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## Short Note

# Regional Differences in Mammalian Pollinators of *Mucuna macrocarpa* (Leguminosae): a Review

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Many angiosperms are pollinated by animals[1]. Among them, certain species are pollinated exclusively by mammals, although mammal-pollinated plants are fewer in number than insect-pollinated plants[2]. Mammal-pollinated plants are known from many taxa which reviewed by Fleming and Kress[3]. In addition, specific groups of mammals are known pollinators. The most well-known of these are bats, but various non-flying mammals pollinate plants[4].

This study focuses on *Mucuna* (Leguminosae). Genus *Mucuna* includes more than 100 species and this genus is distributed throughout tropics and subtropics[5]. *Mucuna* has inflorescences with relatively large flowers and this genus has been considered to be pollinated by bats or birds specifically[6].

Among pollinators of *Mucuna* species, this study reviews the behavior of *Mucuna macrocarpa*'s mammalian pollinators and its flower structure. In addition, we discuss the challenges of pollination studies in this genus. *Mucuna macrocarpa* is an evergreen woody vine. It produces 30–50 cm long inflorescences bearing 10–30 flowers with purple and pale green petals (Fig. 1). Matured flowers emit a fermentation-like odor. *Mucuna macrocarpa* is distributed from Southeast Asia to Japan[7]. In Thailand, it occurs in evergreen and mixed forests in the central to northern regions[8]. In the subtropics or temperate regions, it occurs in evergreen forests. The flowering season changes annually and locally, and is thought to take place over one or two months between January and May.

**Methods of Observation**

Previous observations have been either direct, in which observers stay in front of the target flowers, or via video cameras[9,10]. However, these methods have limitations, given the wariness of mammal visitors and influence of observers on their flower-visiting behavior and staying time. In addition, night-vision scopes are needed,



**FIGURE 1.** Inflorescences of *Mucuna macrocarpa*.

and observation of detailed flower-visiting behavior is difficult. Video cameras are expensive and battery life is short, placing a limitation on observation time. In the 1990s, automatic camera traps were developed for observation of mammalian flower visitors[11]. However, detailed observation of flower-visiting behavior is required, because not all flower visitors contribute to pollination, and some visitors rob nectar or drop flowers[12-14], and this method does not allow for description of flower-visiting behavior from photographs.

We used automatic video camera traps to resolve these problems[15]. There are various types of trigger[16]. Among them, cameras with infrared sensors which detect differences between air temperature and animal (surface) temperature are often used for field surveys of mammals. In this method, 1) mammals do not change their behaviors, 2) researchers can observe

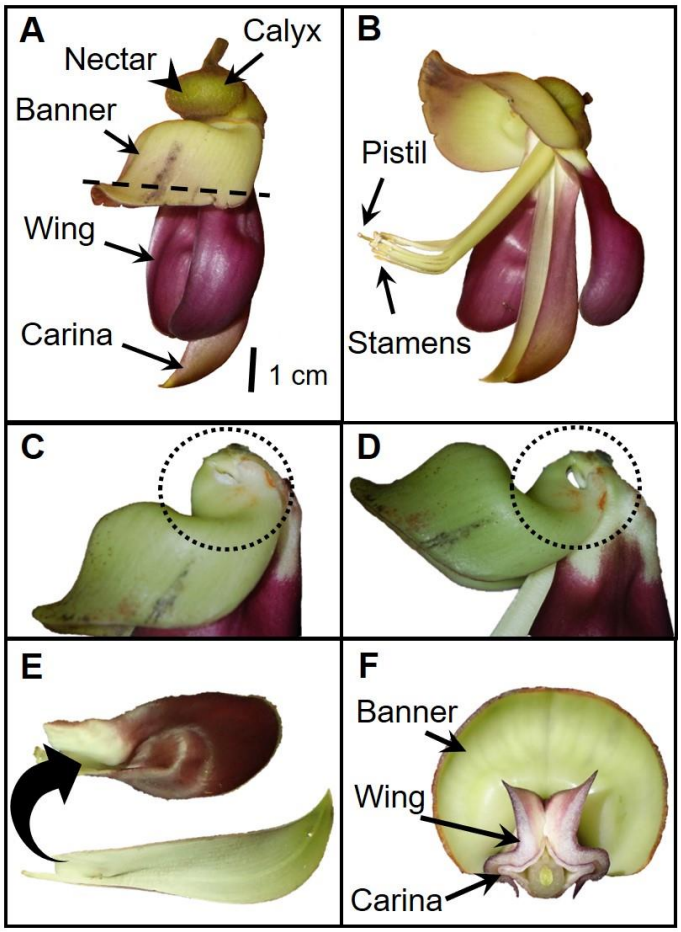



**FIGURE 2.** Flower of *Mucuna macrocarpa* and floral structures. Banner petal is pale green, wing petals are purple, and carina petals are pale purple. (A): Before flower opening, (B): After flower opening, (C): Hook-like structure (before flower opening), (D): Hook-like structure (after flower opening), (E): Connected part of wing and carina petals, (F): Section of the broken line in Fig. 2A. Large amount of sweet nectar is located inside the calyx (see Fig. 2A). When the flower opens and the banner faces upward, nectar flows down from the hook-like structure (see Fig. 2D) to the tip of the carina. Dotted circle in Figs. 2C and D shows the location of the hook-like structure.

throughout the day and night, and 3) flower-visiting behaviors are recorded in detail. This method has been successfully used to observe flower-visiting mammals[17-19].

**Explosive Opening**

The flower shape of *M. macrocarpa* is papilionaceous. Papilionaceous flowers have five petals — a banner, a pair of wings, and a pair of carina petals (Fig. 2A). Nectar, a reward for visitors, is stored inside the calyx. The stamens and pistil are enclosed by a pair of carina petals, preventing automatic pollination. However, specific mammals are able to open the flower,

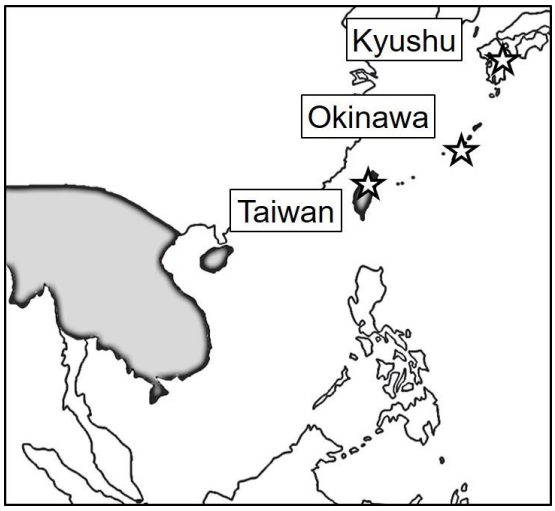



**FIGURE 3.** Distribution map of *Mucuna macrocarpa* and study regions. Shaded areas show distribution. Stars indicate study sites.

exposing stamens and pistil (Fig. 2B) so that pollination can occur. Once the flower of *M. macrocarpa* is opened in this manner the stamens and pistil are not enclosed again. Additionally, the opening of the flower is accompanied by explosive release of pollen, referred to as "explosive opening". This mechanism is also known from other, bee-pollinated genera[20]. The flowers of these plants cannot open on their own, and at least cross-pollination by an animal, or explosive opener, is obligatory.

In *M. macrocarpa*, flower opening takes place when the wing petal is pressed downward, and the banner petal simultaneously pressed upward[21]. Thus, explosive openers must be able to accomplish this movement. Successful pollinators must also be able to release the pair of hook-like structures at the base of the banner petal, which press the wing petals from both sides, preventing the flower from opening automatically[21] (Fig. 2C). When these hook-like structures are released (Fig. 2D), nectar flows away from the calyx, allowing the explosive opener to feed[21]. In addition, because of the wing petal's attachment to the carina (Fig. 2E, F) depressing the wing petal has the simultaneous effect of pushing the carina down. Thus, flower opening requires the strength of a mammal pollinator, as even large bees, such as carpenter bees *Xylocopa appendiculata circumvolans*, cannot open *M. macrocarpa* flowers[22].

Explosive openers were considered pollinators, but their role had not been experimentally verified[9,23,24]. While our observations on fruit set following artificial pollination in this genus suggest self-compatibility, fruits were not observed when flowers did not open[25]. Thus, we assume that explosive opening is necessary for pollination in this genus, even though only one species was tested.

**Shift of Explosive Openers**

Explosive openers were identified *M. macrocarpa*'s range, in Kyushu, Okinawa, and Taiwan[15,18,21] (Fig. 3). Explosive openers are Japanese macaques *Macaca*

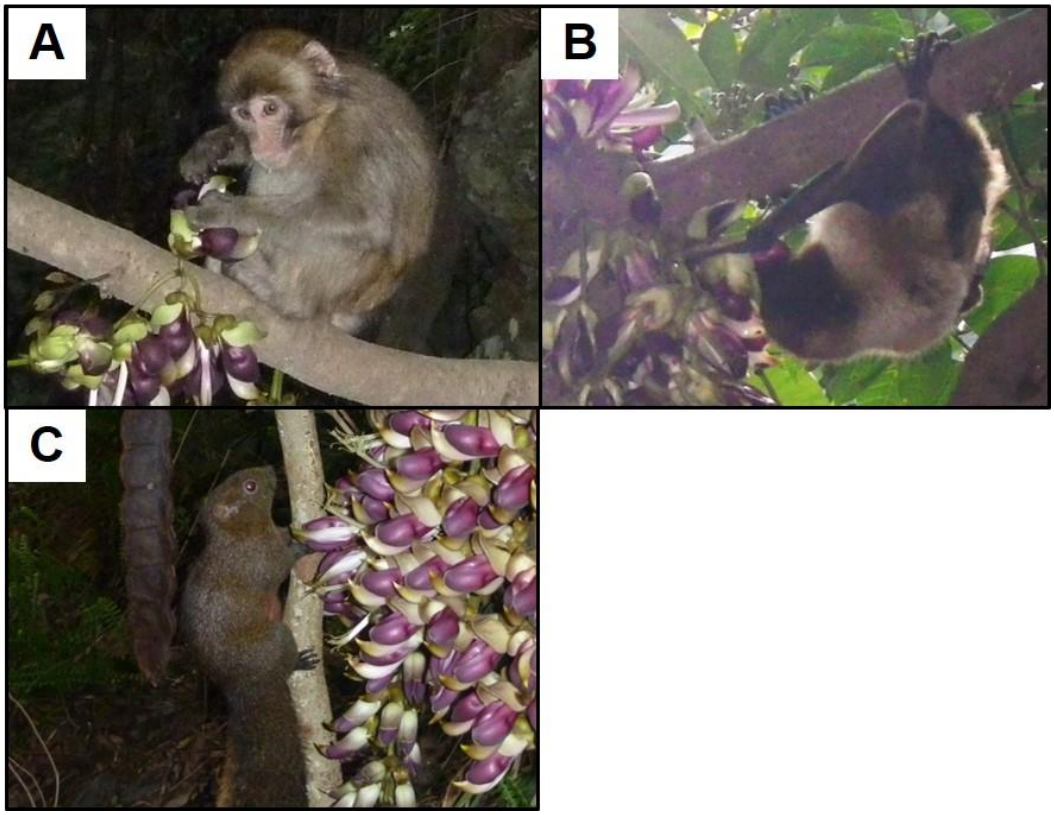



**FIGURE 4.** Explosive openers (effective pollinators) in three study regions. (A): Japanese macaque (*Macaca fuscata*), (B): Ryukyu flying fox (*Pteropus dasymallus*), (C): Red-bellied squirrel (*Callosciurus erythraeus*).

*fuscata* (Fig. 4A) and Japanese martens *Martes melampus* in Kyushu; Ryukyu flying foxes *Pteropus dasymallus* (Fig. 4B) in Okinawa; and red-bellied squirrels *Callosciurus erythraeus* (Fig. 4C), Formosan striped squirrels *Tamiops maritimus* and masked palm civets *Paguma larvata* in Taiwan. Although the openers described above are available, Japanese macaques are the main openers in Kyushu and red-bellied squirrels are the main openers in Taiwan, by virtue of the large number of flowers they open when compared to other openers. Explosive openers differ among regions, but all known openers are mammals. When these species open a flower large amounts of pollen are removed. Supported by the results of experiments, we conclude that explosive openers are effective pollinators.

In *Mucuna*, explosive openers comprise either one or 2–3 species from the same group, as reported in Table 1. Almost all of them are bats or birds (Table 1). On the other hand, mammals from different orders act as pollinators in different regions of *M. macrocarpa*'s range. There were other examples of plants pollinated by different mammals at different sites. Traveler's trees *Ravenala madagascariensis* are pollinated

**TABLE 1.** Explosive openers or flower visitors of *Mucuna* spp.

| Plant name | Study region/Country | Explosive opener (Flower visitor**) | | Pollinator observation method | Literature |
|---|---|---|---|---|---|
| | | Species name | Common name | | |
| *M. macrocarpa* | Kyushu (Japan) | *Macaca fuscata**** | Japanese macaque | Video camera trap / Direct observation | 15 |
| | | *Martes melampus* | Japanese marten | | |
| | Okinawa (Japan) | *Pteropus dasymallus* | Ryukyu flying fox | Direct observation | 21 |
| | Taiwan | *Callosciurus erythraeus**** | Red-bellied squirrel | Video camera trap | 18 |
| | | *Tamiops maritimus* | Formosan striped squirrel | | |
| | | *Paguma larvata* | Masked palm civet | | |
| *M. sempervirens* | Kunming (China) | *Callosciurus erythraeus* | Red-bellied squirrel | Direct observation | 49 |
| | | *Dremomys pernyi* | Perny's long-nosed squirrel | | |
| *M. birdwoodiana** | Hongkong | (*Rousettus leschenaulti*) | (Leschenault's rousette bat) | Direct observation | 50,51 |
| | | (*Paguma larvata*) | (Masked palm civet) | | |
| *M. macropoda* | Papua New Guinea | *Synycteris australis* | Queensland blossom bat | Direct observation | 24 |
| *M. gigantea** | Indonesia | (Bat ?) | | Estimate from the claw mark on flower | 23 |
| *M. reticulata** | Indonesia | (Bat ?) | | Estimate from the claw mark on flower | 23 |
| *M.macrophylla** | Indonesia | (Bat ?) | | Estimate from the claw mark on flower | 23 |
| *M. monosperma** | Indonesia | (Bat ?) | | Estimate from the claw mark on flower | 33 |
| *M. flagellipes* | Kamerun | *Megaloglossus woermanni* | Woermann's fruit bat | Direct observation | 52 |
| *M. urens* | Brazil | *Glossophaga soricina* | Pallas's long-tongued bat | Direct observation | 53 |
| *M. holtonii* | Costa Rica | *Glossophaga commissarisi**** | Commissaris's long-tongued bat | Direct observation / Video camera | 10,54 |
| | | *Hylonycteris underwoodi* | Underwood's long-tongued bat | | |
| | | *Lichonycteris obscura* | Dark long-tongued bat | | |
| *M. rostrata* | Colombia | *Cacicus cela* | Yellow-rumped cacique | Direct observation | 55 |
| *M. japira* | São Paulo (Brazil) | *Cacicus haemorrhous* | Red-rumped cacique | Direct observation | 9 |
| *M. sloanei** | No information | *Glossophaga soricina* | Pallas's long-tongued bat | Direct observation | 56 |
| *M. mutisiana** | No information | (Bat ?) | | No information | 57**** |
| *M. reptans** | Australia | (Rat or Bird ?) | | Estimate from the floral characteristics | 58 |
| *M. pruriens** | No information | (Bat ?) | | No information | 57**** |

*Quantitative observations were not conducted to identify the pollinator. **Parentheses indicate that explosive opening behavior was not observed for this species. *** This is a main pollinator in the region, even when multiple pollinators occur in the region. ****Article suggested the pollinator, but we could not find any evidence of field observation.

by ruffed lemurs *Varecia variegata* in their naturally-occurring range, and by gray-headed flying foxes *Pteropus poliocephalus* in Australia where traveler's trees have been introduced[26,27]. However, to our knowledge, pollinator shifts from one mammal to another within a species' natural range are not known. Pollinator shifts from bats to non-flying mammals or vice versa are also rare.

**Comparisons of Explosive Opening Behaviors**

In *M. macrocarpa*, it is necessary to simultaneously raise banner and push down wing petals for explosive opening to occur. Does explosive opening behavior differ among openers? Our observations clarified that explosive opening behavior is common among openers, who hold wing petals with their forelimbs and raise the banners with their snouts by inserting them into the gap between wing and banner[15,18,21]; a single exception is the Japanese macaque, which holds the wing petal in one hand and raises the banner petal with the other hand[15].

This difference in opening behavior may affect pollination success. The Ryukyu flying fox, the only opener in Okinawa, and the red-bellied squirrel, the main opener in Taiwan, always inserted their snouts into the gap between wing and banner at a similar angle[18,21]. This method results in both the adherence of pollen grains to, and contact of the plant's stigma with the pollinator, on the same part of the pollinator's body, with obvious consequences for pollination efficacy i.e. the pollinator's method maximizes the likelihood of pollen deposition on the stigma. In contrast, when Japanese macaques open flowers, pollen grains may adhere to their hands or faces, depending on the precise opening stance employed i.e. the distance between face and flower when opening occurs. The stigma always attached to the face and does not touch on hand. Thus, the site of attachment of pollen and stigma is not always same in the case of macaques.

Explosive opening behaviors have been described for other *Mucuna* species. In *M. japira*, which is pollinated by red-rumped caciques *Cacicus haemorrhous*, Agostini et al.[9] noted that birds used their heads to "press the base of the wing and carina petals at the same time". In bat-pollinated *M. macropoda*, Hopkins and Hopkins[24] described pollen release when the pressure (exerted by the bat with its head) on the base of the petals released the androecium and gynoecium from within the carina. Other leguminous explosive openers are known among bee-pollinated species in which the weight of bees on the plant's wings appears sufficient to trigger explosive opening without any specialized behavior[20,28]. Compared to these species, the mechanism of explosive opening in *M. macrocarpa* is more complex, its reliance on the use of the mammalian forelimb suggesting co-evolution with mammal pollinators.

**Flower Visitors Other than Explosive Openers**

Flower visitors other than explosive openers were also recorded in the three regions sampled[15,18,21]. While Japanese macaques (in Kyushu) could open and pollinate flowers as described, Formosan rock macaques *Macaca cyclopis* could not open flowers[18]. In a survey spanning at Nanrenshan Ecological Reserve Area, southern Taiwan[16] we used camera traps (Ltl-Acorn 5210; Shenzhen Ltl Acorn Electronics Co., Ltd., China) to ascertain the fate of *M. macrocarpa* inflorescences, discovering that 92.9% (n = 14) of inflorescences were picked and eaten by Formosan rock macaques prior to maturation, while Formosan rock macaques

visited mature flowers in northern Taiwan. Because of regional differences in vegetation in Taiwan[29] food sources exploited by macaques vary with area, and their reliance on *Mucuna* relative to other foods may also vary as a reflection of these differences. Resource requirements may also differ on the basis of troop size, which varies among troops[30] and may influence which food sources are most regularly visited.

Secondly, visitors to opened flowers were observed in all regions. One of them, the honeybee, *Apis cerana* visits to collect pollen, sometimes coming into contact with the stigma[15,18] and potentially acting as a secondary pollinator, although efficiency is unknown. In addition, honeybees frequently visited flowers immediately after explosive opening. Diurnal Japanese macaques and red-bellied squirrels frequently visited flowers in the early morning[25], thus attracting the visits of honeybees at this time.

Interestingly, birds seldom visited *M. macrocarpa* flowers. Japanese white-eyes *Zosterops japonicus* and brown-eared bulbuls *Hypsipetes amaurotis* visited flowers less frequently than explosive openers both in Kyushu and Okinawa, and did not open flowers at all[15,18,21]. In Taiwan, no birds visited flowers[18]. These results suggest that *M. macrocarpa* relies solely on mammal pollinators. While the Okinawa woodpecker *Sapheopipo noguchii* visited relatively frequently and fed on nectar[31] this may reflect a feeding habit related to evolution on a small island[32], and insignificant in terms of pollination.

**Future Challenges**

It will be instructive to identify the pollinators of *Mucuna* spp. A large number of vertebrate-pollinated plant species occur in the tropics[3], and *Mucuna* is a good target group for studies on the diversity and evolution of mammal-dependent pollination systems. Pollinators of several *Mucuna* species have been clarified (Table 1). However, some of these pollinators were identified only by the observations confirmed visits by these species but not necessarily visits resulting in pollination (Table 1). This genus has been considered to be pollinated by bats or birds[6], but this suggestion is not based on enough surveys. For example, although van der Pijl[23,33] conducted pioneering studies, he concluded that bats were pollinators based on the claw marks on flowers. While claw marks of fruit bats may differ from those of other mammals, squirrels and macaques also mark flowers (Fig. 5) and it is sometimes difficult to distinguish between the marks of bats and those of other mammals. In addition, information on flower-visiting frequency and flower-visiting behavior is lacking, and van der Pijl[23] did not consider other possible visitors. Furthermore, the genus *Mucuna* requires specific flower-visiting behaviors (this requirement does not apply only to *M. macrocarpa*). Thus, detailed observations are needed especially in those species. Otherwise, *Mucuna* species may have other additional pollinators, and pollinators may differ in different parts of *Mucuna*'s range.

The genus *Mucuna* originated in tropical Asia[34]. Therefore, in order to understand the pollination system of *Mucuna*, Southeast Asia is the most important region. The fauna in the tropical zone is more diversified than that in the temperate zone, and squirrels and carnivores are the most diversified group in Southeast Asia[35]. The importance of flying foxes[36-38] and squirrels[38,39] as pollinators in Southeast Asia has been noted. In fact, diurnal tree squirrels act as pollinators of number of plants besides *Mucuna*[40-42]. Most studies of non-flying mammal-pollinated

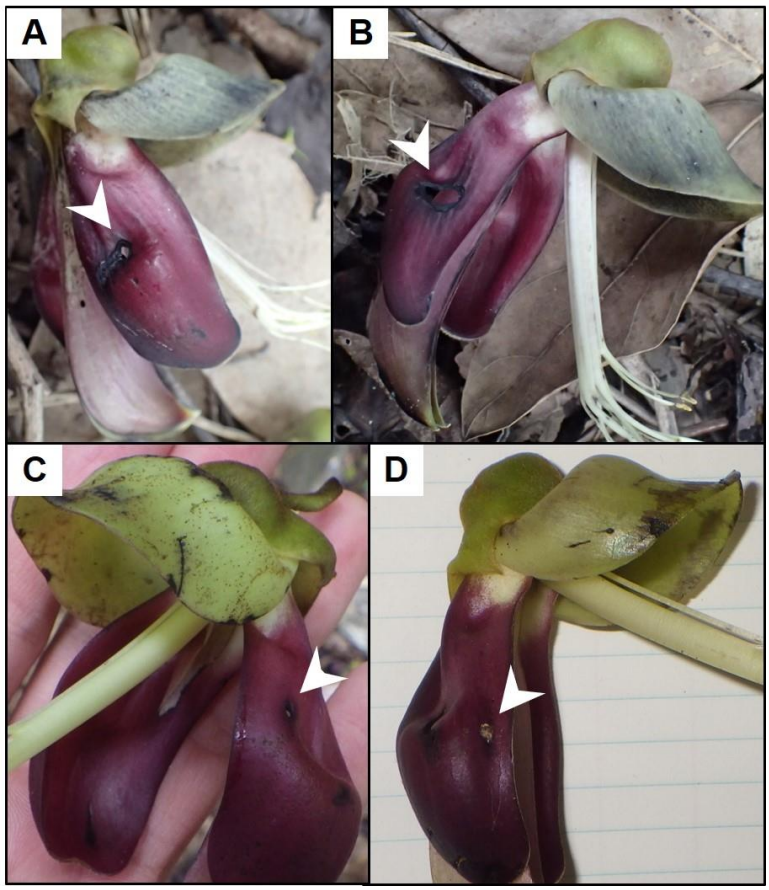



**FIGURE 5.** Claw marks of explosive openers. (A) and (B): Ryukyu flying-fox, (C): Japanese macaque, (D): Red-bellied squirrel. Arrows indicate the claw marks of each opener.

plants have been conducted in Australia, and South Africa, and more research into mammal-dependent pollination systems in Southeast Asia are needed.

One of the important issues for discussion of the evolution of mammal-pollinated plants is that of floral traits. Many plants that are considered bat-pollinated species have floral traits reflecting this pollination syndrome, causing researchers to overlook the possibility of other pollinators. Pollination syndrome is the concept that plants pollinated by same pollinator have common floral traits such as shape, nectar secretion dynamics, and odor (volatile components). Although several *Mucuna* species fit bat-pollination syndromes[10,24,43], floral traits are seldom quantitatively assessed for their fit with pollinators. This represents a significant gap in our knowledge, and there are instances in which pollinators predicted for a species, based on floral characteristics and pollination syndromes, differ from observed pollinators. Many such exceptions have recently been described[44-46] and it appears that prediction

of pollinators based on the pollination syndrome is unrealistic. However, it is known that a specific floral trait attracts a specific pollinator. In mammal-pollinated plants, volatile components are one of the most important attractive traits[47]. Further research on *Mucuna* is needed to clarify floral traits such as shape, nectar production dynamics, and volatile components, and to examine the relationship of these traits with pollinators.

**Conclusion**

Pollinators of *M. macrocarpa* differ among regions but all of them initiate explosive opening, with the exception of the Japanese macaque. Such commonness of behavior indicates that the ability of *M. macrocarpa* to open explosively makes it available to a number of potential pollinators. However, in all regions, non-mammal flower visitors are infrequently observed, suggesting a reliance on mammals at the expense of other groups, and the evolution of flower strength useful for prohibiting small animals from robbing nectar.

The explosive opening behavior of Japanese macaques is distinctive, and this pollinator occurs at the northern limit, or edge, of *M. macrocarpa*'s range[15], where pollinator shift is more likely to occur[48]. In addition, Japanese macaques dropped flowers frequently[15] and other *Macaca* monkeys cannot open and pollinate flowers. Thus, Japanese macaques might have become pollinators as a secondary consequence of learning to prey on *Mucuna* flowers.

In Southeast Asia, non-flying mammals are known to pollinate plants reported as bat-pollinated species[18,44]. Thus, we need to clarify the pollinators of other *Mucuna* species in Asia. In addition, clarifying pollination systems, including floral traits, is needed to enhance understanding of the evolution of mammal pollination.

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