



Ecological Roles of Indian Palm Squirrels (*Funambulus* spp.) as Floral Visitors Across Five Indian States: First Comprehensive Account


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ABSTRACT: Flower visitation by non-flying mammals remains poorly documented in South Asia. The ecological roles of palm squirrels as floral visitors and potential pollinators in India have received limited systematic attention. This study aimed to document flower visitation by all four Indian palm squirrel species (*Funambulus* spp.), assess their roles as nectar robbers, flower predators, or occasional floral visitors across diverse plant species. Floral visitation was recorded opportunistically through direct observation, photographic and video documentation across gardens, agricultural landscapes, forest edges and protected areas in five Indian states, encompassing 40 independent observation events between December 2019 and March 2021. Observations were classified into three functional categories: nectar robbers, flower predators, and occasional visitors. A presence-absence bipartite interaction network was constructed to visualise interaction structure across squirrel species. All four palm squirrel species were recorded visiting flowers of 20 plant species, belonging to 11 families, of which 11 represent novel interaction records. Most visits involved nectar access with floral damage, indicating roles as nectar robbers or flower predators, particularly on small, fragile entomophilous flowers. Visits to large, robust flowers were less destructive and occasionally involved contact with reproductive structures, raising the possibility of opportunistic pollen transfer. The bipartite network indicated unequal interaction occurrence among squirrel species, with *Funambulus tristriatus* recording the maximum number of plant associations, whereas *Funambulus sublineatus* showed the minimum interactions. These findings highlight the underappreciated role of palm squirrels as frequent floral visitors in Indian plant communities.

Keywords: Palm squirrels, *Funambulus*, Nectar robbing, Flower visitation, Mammal-plant interactions, Floral damage, Pollination ecology.

1. INTRODUCTION

Interactions between flowering plants and their visitors constitute one of the most ecologically significant mutualisms in terrestrial ecosystems, sustaining plant reproduction and supporting food webs across diverse

landscapes (Ollerton et al., 2011; Hale et al., 2020; Dicks et al., 2021). Among vertebrate pollinators, bats and birds have received the greatest research attention, while the contribution of non-flying mammals to floral visitation and pollination has remained comparatively neglected, particularly in tropical Asia (Carthew & Goldingay, 1997;

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Ganesh & Devy, 2006; Kobayashi et al., 2019; Kobayashi et al., 2021). Non-flying mammals such as rodents and small marsupials, visit flowers primarily for nectar, and their interactions with plants range from mutualistic pollination to antagonistic behaviours, including nectar robbing and flower predation (Irwin et al., 2010; Kobayashi et al., 2017). Nectar robbing refers to the extraction of nectar without following the normal pollination pathway, typically by piercing floral tissues and avoiding contact with anthers and stigmas, whereas flower predation involves the consumption or destruction of floral structures, including reproductive organs, that can directly reduce plant reproductive success (Richman et al., 2021; Boaventura et al., 2022; Xiao et al., 2025). Consequently, mammalian flower visitors may function as pollinators, nectar robbers or flower predators depending on both floral architecture and their mode of resource exploitation (Kobayashi et al., 2017). Rodents, in particular, have been documented as frequent floral visitors in tropical systems across Asia, Africa and the Americas, where they often exploit nectar rewards opportunistically without consistently delivering pollination services (Deng et al., 2004; Deng et al., 2015). Squirrels (family Sciuridae) are among the more conspicuous rodent floral visitors, having been recorded as pollinators, nectar robbers and incidental flower visitors across a variety of plant species in tropical and subtropical regions (Kobayashi et al., 2015; Kobayashi et al., 2017; Kobayashi et al., 2018a; Kobayashi et al., 2018b). Notably, squirrel pollination has been confirmed for *Mucuna macrocarpa* in Taiwan, where body size and floral architecture are well matched for pollen transfer (Kobayashi et al., 2017), while in the Western Ghats of India, the Indian giant squirrel and the dusky-striped squirrel were recorded as flower predators on *Cullenia exarillata*, consuming floral parts without contributing to pollination (Ganesh & Devy, 2006). Together, these contrasting examples illustrate that the functional role of squirrels at flowers is not fixed, but is contingent on the morphological compatibility between the visiting animal and the flower being exploited. This contingency is best understood through the concept of therophily, the pollination syndrome associated with non-flying mammals, which predicts that flowers tolerant of mammalian visitors typically share a suite of traits: large, robust, bowl-shaped structures capable of withstanding physical disturbance, freely accessible nectar, drab colouration and musty or yeasty scents that appeal to olfactory-oriented foragers (Carthew & Goldingay, 1997;

Wester et al., 2023). Importantly, therophily does not guarantee pollination; where the visitor's body size or foraging posture precludes consistent contact with anthers and stigmas, even structurally accommodating flowers may yield only nectar robbery rather than pollen transfer (Lai et al., 2024)

Palm squirrels of the genus *Funambulus* are among the most widely distributed and ecologically familiar small mammals of the Indian subcontinent, occurring abundantly across natural forests, forest edges, agricultural landscapes, gardens and urban areas (Chakravarthy & Thyagaraj, 2012). Despite their conspicuousness and close association with flowering vegetation, systematic documentation of their interactions with flowers across India remains sparse. Early observations identified palm squirrels as visitors to coconut palm (*Cocos nucifera*) flowers and suggested a possible role in pollination (McCann, 1933). More recently, it was documented that the foraging activities of palm squirrels, *F. palmarum*, on coconut inflorescences in plantation ecosystems highlighted their potential contribution to pollination through therophily (Chakravarthy & Thyagaraj, 2012). Scattered records exist for individual species visiting specific plant species. However, a comprehensive account covering all four Indian *Funambulus* species across a range of plant families and geographic regions has not been attempted. This gap is significant given that palm squirrels, by virtue of their abundance and behavioural flexibility (Perodaskalaki et al., 2023; Abedin et al., 2025), may exert a non-trivial influence on the reproductive ecology of the plants they visit, whether as flower predator and nectar robbers that reduce floral resources available to legitimate pollinators, or as incidental pollen vectors on structurally suitable flowers (Irwin et al., 2010; Chakravarthy & Thyagaraj, 2012).

The present study was therefore undertaken to compile and document opportunistic records of flower visitation by all four Indian palm squirrel species across multiple states, characterise the nature of their interactions with flowering plants and assess their functional roles as nectar robbers, flower predators or occasional visitors. A bipartite interaction network was additionally constructed to examine patterns of interaction structure across squirrel species. By synthesising these observations, the study will contribute to a broader understanding of non-flying mammal floral interactions in South Asia and stimulate further experimental investigations into their ecological consequences.

2. MATERIALS AND METHODS

2.1. Study Area

The present study was carried out across five states of India, namely West Bengal, Odisha, Maharashtra, Tamil Nadu and Kerala, spanning a broad ecological range (Figure 1). These states collectively encompass a diverse array of biogeographic zones, including the Eastern Ghats, Western Ghats, Deccan Plateau and the eastern coastal plains, and support populations of all four Indian palm squirrel species. Observations were made across a variety of land-use types, including home gardens, urban parks, agricultural landscapes, forest edges and protected areas. The wide geographic scope of the study reflects the opportunistic nature of the documentation, which was carried out wherever palm squirrels were encountered visiting flowers during the study period. Direct observations by the first

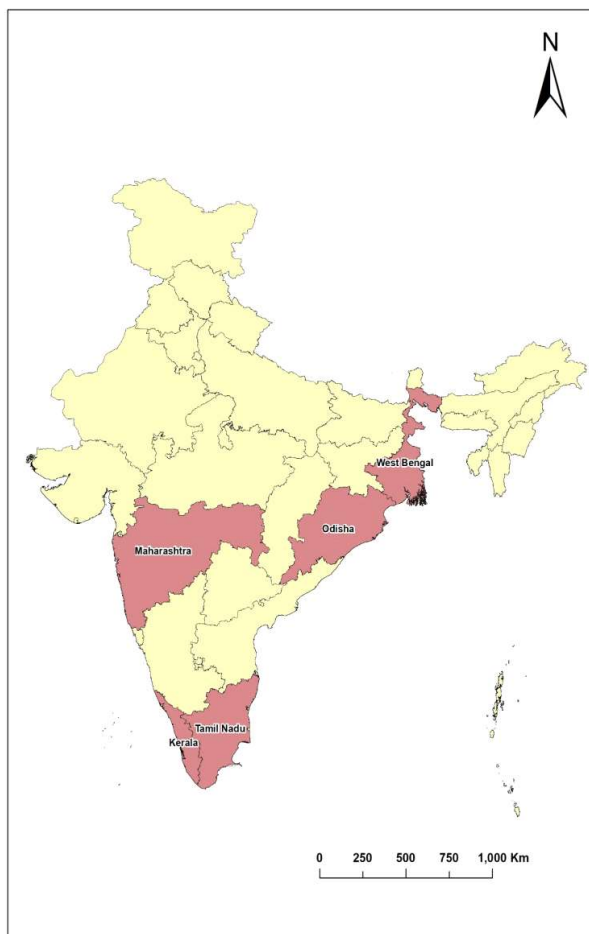


Figure 1. Study area map of India showing the five states, West Bengal, Odisha, Maharashtra, Tamil Nadu and Kerala, from which opportunistic records of flower visitation by palm squirrels (*Funambulus* spp.) were documented

author were carried out at the AJC Bose Indian Botanical Garden, Howrah, West Bengal, India (22°33'31"N, 88°17'28"E; ca. 10 m a.s.l.), where *Funambulus pennantii* was recorded visiting the flowers of *Asystasia gangetica* in an urban botanical garden setting.

2.2. Study Species

The four palm squirrel species native to India, namely *Funambulus palmarum* (Linnaeus, 1766), *Funambulus pennantii* Wroughton, 1905, *Funambulus tristriatus* (Waterhouse, 1837) and *Funambulus sublineatus* (Waterhouse, 1838), were the focal taxa of the present study. All four species are diurnal, arboreal to semi-arboreal rodents belonging to the family Sciuridae that collectively occupy a broad geographic range across India. However, individual species differ in their distributions and habitat associations (Wilson & Reeder, 2005). They are omnivorous, consuming fruits, seeds, insects, bark and plant exudates, and are commonly observed in close association with flowering vegetation across both natural and human-modified landscapes (Chakravarthy & Thyagaraj, 2012).

All four native Indian *Funambulus* species were easily identified from photographs and videos using a standardised matrix of diagnostic phenotypic traits and geographic distribution boundaries (Dissanayake et al. 2012; Nivetha et al. 2023). The Northern Palm Squirrel (*F. pennantii*) was identified by its characteristic five pale dorsal stripes (Yousefi et al., 2013). The remaining three-striped congeners were differentiated based on body size, stripe prominence, pelage characteristics, habitat preference, and geographic occurrence (Talmale et al., 2013). The Three-striped Palm Squirrel (*F. palmarum*) was recognised by its distinct three-striped pattern and its occurrence in southern and central India (Samson et al., 2017). The Jungle Palm Squirrel (*F. tristriatus*) was distinguished by its relatively larger body size, darker pelage, and association with woodland habitats of the Western Ghats (Talmale et al., 2013). The Nilgiri Striped Squirrel (*F. sublineatus*) was identified by its notably small size, faint dorsal striping, and restriction to high-altitude montane forests of the southern Western Ghats (Dissanayake et al., 2012; Rajamani, 2021). The squirrel species was identified by the co-author, Muhamed Jafer Palot (Zoological Survey of India), who is an expert on Indian small mammals.

2.3. Focal Observation

Floral visitation by palm squirrels was documented

opportunistically between December 2019 and March 2021. Observations were made whenever squirrels were encountered interacting with flowers during the course of routine field activities and dedicated wildlife surveys. A few records were contributed by citizen-science observers across India, who submitted photographic documentation of palm squirrel floral visitation via personal communication (see Acknowledgement section). Independent observation events from 5 states of India were recorded. Each interaction was recorded through direct observation, supplemented, wherever possible, by photographic and video documentation to facilitate subsequent verification of both squirrel identity and the nature of the interaction. No animals

were handled, or subjected to any form of experimental manipulation during the course of this study.

Plant species visited were identified to species level using standard floristic references and verified against herbarium records where necessary. In addition to original observations, published records of floral visitation by *Funambulus* species in India were reviewed and incorporated (Ganesh & Devy, 2006; Chakravarthy & Thyagaraj, 2012). Literature records were included only when squirrel and plant species could be reliably identified and floral visitation was clearly documented. These records were incorporated to complement original observations and provide a broader overview of palm squirrel-flower interactions in India. Because the present study compiled opportunistic natural-history observations from multiple observers, only conspicuous, day-active behaviour of palm squirrels in human-frequented areas was documented.

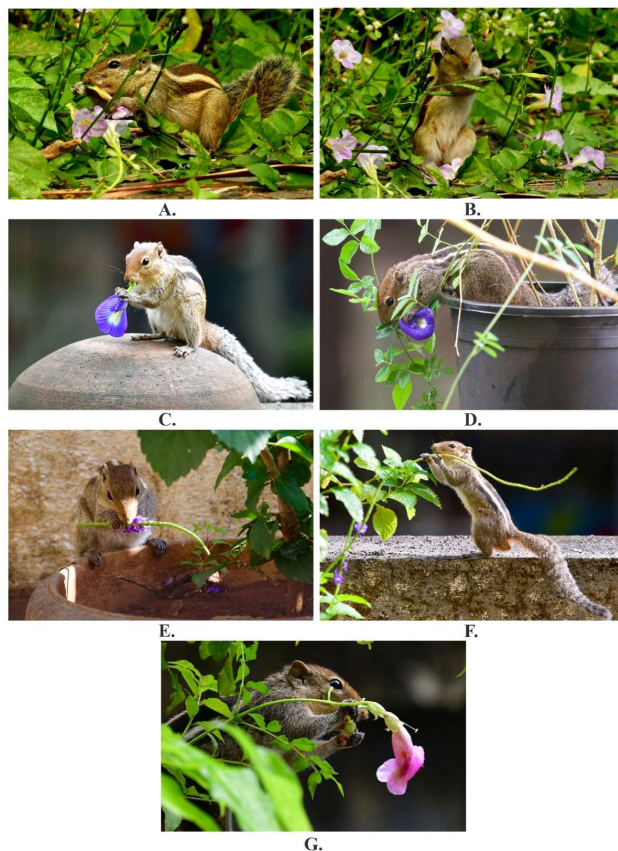


Figure 2. A. *Funambulus pennantii* was found feeding nectar from the corolla of *Asystasiagangetica*, B. *F. pennantii* dislodged several flowers of *A. gangetica*, C. *F. tristriatus* was found feeding on floral parts by plucking the entire flower of *Clitoriaternatea*, D. *F. tristriatus* was biting the corolla tube of *C. ternatea*, E and F. *F. tristriatus* was nectaring from *Stachytarpheta jamaicensis* by taking away the entire flower spike, G. *F. tristriatus* was nectaring on flowers of *Tecoma stans*

2.4. Floral Interactions

Each recorded interaction was assigned to one of three functional categories (Inouye, 1980; Irwin et al., 2010). Interactions were classified as nectar robbing when squirrels obtained nectar by piercing or biting floral tissues such as the corolla tube or calyx, causing structural damage and often facilitating subsequent visits by secondary robbers. Interactions were classified as flower predation when squirrels consumed floral parts, including petals, anthers, ovaries or entire flowers. Interactions were classified as occasional visitation when squirrels accessed floral rewards without exhibiting morphological or behavioural specialisation for pollination, making incidental, and generally non-destructive contact with anthers and stigmas. Pollen adhesion to body fur and nasal bristles was observed during some visits, suggesting the possibility of incidental pollen contact. However, quantitative pollen load analysis was beyond the scope of the present study. These visits were distinguished from nectar robbing by the absence of visible floral damage and from flower predation by the absence of flower or floral-part consumption.

2.5. Bipartite Network Analysis

To visualise the structure of interactions between squirrel species and plant species, a presence-absence bipartite interaction network was constructed based on the recorded visitation data (Robinson et al., 2015; Khorsand et al., 2025). Each squirrel-plant pair with at least one confirmed interaction was treated as a binary link. Binary network metrics, including connectance, nestedness (NODF), and

modularity, were calculated using the 'networklevel' function in the bipartite package to characterise the structural properties of the network. The network was constructed and visualised using the bipartite package v2.18 (Dormann et al., 2008) in R v4.1.2 (R Core Team, 2023) to summarise interaction patterns among the four *Funambulus* species. As the study was conducted in citizen-science mode, interaction frequencies were not recorded, and weighted metrics were therefore not calculated. Only squirrel-plant interactions recorded during the study period were included as binary links, representing the occurrence of interactions (Chacoff et al., 2012).

3. RESULTS AND DISCUSSION

3.1. Floral Visitation Records and Plant Diversity

All four palm squirrel species occurring in India, *Funambulus palmarum*, *F. pennantii*, *F. tristriatus* and *F. sublineatus* were observed visiting flowers. Across all four species, 40 observation events were recorded on 20 plant species belonging to 11 families (Table 1). *Funambulus tristriatus* contributed the highest number of observation events, followed by *F. pennantii*, *F. palmarum*, and *F. sublineatus*. Of the 20 plant species recorded, 8 were associated exclusively with occasional visitation, 5 exclusively with flower predation, and 1 exclusively with nectar robbing, while 6 species exhibited multiple interaction behaviours. During most visits, squirrels accessed nectar by biting or tearing floral tissues. This often resulted in damage to corollas or removal of entire flowers, particularly in small or delicate entomophilous species such as *Asystasia gangetica*, *Stachytarpheta jamaicensis* and *Lantana camara*. In several instances, flowers were plucked and discarded after nectar extraction.

In contrast, visits to large and robust flowers and inflorescences, including *Butea monosperma*, *Callistemon citrinus*, *Musa* spp. and *Cocos nucifera*, involved nectar feeding with comparatively little floral damage. In these cases, contact between the squirrel's head or snout and floral reproductive structures was occasionally observed while accessing nectar (Figure 3F & 3G for the pollen attached to the snout of the squirrel).

3.2. Bipartite Interaction Network

The bipartite interaction network (Figure 4) illustrated the visitation pattern of all four *Funambulus* species across the 20 recorded plant species (Figure 4). Binary network metrics revealed a connectance of 0.325. The network exhibited moderate nestedness (temperature = 34.16; NODF

= 26.53) and moderate modularity ($Q = 0.450$), with four distinct modules identified, each predominantly associated with a single squirrel species. Network-level specialisation, $H2'$ was 0.704. All metrics were computed from presence-absence data, and weighted metrics were not calculated as recording interaction frequencies were not a part of this study.

Funambulus tristriatus, a widely distributed species showed the maximum host visits, with floral interactions recorded across the highest number of plant species, while *F. sublineatus*, being a forest species had the least interaction, with only two observation events (Table 1) both recorded on

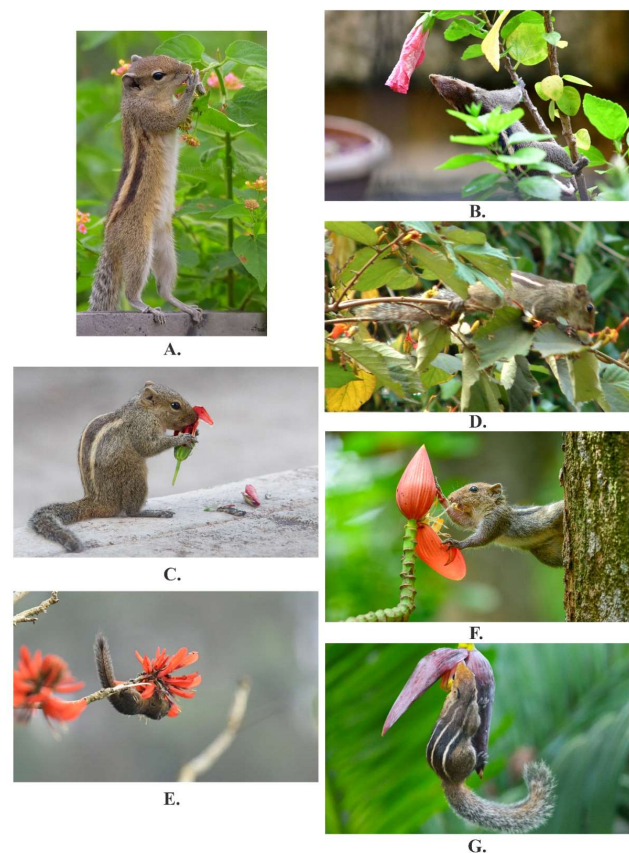


Figure 3. A. *F. palmarum* was taking nectar and damaging the entire inflorescence of *Lantana camara*, B. *F. tristriatus* was nectaring on the flowers of *Hibiscus* sp., C. *F. tristriatus* was plucking the flowers of *Hibiscus* sp., D. *F. tristriatus* was feeding nectar of *Helicteresisora*, without damaging the flower heads, E. *F. sublineatus* found feeding on the flowers of *Erythrina variegata*, F. *F. tristriatus* was feeding nectar from the inflorescence of *Musa ornata* and the entire flowers are taken away G. *F. tristriatus* was visiting inflorescence of *Musa paradisiaca*

Table 1. Flower visitation by Indian palm squirrels (*Funambulus* spp.) recorded across selected states in India

Plant species (Common name; Scientific name; Family)	Pollination syndrome	Observation locality	Date and documentation	Number of times observed	Behaviour category	Remark
* Chinese violet; <i>Asystasia gangetica</i> ; Acanthaceae	Entomophilous (Liow et al. 2001).	Howrah (Kolkata, West Bengal)	13-12-2019	8	Flower predator & Nectar robber	<i>F. pennantii</i> fed on nectar from the corolla (Fig.2A) and dislodged flowers (Fig.2B).
*Asian pigeonwing; <i>Clitoria ternatea</i> ; Fabaceae	Entomophilous (Girish, 2017)	Thane (Mumbai, Maharashtra)	23-09-2020	2	Flower predator	<i>F. tristriatus</i> fed on floral parts by plucking the entire flower (Fig.2C) or biting the corolla tube (Fig. 2D)
*Blue porterweed; <i>Stachytarpheta jamaicensis</i> ; Verbenaceae	Entomophilous; butterfly nectar plant (Manoj et al. 2021)	Thane (Mumbai, Maharashtra)	22-03-2020	2	Flower predator	<i>F. tristriatus</i> removed entire flower spikes while nectaring (Fig. 2E, Fig. 2F)
*Yellow elder; <i>Tecoma stans</i> ; Bignoniaceae	Entomophilous and ornithophilous (Dhnaya et al. 2013)	Thana (Mumbai, Maharashtra)	02-12-2020	1	Occasional visitor	<i>F. tristriatus</i> nectaring on flowers (Fig. 2G)
*Common lantana; <i>Lantana camara</i> ; Verbenaceae	Entomophilous; butterfly nectar plant (Manoj et al. 2021)	Coimbatore (Tamil Nadu)	02-12-2020	2	Nectar robber & Flower predator	<i>F. palmarum</i> nectaring and damaging the inflorescence (Fig.3A)
*Red powder puff; <i>Calliandra haematocephala</i> ; Fabaceae	Entomophilous, chiropterophilous; butterfly nectar plant (Churiet al. 2021)	Vaniyambalam, (Malappuram district Kerala)	11-10-2020	1	Occasional visitor	No photo documentation, but observed <i>F. tristriatus</i> nectaring on flowers (personal Communication by Dasan)
* <i>Hibiscus</i> sp.; Malvaceae	Butterfly nectar plant (Churiet al. 2021)	Thane (Mumbai, Maharashtra)	15-07-2020	2	Nectar robber & Flower predator	<i>F. tristriatus</i> nectaring (Fig.3B) and plucking flowers (Fig.3C)
Silk cotton tree; <i>Bombax ceiba</i> ; Malvaceae	Ornithophilous, chiropterophilous, occasionally entomophilous (Raju et al. 2005)	Payangadi Kannur, (Kerala)	18-02-2020	1	Occasional visitor	Though not photo documented, observed <i>F. tristriatus</i> visiting flowers.
Indian coral tree; <i>Erythrina variegata</i> ; Fabaceae	Entomophilous; ornithophilous; chiropterophilous (Fleming et al. 2009)	Munnar, Idukki, (Kerala)	22-10-2020	2	Flower predator	<i>F. sublineatus</i> (Fig.3E) and <i>F. tristriatus</i> observed feeding on flowers
Drumstick tree; <i>Moringa oleifera</i> ; Moringaceae	Entomophilous; nectar plant & ornithophilous (Jyothi et al. 1990; Sharma, 2019)	Bhuvaneswar, (Odisha) Patnadevi, Gautala-Autramghat WLS, Jalgaon, (Maharashtra)	18-06-2020 14-01-2021	2	Occasional visitor	<i>F. palmarum</i> frequently visited flowers; frequent nectar-feeding visits by <i>F. pennantii</i> were observed.
*Copperpod; <i>Peltophorum pterocarpum</i> ; Fabaceae	Entomophilous (Aluri & Reddi, 1996)	Pune, (Maharashtra)	29-03-2021	2	Flower predator	<i>F. pennantii</i> and <i>F. palmarum</i> skimmed through flower clusters feeding on flowers.

Cont...

Table 1. Flower visitation by Indian palm squirrels (*Funambulus* spp.) recorded across selected states in India

Plant species (Common name; Scientific name; Family)	Pollination syndrome	Observation locality	Date and documentation	Number of times observed	Behaviour category	Remark
*Lindley's aporosa; <i>Aporosa cardiosperma</i> ; Phyllanthaceae	Pollinators unknown (Schot, 2004)	Aralam WLS, Kannur, (Kerala)	January, 2020	2	Occasional visitor & Flower predator	<i>F. tristriatus</i> frequently visited and fed on flowers.
Champak tree; <i>Magnolia champaca</i> ; Magnoliaceae	Entomophilous (WWF 2019)	Bhuvaneswar, (Odisha)	2-07-2020	2	Occasional visitor	Regular visits by <i>F. palmarum</i> on flowers.
*Indian laburnum; <i>Cassia fistula</i> ; Fabaceae	Entomophilous (Murali, 1993)	Pune, (Maharashtra)	27-03-2021	2	Flower predator	<i>F. pennantii</i> attended flowers while skimming through flower clusters.
Bottle brush tree; <i>Callistemon citrinus</i> ; Myrtaceae	Entomophilous & ornithophilous (Sharanya et al. 2014)	Raichak, (West Bengal) and Uttar Pradesh	14-02-2020	1	Occasional visitor, Nectar robber	<i>F. pennantii</i> nectaring with little flower damage.
Indian screw tree; <i>Helicteresisora</i> ; Malvaceae	Entomophilous & ornithophilous (Atluri, 2000)	Calicut University Campus, Malappuram, (Kerala)	01-04-2020	1	Occasional visitor	<i>F. tristriatus</i> fed on nectar without damaging flower heads (Fig.3D),
Flame of the forest; <i>Butea monosperma</i> ; Fabaceae	Ornithophilous, therophilous, chiropterophilous (Tandon et al. 2003; Fleming et al. 2009)	Akurdi, Pune, (Maharashtra)Mukkali, Silent Valley National Park, Palakkad, (Kerala)	28.03. 2020	3	Occasional visitor	<i>F. palmarum</i> , <i>F. pennantii</i> and <i>F. tristriatus</i> observed nectar feeding.
Ornamental banana; <i>Musa ornata</i> ; Musaceae	Ornithophilous, therophilous, chiropterophilous (Nur, 1976; Subbaraya & Baudoin, 2006)	Kozhikode (Kerala) Several places in Maharashtra	Feb, 2020 Throughout the year	2	Flower predator / Occasional visitor	<i>F. tristriatus</i> removed flowers while feeding (Fig. 3F); <i>F. palmarum</i> nectaring observed.
Common banana; <i>Musa paradisiaca</i> ; Musaceae	Chiropterophilous (Fleming et al. 2009)	Malappuram, (Kerala)	10-01-2020	1	Occasional visitor	<i>F. tristriatus</i> visiting inflorescences (Fig. 3G).
Coconut palm; <i>Cocos nucifera</i> ; Arecaceae	Entomophilous, ornithophilous, therophilous (Thomas & Kumar, 2013; Chakravarthy & Thyagaraj, 2012)	Karnataka and northern part of Kerala.	16-03- 2020	1	Occasional visitor	<i>F. tristriatus</i> observed on coconut palms.

*Indicates first report of flower visitation by palm squirrels

a single plant species (Figure 4), *Erythrina variegata*. *Funambulus palmarum* and *F. pennantii* showed intermediate host breadths. Nonetheless, the pattern is consistent with the known habitat associations of these species: *F. tristriatus* is a generalist of disturbed and edge habitats where floral diversity is high, whereas *F. sublineatus* is a forest interior specialist with a more limited geographic and ecological range (Chandrasekar & Sunquist, 1996; Molur & Nameer, 2016; Middleton & Ferguson, 2020;

Rajamani, 2021). The network further revealed that several plant species, including *Musa* spp. and *Moringa oleifera*, were associated with more than one *Funambulus* species, suggesting overlap in floral resource use at the species level.

3.3. Nectar Feeding and Floral Damage

Nectar feeding by palm squirrels appears to be opportunistic and primarily related to energy acquisition. Frequent damage or removal of flowers indicates that

squirrels often function as nectar robbers or flower predators, especially on flowers not structurally adapted to mammalian visitors. Similar patterns of nectar robbing and floral damage by rodents and other mammals have been documented in tropical systems (Deng et al., 2004; Irwin et al., 2010). Such damage is likely to reduce floral longevity and may limit access to nectar for legitimate pollinators.

3.4. Context-dependent Pollination Potential

In contrast to damaging visits on small, fragile entomophilous flowers, palm squirrels visiting large, structurally robust flowers occasionally came into contact with anthers and stigmas. Nine plant species recorded in this study, *Tecoma stans*, *Calliandra haematocephala*, *Bombax ceiba*, *Moringa oleifera*, *Magnolia champaca*, *Helicteres isora*, *Butea monosperma*, *Musa paradisiaca*, and *Cocos nucifera*, were categorised exclusively as occasional visitors, with no flower damage recorded. This behavioural distinction suggests that floral morphology plays a decisive role in determining visit outcome.

Among these, several species possess floral traits particularly conducive to incidental pollen transfer. *Bombax ceiba* produces large, open, cup-shaped flowers with a prominent exerted stamen column, with no morphological restriction for access to nectar, making anther contact with the squirrel's muzzle or facial fur highly probable during nectar feeding (Raju et al., 2005). Similarly, *Magnolia champaca* bears large, robust tepals with anthers and stigmas in close spatial proximity along a central receptacle axis, a floral architecture associated with generalist vertebrate visitation (Thien et al., 2000). *Callistemon citrinus* displays a bottlebrush inflorescence architecture in which stamens are exerted several centimetres beyond the corolla, virtually ensuring contact with a visiting mammal (Sharanya et al., 2014). *Butea monosperma*, visited by all three *Funambulus* species in the present study, has previously been reported to be squirrel-pollinated. *Funambulus tristriatus* was observed to contact both the anthers and the stigma while foraging for nectar, thereby facilitating pollen deposition and fruit set (Tandon et al., 2003). *Helicteres isora* is particularly noteworthy: the observed individual fed on nectar without damaging flower heads, suggesting a non-destructive foraging mode compatible with pollinator function; its flowers are large, zygomorphic, with a prominent androgynophore that positions stamens accessibly for vertebrate visitors (Atluri et al. 2000).

This raises the possibility that they may function as potential incidental pollen vectors when floral morphology is compatible with their body size and handling behaviour. However, pollen deposition and transfer were not directly measured in this study. Similar interactions have been reported where squirrels act as opportunistic rather than specialised pollinators, and pollen transfer has been inferred in flowers with sturdy construction, accessible nectar, and exposed reproductive organs (Ganesh & Devy, 2006;

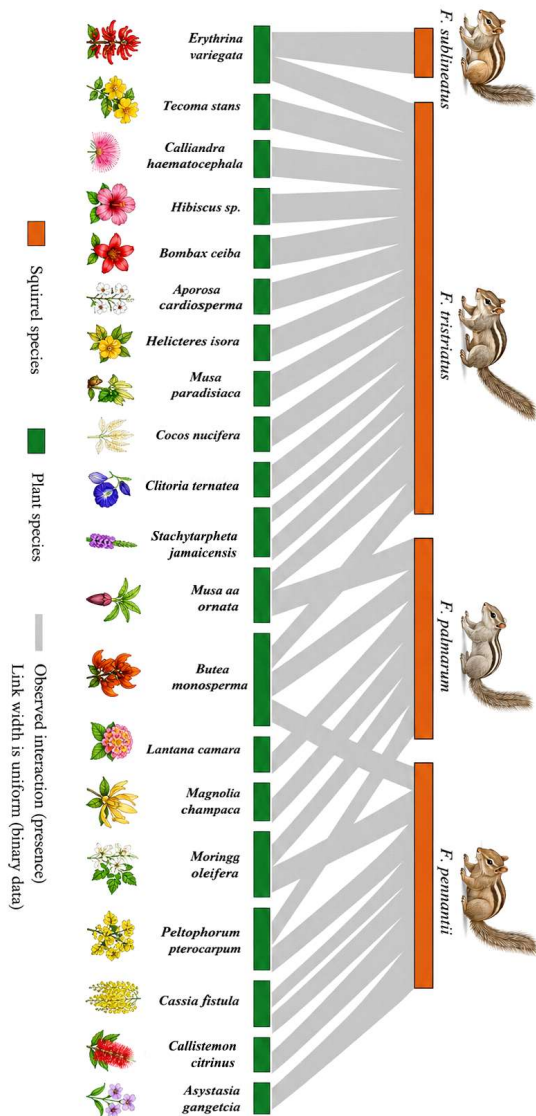


Figure 4. Bipartite network illustrating the flower visitation interactions between four *Funambulus* species (orange nodes, top) and 20 plant species from 11 families (green nodes, bottom) documented across five Indian states. Lines connect each squirrel species to the plant species it was recorded visiting

Kobayashi et al., 2017). Such trait matching between floral architecture and mammalian foragers is a recurring feature of non-flying mammal pollination systems (Carthew & Goldingay, 1997), and future studies incorporating pollen load analysis would be needed to confirm whether palm squirrels contribute meaningfully to pollination in Indian plant communities.

3.5. Ecological Implications

The wide taxonomic range of flowers visited and the occurrence of floral visitation across diverse landscapes indicate substantial behavioural flexibility in palm squirrels. As common and abundant mammals in many Indian ecosystems, their frequent nectar feeding may influence plant-pollinator interactions by competing with legitimate pollinators and altering floral resource availability (Irwin et al., 2010; Chakravarthy & Thyagaraj, 2012).

The bipartite interaction network provides a preliminary structural overview of the squirrel-plant interaction system documented in this study. The asymmetry in host breadth across species with *F. tristriatus* being notably more generalist than *F. sublineatus* likely reflects a combination of unequal observation effort and biological differences in distribution range, habitat use and abundance rather than dietary specialization per se, as all four species appear to exploit floral resources opportunistically. The occurrence of shared plant species across multiple squirrel species raises the possibility of interspecific competition for floral resources, though this cannot be evaluated without quantitative visitation data. Such interaction networks, even when based on presence-absence records, can serve as a useful baseline for future studies that incorporate visit frequency, pollen load analysis and experimental studies to rigorously assess the ecological roles of non-flying mammals in Indian plant communities (Dormann et al., 2017; Blüthgen & Staab, 2021)

4. CONCLUSION

The study highlights floral visits of palm squirrels in India, spanning a taxonomically diverse range of plant species and providing a comprehensive synthesis of squirrel-flower interactions from the country to date. The interactions involved nectar robbing or florivory on delicate entomophilous flowers, particularly species lacking morphological traits associated with conspicuous therophilic syndromes. However, they may serve as potential pollen vectors for structurally robust therophilous flowers such as *Butea monosperma* and *Musa* spp. Floral

visitation by palm squirrels is not always ecologically neutral; nectar robbing and florivory can deplete floral rewards and damage reproductive structures, reducing resource availability for legitimate pollinators such as bees, butterflies, birds or mammals and potentially compromising plant reproductive fitness. Non-flying mammals, often overlooked in pollination ecology research, can meaningfully influence plant-animal interaction networks, and future studies should move beyond natural history observations toward experimental evaluation of the ecological consequences of floral visitation by Indian palm squirrels.

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CRediT authorship contribution statement

Prodipta Biswas: Data collection, Methodology, Software, Writing original draft, Formal analysis, Tabulation, Data curation. **K. Rajmohana:** Conceptualization, Supervision, Reviewing and editing, Visualization. **Muhamed Jafer Palot:** Methodology, Reviewing and editing, Visualization.

Conflict of interest

The authors declare that they have no conflicts of interest

Data availability statement

All data generated or analysed during this study are included in this published article. The interaction records are presented in their entirety in Table 1. The corresponding author retains raw photographic and video evidence supporting the documented observations and will be made available upon reasonable request.

Declaration of generative AI AND AI-assisted technologies in the writing process

The authors declare that no artificial intelligence tools were used to write this manuscript.

REFERENCES

Abedin, I., Chatterjee, P., Singha, H., Kim, H.W., & Kundu, S. (2025). Climate-Driven habitat shifts of two palm squirrel species (Sciuridae: Funambulus) and projected

- expansion of their range overlap with Indian agroecosystems. *Biology*, 14(12), 1666.
- Agrawal, V.C., & Chakraborty, S. (1979). Catalogue of mammals in the Zoological Survey of India. Rodentia. Part I. Sciuridae. *Records of the Zoological Survey of India*, 74(4): 333-481.
- Aluri, J.S.R., & Reddi, C.S. (1996). Vibrational pollination in *Peltophorumpterocarpum* (Caesalpinaceae). *Journal of Nature Conservation*, 8, 99-100.
- Aravind, P.S., Joe, G., Dhanesh, P., & Nandini, R. (2021). Food habits of the dusky-striped squirrel *Funambulussublineatus* (Mammalia: Rodentia: Sciuridae). *Journal of Threatened Taxa*, 13, 17827-17831.
- Atluri, J.B., Rao, S.P., & Subba Reddi, C. (2000). Pollination ecology of *Helicteresisora* Linn. (Sterculiaceae). *Current Science*, 78(6), 713-718.
- Bascompte, J., Jordano, P., Melian, C.J., & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16), 9383-9387.
- Blüthgen, N., & Staab, M. (2021). Mammals, interaction networks and the relevance of scale. *Current Biology*, 31, R850-R853.
- Boaventura, M.G., Villamil, N., Teixido, A.L., Tito, R., Vasconcelos, H.L., Silveira, F.A., & Cornelissen, T. (2022). Revisiting florivory: an integrative review and global patterns of a neglected interaction. *New Phytologist*, 233(1), 132-144.
- Carthew, S.M., & Goldingay, R.L. (1997). Non-flying mammals as pollinators. *Trends in Ecology & Evolution*, 12(3), 104-108.
- Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J., & Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology*, 81(1), 190-200.
- Chakravarthy, A.K., & Thyagaraj, N.E. (2012). The palm squirrel in coconut plantations: Ecosystem services by therophily. *Mammalia*, 76, 193-199.
- Chandrasekar-Rao, A., & Sunquist, M.E. (1996). Ecology of small mammals in tropical forest habitats of southern India. *Journal of Tropical Ecology*, 12(4), 561-571.
- Churi, P., Manoj, P., & Sawant, D. (2021). Nectar plants - Malvaceae. In K. Kunte, S. Kalesh, & U. Kodandaramaiah (Eds.), *Butterflies of India* (Version 2.00). Indian Foundation for Butterflies. <http://www.ifoundbutterflies.org/nectar-plants/Malvaceae>
- Deng, X.B., Ren, P.Y., Gao, J.Y., & Li, Q.J. (2004). The striped squirrel (*Tamias swinhoi hainanus*) as a nectar robber of ginger (*Alpinia kwangsiensis*). *Biotropica*, 36, 633-636.
- Deng, X., Deng, W., Hughes, A.C., & Mohandass, D. (2015). Diverse nectar robbers on *Alpinia roxburghii* Sweet (Zingiberaceae). *Journal of Asia-Pacific Biodiversity*, 8, 238-241.
- Dhanya, R., Azeez, P.A., & Das, K. S. A. (2013). Floral visits and floral damage by avian nectar robbers on an exotic shrub, *Tecoma stans* (L.) Kunth, in the Western Ghats, India. *Tropical Natural History*, 13, 49-52.
- Dissanayake, R., & Oshida, T. (2012). The systematics of the dusky striped squirrel, *Funambulussublineatus* (Waterhouse, 1838) (Rodentia: Sciuridae) and its relationships to Layard's squirrel, *Funambuluslayardi* Blyth, 1849. *Journal of Natural History*, 46(1-2): 91-116.
- Dissanayake, R., & Oshida, T. (2012). The systematics of the dusky striped squirrel, *Funambulussublineatus* (Waterhouse, 1838)(Rodentia: Sciuridae) and its relationships to Layard's squirrel, *Funambuluslayardi* Blyth, 1849. *Journal of Natural History*, 46(1-2), 91-116.
- Dormann, C.F., Fründ, J., & Schaefer, H.M. (2017). Identifying causes of patterns in ecological networks: Opportunities and limitations. *Annual Review of Ecology, Evolution, and Systematics*, 48, 559-584.
- Dormann, C.F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, 8(2), 8-11.
- Fleming, T.H., Geiselman, C., & Kress, W.J. (2009). The evolution of bat pollination: A phylogenetic perspective. *Annals of Botany*, 104, 1017-1043.
- Galetto, L., Bernardello, G., Isele, I.C., Vesprini, J., Speroni, G., & Berduc, A. (2000). Reproductive biology of *Erythrina crista-galli* (Fabaceae). *Annals of the Missouri Botanical Garden*, 87, 127-145.
- Ganesh, T., & Devy, M.S. (2006). Interactions between non-flying mammals and flowers of *Culleniaaxarillata* Robyns (Bombacaceae), a canopy tree from the wet forests of the Western Ghats, India. *Current Science*, 91, 1674-1679.
- Girish, E. (2017). An integrated study on effect of climate change on biodiversity, insect pollinator visitation and seed germination in *Clitoriaternatea*. *Journal of Medical Science and Clinical Research*, 5, 18331-18336.
- Hale, K.R., Valdovinos, F.S., & Martinez, N.D. (2020). Mutualism increases diversity, stability, and function of multiplex networks that integrate pollinators into food webs. *Nature Communications*, 11(1), 2182.
- Inouye, D.W. (1980). The terminology of floral larceny. *Ecology*, 61, 1251-1253.
- Irwin, R.E., Bronstein, J.L., Manson, J.S., & Richardson, L. (2010). Nectar robbing: Ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution, and Systematics*, 41, 271-292.
- Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal. *American Naturalist*, 129, 657-677.
- Jyothi, P.V., Atluri, J.B., & Reddi, C.S. (1990). Pollination ecology of *Moringa oleifera*. *Proceedings of the Indian Academy of Sciences (Plant Sciences)*, 100, 33-42.
- Khorsand, R.S., Ginn, Z.R., & Sancier-Barbosa, F. (2025). Spatio-temporal patterns in floral resources and plant-

- pollinator network structure in the Alaskan Arctic. *Frontiers in Plant Science*, 16, 1552422.
- Kobayashi, S., Denda, T., Liao, C.C., Lin, Y.H., Liu, W.T., & Izawa, M. (2018a). Comparison of visitors and pollinators of *Mucuna macrocarpa*. *Mammal Study*, 43, 219-228.
- Kobayashi, S., Denda, T., Liao, C.C., Placksanoi, J., Waengsothorn, S., Aryuthaka, C., Panha, S., & Izawa, M. (2018b). Regional differences in mammalian pollinators. *Tropical Natural History*, 18, 135-145.
- Kobayashi, S., Denda, T., Liao, C.C., Wu, S.H., Lin, Y.H., & Izawa, M. (2017). Squirrel pollination of *Mucuna macrocarpa*. *Journal of Mammalogy*, 98, 533-541.
- Kobayashi, S., Denda, T., Mashiba, S., Iwamoto, T., Doi, T., & Izawa, M. (2015). Pollination partners of *Mucuna macrocarpa*. *Plant Species Biology*, 30, 272-278.
- Kobayashi, S., Denda, T., Placksanoi, J., Waengsothorn, S., Aryuthaka, C., Panha, S., & Izawa, M. (2019). The pollination system of the widely distributed mammal-pollinated *Mucuna macrocarpa* (Fabaceae) in the tropics. *Ecology and Evolution*, 9(11), 6276-6286.
- Kobayashi, S., Panha, S., Seesamut, T., Nantarat, N., Likhitrakarn, N., Denda, T., & Izawa, M. (2021). First record of non-flying mammalian contributors to pollination in a tropical montane forest in Asia. *Ecology and Evolution*, 11(24), 17604-17608.
- Lai, H. R. et al. (2024). Canids as pollinators? Nectar foraging by Ethiopian wolves may contribute to the pollination of *Kniphofia foliosa*. *Ecology*, 106, e4470.
- Liow, L.H., Sodhi, N.S., & Elmqvist, T. (2001). Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology*, 38(1): 180-192.
- Marod, D., Pinyo, P., Duengkae, P., & Hiroshi, T. (2010). The role of wild banana (*Musa acuminata*) on wildlife diversity. *Agriculture and Natural Resources*, 44, 35-43.
- McCann, C. (1933). The flying fox and palm squirrel as pollinators. *Journal of the Bombay Natural History Society*, 36, 761-764.
- Middleton, K., & Ferguson, A. 2020. *Funambulus sublineatus*. The IUCN Red List of Threatened Species 2020: e.T88813572A22259638. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T88813572A22259638.en>. Accessed on 05 June 2026.
- Molur, S., & Nameer, P.O. 2016. *Funambulus tristriatus*. The IUCN Red List of Threatened Species 2016: e.T8704A22259512. <https://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T8704A22259512.en>. Accessed on 05 June 2026.
- Moore, J.C., & Tate, G.H.H. (1965). A study of the diurnal squirrels, Sciurinae, of the Indian and Indo-Chinese subregions. *Fieldiana: Zoology*, 48: 1-351.
- Murali, K.S. (1993). Differential reproductive success in *Cassia fistula*. *Current Science*, 65, 270-272.
- Nivetha, M., D'Souza, S., Shijisha, A.C., Ligon, R.A., & Nandini, R. (2023). *Multifunctional evolution of palm squirrel coat colour and pattern*. bioRxiv, 2023-09
- Nur, N. (1976). Studies on pollination in Musaceae. *Annals of Botany*, 40, 167-177.
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321-326.
- Perodaskalaki, A., Rammou, D.L., Thapamagar, T., Bhandari, S., Bhusal, D.R., & Youlatos, D. (2023). Habitat use and positional behavior of northern palm squirrels (*Funambulus pennantii*) in an urban forest in central Nepal. *Land*, 12(3), 690.
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rajamani, N. (2021). Food habits of the Dusky-striped Squirrel *Funambulus sublineatus* (Mammalia: Rodentia: Sciuridae). *Journal of Threatened Taxa*.
- Raju, A.J.S., Rao, S.P., & Rangaiyah, K. (2005). Pollination by bats and birds in *Bombax ceiba*. *Ornithological Science*, 4, 81-87.
- Raju, A.J.S., Rao, S.P., & Victorbabu, K. (2005). Pollination by bats and birds in the obligate outcrosser *Bombax ceiba* L. (Bombacaceae), a tropical dry season flowering tree species in the Eastern Ghats forests of India. *Ornithological Science*, 4(1), 81-92.
- Richman, S.K., Barker, J.L., Baek, M., Papaj, D.R., Irwin, R.E., & Bronstein, J.L. (2021). The sensory and cognitive ecology of nectar robbing. *Frontiers in Ecology and Evolution*, 9, 698137.
- Robinson, K.M., Hauzy, C., Loeuille, N., & Albrechtsen, B.R. (2015). Relative impacts of environmental variation and evolutionary history on the nestedness and modularity of tree-herbivore networks. *Ecology and Evolution*, 5(14), 2898-2915.
- Samson, A., Ramakrishnan, B., & Bargavi, S. (2017). Leucism in the three-striped palm squirrel (*Funambulus palmarum*) at Gudalur Forest Division, Tamil Nadu, Southern India. *Therya*, 8(3), 261-262.
- Schot, A.M. (2004). Systematics of *Aporosa* (Euphorbiaceae). *Blumea Supplement*, 17, 1-380.
- Sharanya, C.G., Arya, K., & Devipriya, S.P. (2014). A review on the traditional uses, phytochemistry and pharmacology of bottlebrush plant (*Callistemon citrinus*). *International Journal of Phytopharmacy*, 4(1), 1-8.
- Sharanya, M., Aswani, K., & Sabu, M. (2014). Pollination biology of *Callistemon citrinus*. *International Journal of Plant Reproduction Biology*, 6, 105-110.
- Sharma, D. (2019). *Moringa oleifera*: The honey bee heaven plant. *Bee World*, 96, 120-122.
- Soh, Z.W.W., & Ngiam, R.W.J. (2013). Flower-visiting bees and wasps in Singapore parks. *Nature in Singapore*, 6, 153-172.
- Srivastava, M. (2020). Flowers of *Moringa oleifera*: A preferred food of Indian palm squirrel. *International Journal of Recent Scientific Research*, 11, 38105-38106.
- Subbaraya, U., Litaladio, N., & Baudoin, W.O. (2006). *Farmer's knowledge of wild Musa in India*. FAO.
- Suneetha, T., & Solomon Raju, A.J. (2019). Foraging

- activity of carpenter bees. *Journal of Palynology*, 55, 99-108.
- Talmale, S.S. (2013). Taxonomic studies on jungle palm squirrel *Funambulustristriatus* (Waterhouse) from Northern Western Ghats. *Records of the Zoological Survey of India*, 61-66.
- Tandon, R., Shivanna, K.R., & Mohan Ram, H.Y. (2003). Reproductive biology of *Butea monosperma*. *Annals of Botany*, 92, 715-723.
- Tandon, R., Shivanna, K.R., & Mohan Ram, H.Y. (2003). Reproductive biology of *Butea monosperma* (Fabaceae). *Annals of Botany*, 92(5), 715-723.
- Thien, L.B., Azuma, H., & Kawano, S. (2000). New perspectives on the pollination biology of basal angiosperms. *International Journal of Plant Sciences*, 161(S6), S225-S235.
- Thomas, R.J., & Kumar, J.A. (2013). Flowering and pollination biology in coconut. *Journal of Plantation Crops*, 41, 109-117.
- Wester, P. et al. (2023). Non-flying mammal pollination in *Massonia grandiflora*. *South African Journal of Botany*, 163, 612-621.
- Willson, M.F., Smith-Ramírez, C., Sabag, C., & Hernández, J.F. (1996). Mutualisms between plants and animals. In J.J. Armesto, C. Villagrán, & M.T.K. Arroyo (Eds.), *Ecología de los bosques nativos de Chile* (pp. 251-264). Editorial Universitaria.
- Wilson, D.E., & Reeder, D.M. (Eds.). (2005). *Mammal species of the world* (3rd ed.). Johns Hopkins University Press.
- WWF. (2019). *Champ monograph (Michelia champaca)*. WWF Nepal.
- Xiao, H.W., & Huang, Y.B. (2025). Spatiotemporal Variations in Nectar Robbing and Its Effects on Reproduction in *Salvia castanea* Diels (Lamiaceae). *Plants*, 14(15), 2266.
- Yousefi, S., Izadian, M., & Kheradpir, N. (2013). Survey of morphometric features of palm squirrel, *Funambulus pennantii* Wroughton, 1905 in Iran. *Mun. Ent. Zool*, 8(1), 154-61.
- Yumoto, T. (2000). Bird pollination of *Durio species*. *American Journal of Botany*, 87, 1181-1188.