER W.A. & FRANKIE G.W. 1982: Pollination of *Leuhea* (Tiliaceae) In Costa Rican deciduous forest. — *Ecology* **63**: 1740–1750.
- HABER W.A. & FRANKIE G.W. 1989: A tropical hawkmoth community: Costa Rican dry forest Sphingidae. — *Biotropica* **21**: 155–172.
- HANSMAN D.J. 2001: Floral biology of dry rainforest in north Queensland and a comparison with adjacent savanna woodland. — *Aust. J. Bot.* **49**: 137–153.
- HEINRICH B. 1975: Energetics of pollination. — *Annu. Rev. Ecol. Syst.* **6**: 139–170.
- HERNÁNDEZ-MONTERO J.R. & SOSA V.J. 2016: Reproductive biology of *Pachira aquatica* Aubl. (Malvaceae: Bombacoideae): A tropical tree pollinated by bats, sphingid moths and honey bees: Reproductive biology of *Pachira aquatica*. — *Plant Species Biol.* **31**: 125–134.

- INOUE D.W. 1980: The terminology of floral larceny. — *Ecology* **61**: 1251–1253.
- IRWIN R.E., BRODY A.K. & WASER N.M. 2001: The impact of floral larceny on individuals, populations, and communities. — *Oecologia* **129**: 161–168.
- IRWIN R.E., BRONSTEIN J.L., MANSON J.S. & RICHARDSON L. 2010: Nectar robbing: Ecological and evolutionary perspectives. — *Annu. Rev. Ecol. Evol. Syst.* **41**: 271–292.
- JANEČEK Š., CHMEL K., EWOME F.L., HRUBÁ K., KLOMBERG Y., KOBE I.N., KOUÉDE R.D., MERTENS J.E.J., NJIE M.M. & TROPEK R. 2021: Differences in nectar traits between ornithophilous and entomophilous plants on Mount Cameroon. — *Plants* **10**: 1161.
- JOHNSON S.D. 2001: Hawkmoth pollination and hybridization in *Delphinium leroyi* (Ranunculaceae) on the Nyika Plateau, Malawi. — *Nord. J. Bot.* **21**: 599–605.
- JOHNSON S.D. & RAGUSO R.A. 2016: The long-tongued hawkmoth pollinator niche for native and invasive plants in Africa. — *Ann. Bot.* **117**: 25–36.
- JOSENS R. & FARINA W. 2001: Nectar feeding by the hovering hawk moth *Macroglossum stellatarum*: Intake rate as a function of viscosity and concentration of sucrose solutions. — *J. Comp. Physiol. [A]* **187**: 661–665.
- KARIMI N., SAGHAFI S., KEEFOVER-RING K., VENTER S.M., ANÉ C. & BAUM D.A. 2021: Evidence for hawkmoth pollination in the chiropterophilous African baobab (*Adansonia digitata*). — *Biotropica* **00**: 1–12.
- KATO M. 1996: Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. — *Am. J. Bot.* **83**: 732–743.
- KATO M., KOSAKA Y., KAWAKITA A., OKUYAMA Y., KOBAYASHI C., PHIMMINITH T. & THONGPHAN D. 2008: Plant-pollinator interactions in tropical monsoon forests in Southeast Asia. — *Am. J. Bot.* **95**: 1375–1394.
- KATO M., TAKIMURA A. & KAWAKITA A. 2003: An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). — *Proc. Natl. Acad. Sci.* **100**: 5264–5267.
- KAWAHARA A.Y., PLOTKIN D., ESPELAND M., MEUSEMANN K., TOUSSAINT E.F.A., DONATH A., GIMNICH F., FRANDBEN P.B., ZWICK A., DOS REIS M., ET AL. 2019: Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. — *Proc. Natl. Acad. Sci.* **116**: 22657–22663.
- KAWAKITA A. 2010: Evolution of obligate pollination mutualism in the tribe Phyllanthaceae (Phyllanthaceae). — *Plant Species Biol.* **25**: 3–19.
- KAWAKITA A., SATO A.A.W., SALAZAR J.R.L. & KATO M. 2019: Leaf-flower–leaf-flower moth mutualism in the Neotropics: Successful transoceanic dispersal from the Old World to the New World by actively-pollinating leaf-flower moths. — *PLoS ONE* **14**: e0210727.

- KELBER A. 2003: Colour vision in diurnal and nocturnal hawkmoths. — *Integr. Comp. Biol.* **43**: 571–579.
- KISLEV M. 1972: A study of hawkmoth pollination, a palynological analysis of the proboscis. — *Isr. J. Bot.* **21**: 57–75.
- KLAHRE U., GURBA A., HERMANN K., SAXENHOFER M., BOSSOLINI E., GUERIN P.M. & KUHLEMEIER C. 2011: Pollinator choice in *Petunia* depends on two major genetic loci for floral scent production. — *Curr. Biol.* **21**: 730–739.
- KLOMBERG Y., TROPEK R., MERTENS J.E.J., KOBE I.N., HODEČEK J., RAŠKA J., FOMINKA N.T., SOUTO-VILARÓS D., JANEČKOVÁ P. & JANEČEK Š. 2022: Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. — *Ecol. Lett.* **00**: 1–12.
- KNUDSEN J.T. & TOLLSTEN L. 1993: Trends in floral scent chemistry in pollination syndromes: Floral scent composition in moth-pollinated taxa. — *Bot. J. Linn. Soc.* **113**: 263–284.
- VAN DER KOOI C.J. 2021: How much pigment should flowers have? Flowers with moderate pigmentation have highest color contrast. — *Front. Ecol. Evol.* **9**: 731626.
- KRENN H.W. 2010: Feeding mechanisms of adult Lepidoptera: Structure, function, and evolution of the mouthparts. — *Annu. Rev. Entomol.* **55**: 307–327.
- LINHART Y.B. & MENDENHALL J.A. 1977: Pollen dispersal by hawkmoths in a *Lindenia rivalis* Benth. population in Belize. — *Biotropica* **9**: 143–143.
- LU Q., LIU C. & HUANG S. 2021: Moths pollinate four crops of Cucurbitaceae in Asia. — *J. Appl. Entomol.* **145**: 499–507.
- MACHADO I.C. & LOPES A.V. 2004: Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry forest. — *Ann. Bot.* **94**: 365–376.
- MAKHOLELA T. & MANNING J.C. 2006: First report of moth pollination in *Struthiola ciliata* (Thymelaeaceae) in southern Africa. — *South Afr. J. Bot.* **72**: 597–603.
- MANNING J.C. & GOLDBLATT P. 2005: Radiation of pollination systems in the Cape genus *Tritoniopsis* (Iridaceae: Crocoideae) and the development of bimodal pollination strategies. — *Int. J. Plant Sci.* **166**: 459–474.
- MANNING J.C., GOLDBLATT P., PARKER E. & KAISER R. 2012: First record of pollination in the Afro-Eurasian *Dipcadi* Medik. (Hyacinthaceae): Pollination of *D. brevifolium* by the owlet moth *Syngrapha circumflexa* (Noctuidae). — *South Afr. J. Bot.* **81**: 15–18.
- MARTÉN-RODRÍGUEZ S., MUÑOZ-GAMBOA P., DELGADO-DÁVILA R. & QUESADA M. 2013: Asymmetric pollen transfer and reproductive success of the hawkmoth-pollinated distylous tree *Palicourea tetragona* (Rubiaceae) at La Selva, Costa Rica. — *J. Trop. Ecol.* **29**: 501–510.

- MARTINS D.J. & JOHNSON S.D. 2007: Hawkmoth pollination of aerangoid orchids in Kenya, with special reference to nectar sugar concentration gradients in the floral spurs. — *Am. J. Bot.* **94**: 650–659.
- MARTINS D.J. & JOHNSON S.D. 2013: Interactions between hawkmoths and flowering plants in East Africa: Polyphagy and evolutionary specialization in an ecological context: Hawkmoth pollination in East Africa. — *Biol. J. Linn. Soc.* **110**: 199–213.
- MARUYAMA P.K., AMORIM F.W. & OLIVEIRA P.E. 2010: Night and day service: Distyly and mixed pollination system in *Faramea cyanea* (Rubiaceae). — *Flora - Morphol. Distrib. Funct. Ecol. Plants* **205**: 818–824.
- MERTENS J.E.J., BRISSON L., JANEČEK Š., KLOMBERG Y., MAICHER V., SÁFIÁN S., DELABYE S., POTOCKÝ P., KOBE I.N., PYRCZ T., ET AL. 2021: Elevational and seasonal patterns of butterflies and hawkmoths in plant-pollinator networks in tropical rainforests of Mount Cameroon. — *Sci. Rep.* **11**: 9710.
- MIRANDA-JÁCOME A., RODRÍGUEZ-GARCÍA R. & MUNGUÍA-ROSAS M.A. 2020: Bats and moths contribute to the reproductive success of the columnar cactus *Pilosocereus leucocephalus*. — *J. Arid Environ.* **174**: 103990.
- MOMOSE K., YUMOTO T., NAGAMITSU T., MAKOTO K., NAGAMASU H., SAKAI S., HARRISON R., HAMID A. & TAMIJI I. 1998: Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. — *Am. J. Bot.* **85**: 1477–1501.
- NETO H.F.P. 2013: Floral biology and breeding system of *Bauhinia forficata* (Leguminosae: Caesalpinioideae), a moth-pollinated tree in southeastern Brazil. — *Braz. J. Bot.* **36**: 55–64.
- VAN NIEUKERKEN E.J., KAILA L., KITCHING I.J., KRISTENSEN N.P., LEES D.C., MINET J., MITTER C., MUTANEN M., REGIER J.C., SIMONSEN T.J., ET AL. 2011: Order Lepidoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. — *Zootaxa* **3148**: 212.
- NILSSON L.A., JOHNSON L., RALISON L. & RANDRIANJOHANY E. 1987: Angraecoid orchids and hawkmoths in central Madagascar: Specialized pollination systems and generalist foragers. — *Biotropica* **19**: 310–318.
- NILSSON L.A., JONSSON L., RASON L. & RANDRIANJOHANY E. 1985: Monophily and pollination mechanisms in *Angraecum arachnites* Schltr. (Orchidaceae) in a guild of long-tongued hawk-moths (Sphingidae) in Madagascar. — *Biol. J. Linn. Soc.* **26**: 1–19.
- NILSSON L.A., RABAKONANDRIANINA E., RAZANANAIVO R. & RANDRIAMANINDRY J.-J. 1992: Long pollinia on eyes: Hawk-moth pollination of *Cynorkis uniflora* Lindley (Orchidaceae) in Madagascar. — *Bot. J. Linn. Soc.* **109**: 145–160.
- OLIVEIRA P.E., GIBBS P.E. & BARBOSA A.A. 2004: Moth pollination of woody species in the Cerrados of Central Brazil: A case of so much owed to so few? — *Plant Syst. Evol.* **245**: 41–54.

- OLIVEIRA W., SILVA J.L.S., PORTO R.G., CRUZ-NETO O., TABARELLI M., VIANA B.F., PERES C.A. & LOPES A.V. 2019: Plant and pollination blindness: Risky business for human food security. — *BioScience* **70**: 109–110.
- OLLERTON J. & CRANMER L. 2002: Latitudinal trends in plant-pollinator interactions: Are tropical plants more specialised? — *Oikos* **98**: 340–350.
- OLLERTON J., WINFREE R. & TARRANT S. 2011: How many flowering plants are pollinated by animals? — *Oikos* **120**: 321–326.
- PELLMYR O. 2003: Yuccas, yucca moths, and coevolution: A review. — *Ann. Mo. Bot. Gard.* **90**: 35–55.
- PELLMYR O. & LEEBENS-MACK J. 1999: Forty million years of mutualism: Evidence for Eocene origin of the yucca-yucca moth association. — *Proc. Natl. Acad. Sci.* **96**: 9178–9183.
- PÉREZ-NASSER N., EGUIARTE L.E. & PIÑERO D. 1993: Mating system and genetic structure of the distylous tropical tree *Psychotria faxlucens* (Rubiaceae). — *Am. J. Bot.* **80**: 45–52.
- PORTO R.G., CRUZ-NETO O., TABARELLI M., VIANA B.F., PERES C.A. & LOPES A.V. 2021: Pollinator-dependent crops in Brazil yield nearly half of nutrients for humans and livestock feed. — *Glob. Food Secur.* **31**: 100587.
- POTASCHEFF C. DE M., DE BRITO V.L.G., GALETTO L., SEBBENN A.M. & OLIVEIRA P.E. 2020: Nectar features, diurnal and nocturnal pollinators, and male fitness in *Qualea grandiflora* (Vochysiaceae). — *Plant Syst. Evol.* **306**: 3.
- POWELL J.A. 1992: Interrelationships of yuccas and yucca moths. — *Trends Ecol. Evol.* **7**: 10–15.
- POWELL J.A. 2009: Chapter 151 - Lepidoptera: Moths, butterflies. In Resh V.H. & Cardé R.T. (eds): *Encyclopedia of insects* (second edition). Academic Press, San Diego, pp. 559–587.
- POWERS J.M., SECO R., FAIOLA C.L., SAKAI A.K., WELLER S.G., CAMPBELL D.R. & GUENTHER A. 2020: Floral scent composition and fine-scale timing in two moth-pollinated Hawaiian *Schiedea* (Caryophyllaceae). — *Front. Plant Sci.* **11**: 1116.
- PRIMO L.M., DUARTE J.A. & MACHADO I.C. 2013: Hawkmoth fauna (Sphingidae, Lepidoptera) in a semi-deciduous rainforest remnant: Composition, temporal fluctuations, and new records for Northeastern Brazil. — *An. Acad. Bras. Ciênc.* **85**: 1177–1188.
- QUIRINO Z. & MACHADO I. 2014: Pollination syndromes in a Caatinga plant community in Northeastern Brazil: Seasonal availability of floral resources in different plant growth habits. — *Braz. J. Biol.* **74**: 62–71.
- RAGUSO R.A. & WILLIS M.A. 2002: Synergy between visual and olfactory cues in nectar feeding by naïve hawkmoths, *Manduca sexta*. — *Anim. Behav.* **64**: 685–695.

- RAJU A.J.S. 2019: Pollination ecology of oviparous semi-evergreen mangrove tree species, *Xylocarpus granatum* Koen and *X. mekongensis* Pierre. (Meliaceae) at Coringa mangrove forest, Andhra Pradesh, India. — *Ann. Bot.* **10**: 67–76.
- RAMÍREZ N. 2004: Pollination specialization and time of pollination on a tropical Venezuelan plain: Variations in time and space. — *Bot. J. Linn. Soc.* **145**: 1–16.
- REGAL P.J. 1982: Pollination by wind and animals: Ecology of geographic patterns. — *Annu. Rev. Ecol. Syst.* **13**: 497–524.
- ROBERTSON S.M., DOWLING A.P.G., WIEDENMANN R.N., JOSHI N.K. & WESTERMAN E.L. 2021: Nocturnal pollinators significantly contribute to apple production. — *J. Econ. Entomol.* **114**: 2155–2161.
- ROCHA E.A., DOMINGOS-MELO A., ZAPPI D.C. & MACHADO I.C. 2019: Reproductive biology of columnar cacti: Are bats the only protagonists in the pollination of *Pilosocereus*, a typical chiropterophilous genus? — *Folia Geobot.* **54**: 239–256.
- ROCHA M., VALERA A. & EGUIARTE L.E. 2005: Reproductive ecology of five sympatric *Agave Littaea* (Agavaceae) species in central Mexico. — *Am. J. Bot.* **92**: 1330–1341.
- SAZATORNIL F.D., MORÉ M., BENITEZ-VIEYRA S., COCUCCI A.A., KITCHING I.J., SCHLUMPBERGER B.O., OLIVEIRA P.E., SAZIMA M. & AMORIM F.W. 2016: Beyond neutral and forbidden links: Morphological matches and the assembly of mutualistic hawkmoth–plant networks. — *J. Anim. Ecol.* **85**: 1586–1594.
- SCHULZE C.H., LINSENMAIR K.E. & FIEDLER K. 2001: Understorey versus canopy: Patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. — *Plant Ecol.* **153**: 133–152.
- SINGER R.B. 2002: The pollination biology of *Sauroglossum elatum* Lindl. (Orchidaceae: Spiranthinae): Moth-pollination and protandry in neotropical Spiranthinae. — *Bot. J. Linn. Soc.* **138**: 9–16.
- SONDHI Y., ELLIS E.A., BYBEE S.M., THEOBALD J.C. & KAWAHARA A.Y. 2021: Light environment drives evolution of color vision genes in butterflies and moths. — *Commun. Biol.* **4**: 177.
- SOUZA I.M., HUGHES F.M., FUNCH L.S. & QUEIROZ L.P. DE. 2021: Nocturnal and diurnal pollination in *Copaifera coriacea*, a dominant species in sand dunes of the Middle São Francisco River Basin, Northeastern Brazil. — *Plant Ecol. Evol.* **154**: 207–216.
- STEEN R. 2012: Pollination of *Platanthera chlorantha* (Orchidaceae): New video registration of a hawkmoth (Sphingidae). — *Nord. J. Bot.* **30**: 623–626.
- STÖCKL A.L. & KELBER A. 2019: Fuelling on the wing: Sensory ecology of hawkmoth foraging. — *J. Comp. Physiol. A* **205**: 399–413.
- SZYSZKA P., GERKIN R.C., GALIZIA C.G. & SMITH B.H. 2014: High-speed odor transduction and pulse tracking by insect olfactory receptor neurons. — *Proc. Natl. Acad. Sci.* **111**: 16925–16930.

- TAYLOR P.J., VISE C., KRISHNAMOORTHY M.A., KINGSTON T. & VENTER S. 2020: Citizen science confirms the rarity of fruit bat pollination of baobab (*Adansonia digitata*) flowers in Southern Africa. — *Diversity* **12**: 106.
- WANG X., WEN M., QIAN X., PEI N. & ZHANG D. 2020: Plants are visited by more pollinator species than pollination syndromes predicted in an oceanic island community. — *Sci. Rep.* **10**: 13918.
- WARDHAUGH C.W. 2015: How many species of arthropods visit flowers? — *Arthropod-Plant Interact.* **9**: 547–565.
- WELLER S.G., SAKAI A.K., CAMPBELL D.R., POWERS J.M., PEÑA S.R., KEIR M.J., LOOMIS A.K., HEINTZMAN S.M. & WEISENBERGER L. 2017: An enigmatic Hawaiian moth is a missing link in the adaptive radiation of *Schiedea*. — *New Phytol.* **213**: 1533–1542.
- WHITTALL J.B. & HODGES S.A. 2007: Pollinator shifts drive increasingly long nectar spurs in columbine flowers. — *Nature* **447**: 706–709.
- WILLMER P. 2011: *Pollination and floral ecology*. Princeton University Press, Princeton, N.J., 778 pp.
- WOLFF D., BRAUN M. & LIEDE S. 2003: Nocturnal versus diurnal pollination success in *Isertia laevis* (Rubiaceae): A sphingophilous plant visited by hummingbirds. — *Plant Biol.* **5**: 71–78.
- XIONG Y., JIA L., LIU C. & HUANG S. 2020: Effective pollinia transfer by settling moths' legs in an orchid *Habenaria aitchisonii*. — *J. Syst. Evol.* **58**: 174–181.
- XU Y., LUO Z., GAO S. & ZHANG D. 2018: Pollination niche availability facilitates colonization of *Guettarda speciosa* with heteromorphic self-incompatibility on oceanic islands. — *Sci. Rep.* **8**: 13765.
- YANG M., WAN T., DAI C., ZOU X., LIU F. & GONG Y. 2021: Modern honey bees disrupt the pollination of an ancient gymnosperm, *Gnetum luofuense*. — *Ecology* **00**: e03497.
- ZASPEL J.M., SCOTT C.H., HILL S.R., IGNELL R., KONONENKO V.S. & WELLER S.J. 2014: Geographic distribution, phylogeny, and genetic diversity of the fruit- and blood-feeding moth *Calyptra thalictri* Borkhausen (Insecta: Lepidoptera: Erebidae). — *J. Parasitol.* **100**: 583–591.

* secondary citation