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P Athira

Research Scholar, PG and
Research Department of Botany,
Kongunadu Arts and Science
College, GN Mills, Coimbatore,
Tamil Nadu, India

K Thenmozhi

Assistant Professor and Head,
PG and Research Department of
Botany, Kongunadu Arts and
Science College, GN Mills,
Coimbatore, Tamil Nadu, India

Cockroach associated pollination links: A proof to the complexity of plant-insect alliance

P Athira and K Thenmozhi

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Abstract

Reconnaissance on the spectacle whereby cockroaches fertilize plants has grown in attractiveness amongst botanical investigators. The present comprehension culminates about the cockroach species *Blattodea* as the primary pollinators of plant species and illuminates on the 11 plant species that have been distinguished to be predominantly pollinated by cockroaches. The review deduces the environmental congruity of cockroach pollination by endorsing it as an enthralling plant-pollinator technique through an in-depth review of literature that is presently accessible. The exclusive acquaintance that progresses between the plants and cockroach species shed light on the heterogeneity of stratagems that plants use to reassure efficacious reproduction. The research additionally emphasizes the need for further research on cockroach pollination, arguing that this process has substantial ramifications on both ecological and evolutionary biology. Acknowledging these interactions stipulates insight knowledge towards complexities of cockroach-mediated plant pollination, which underpin our cognizance of plant-pollinator reciprocations and conceives novel prospects for ecological and evolutionary biology exploration.

Keywords: *Blattodea*, cockroach, floral rewards, geitonogamy, pollination mechanism, saprophytes

Introduction

In Angiosperms, the initial contact of the pollen on the stigma and the resulting germination of the plant are cooperatively implied to as pollination. As an aftermath, there is an affiliation between the pollen of the female sporophytic generation—the stigmatic surface of the carpel—and that of the male gametophytic generation^[1]. Pollination is analytical to sustaining biodiversity and security of natural ecosystem. It emboldens genetic variation amid plant populations, which makes them extra tolerant and compliant to vicissitudes in their environment. Plant reproduction is bolstered by pollinators such as the wind, water, insects, birds, bats, mammals, amphibians, and mollusks^[2]. Perceiving the communications between the behavior of pollinators visiting a flower and the biology of the flower, which necessitates self or cross-pollination is decisive in comprehending pollination processes^[3]. Cross-pollination habitually facilitates superior genetic diversity and erraticism as opposed to self-pollinated flowers^[4]. Pollination is consequently indispensable for ecological functioning and obligatory to promise genetic divergence together with proper fruit and seed sets.

Flowers function as vital rudiments in sexual reproduction. They reconcile numerous opposing requirements. These include offering pollen as a floral attractant vs preserving pollen for reproduction, balancing access to reserves with the prerequisite for extravagant displays to draw pollinators, and warranting self-pollination-based progeny creation, contrary to the stipulation of outcrossing to enhance genetic variety^[5]. For this reason, individual flowers are distinguished as a species-specific bargain intended to standardize sexual reproduction. Additionally, the enormity of the association between pollinators and flowers cannot be ignored.

In various fields of ecological research, plant-pollinator interactions are considered instrumental mutualisms that underwrite to detailed environmental systems that endure biodiversity worldwide. In plants, pollinators persist as essential competitive assets, and the variables constraining seed production determine this competition. Although plant reproduction can be limited by mineral resources, leading to an uncorrelated relationship between pollinator richness and fruit development, there are scenarios in which low pollinator

Corresponding Author:

K Thenmozhi

Assistant Professor and Head,
PG and Research Department of
Botany, Kongunadu Arts and
Science College, GN Mills,
Coimbatore, Tamil Nadu, India

availability concedes plant reproductive attainment [6]. Pollinators embrace a broad category of animal species that aid in the angiosperm pollen transfer [7]. Insects are the most copious and diversified pollinators. At present, the four insect orders that are most commonly recognized as pollinators are true flies (Diptera), beetles (Coleoptera), butterflies and moths (Lepidoptera), and bees and wasps (Hymenoptera) [8]. Alternatively, there are only a few indications that certain insect groups, such as Blattodea (cockroaches), Hemiptera (true bugs), Neoptera (net-winged insects), and Orthoptera (crickets), have been documented often and are proficient at devouring flowers [7]. Cockroaches maintain to be the exclusion among all the animals and insects scrutinized as potential pollinators. In addition to functioning as essential pollinators, cockroaches are also central manifestations of environmental degradation, given that they are acclimatizing to oscillating environments and are indispensable to ecosystems universally. Pollination is one of these functions, as it is fundamental to plant growth and food safety [9]. Only eleven plant species globally—including one member of the Apocynaceae family—have been reported to be pollinated by cockroaches [10]. The nonexistence of a well-defined floral syndrome coupled with cockroach pollination accentuates the convolution of plant-insect interactions. This review aims to expound the diversity of plant species pollinated by cockroaches and shed light on the systems underlying this unique mode of pollination. Relevant conclusions into the coevolutionary techniques between plants and their own unique pollinators could perchance be perceived through examining the morphological and behavioral adaptations of these plant species.

Materials and Methods

In conducting this review, an extensive literature search was performed using multiple academic databases, including Google Scholar, PubMed, Science Direct and JSTOR, to ensure comprehensive coverage of relevant research. These databases were chosen to provide this review a strong basis owing to their extensive collections of peer-reviewed scientific literatures.

Mechanism of Cockroach Pollination

Cockroach pollination is a comparatively sporadic mechanism for pollination, discrete from more customary schemes involving bees, butterflies, or birds [11]. Cockroaches are enticed to plants by musty odors and food incentives throughout this phase, which mistakenly encourages pollen transport between the flowers while the insects feed or look for cover. This mutualistic collaboration is a crucial illustration of the multifaceted adaptations and coevolutionary dynamics that occur between plants and insects in various settings. Contrary to other pollination syndromes, the singularity and rarity of this relationship are demonstrated by the small number of plant species that depend on cockroaches for pollination [11], [12]. Certain morphological adaptations have been noticed in the flowers of the plants that have evolved to rely on cockroaches for pollination, facilitating these insects to successfully attract and use the flowers. These flowers are frequently distinguished by their modest size, inconspicuous nature, and grouped organization, all of which work together to exploit cockroach-plant association. These flowers' tubular, narrow forms make them superlative for lodging the cockroach mouth parts, which facilitates most favorable pollen delivery. Moreover, the flowers frequently emit potent scents that lure cockroaches, augmenting the pollination

technique [13]. When a cockroach visits a flower seeking food or shelter, it inadvertently contacts the flower's reproductive structures, including the stigma and anthers, facilitating pollen transfer between flowers and enabling pollination [2]. Due to their nocturnal feeding habits, plants pollinated by cockroaches often release scent and nectar at night to attract these insects (Fig. 1). This nocturnal strategy, coupled with the provision of food resources such as nectar, pollen, and shelter from flowers, heightens the attractiveness of flowers to cockroaches, encouraging them to visit and potentially contribute to pollination [14].

Plant Species Pollinated by Cockroaches

*Balanophora kuroi*wae Makino and *Balanophora tobiracola* Makino

*Balanophora kuroi*wae is a low, perennial root holoparasite that parasitizes *Pongamia pinnata* (Leguminosae) and *Macaranga tanarius* (Euphorbiaceae) [15], [16]. Its short, pale-pink aboveground parts consist of an egg-like inflorescence and scaly leaves. Each plant produces two to thirteen inflorescences in winter, with numerous female flowers grouped among small spadices on the inflorescence's top and a cluster of male flowers at the base. The female flowers are typically larger and more prominent than the male flowers, with each containing a single ovule. The male flowers are smaller and contain numerous pollen-producing anthers. The unique arrangement of these flowers is thought to facilitate pollination by cockroaches, which are attracted to the fermented odor emitted by the female flowers [17]. Male flowers have extrafloral nectarines at their pedicel bases, and some spadices also release nectar, which accumulates on the surface of the female portion. The inflorescences are odorless. The tiny, numerous seeds are indistinguishable from unfertilized ovules. *B. kuroi*wae is distributed eastwards from Celebes and the Philippines to Australia and Fiji [17]. *B. tobiracola* parasitizes *Ligustrum japonicum* (Oleaceae), *Raphiolepis indica* var. *umbellata* (Rosaceae), and *Pittosporum tobira* (Pittosporaceae) [15]. Male flowers are sporadically interspersed with female flowers in the yellow aboveground parts. Nectarines are limited to the bases of pedicels in male flowers. Each plant produces 1–6 inflorescences, lasting 3–5 days [17]. Both *B. kuroi*wae and *B. tobiracola* manifested sporophytic self-compatibility, with varied outcrossing rates across inflorescences and geitonogamy caused by ants. Pyralid moths were thought to be the most likely cross-pollinators of *Balanophora* species, while ants and flightless cockroaches were found to be effective sources of geitonogamous self-pollination. This discovery offers a fresh illustration of mutualism in pollination between a plant and its pollinating insect [17].

Clusia blattophila M.H.G. Gust. & Vlasáková and *Clusia sellowiana* Schldl.

The dioecious shrub *Clusia blattophila* typically reaches heights ranging from 2 to 10 meters [18]. Its nocturnal, light-yellow flowers measure approximately 1 centimeter in diameter and are arranged in dichasial cymes. Male flowers exhibit single-night blooming, while female flowers remain open for two nights. Generally, only a few flowers open each night, and nocturnal visitors such as cockroaches are the primary pollinators. Male flowers secrete fluid from glands located at the base of the androecium, while female flowers do not offer any rewards [19]. Most of the pollen was dispersed in *C. blattophila* by crickets, Diptera, and *Amazonina platystylata* cockroaches; however, ovule fertilization was

more effective with the help of cockroaches than with Diptera. Hence, it is clear that cockroach pollination could be more common and significant than previously believed, emphasizing the underappreciated function of cockroaches as pollinators [20].

The floral morphology of *C. sellowiana* is similar to that of *C. blattophila*. The inflorescence of this plant has a dichasial cyme, bearing 2–16 actinomorphic flowers without resin secretion. There were no morphological differences reported between pistillate and staminate flowers except in terms of reproductive structures [21]. Each flower is surrounded by two pairs of bracteoles that are thick, yellow-green, and up to 4 mm in diameter. The calyx consists of two pairs of sepals that resemble the bracteoles in color and shape, being free, circular-to-elliptic, convex, 3–4 mm wide, and 4–5 mm long, with the inner sepals having a scarious margin [21]. *C. sellowiana* reproduces exclusively through sexual reproduction. Its nocturnal flowers are visited by crickets, ants, moths, and cockroaches, with *A. platystylata* cockroaches being the primary pollinators. Cockroaches exhibit significant electroantennography (EAG) reactions to floral volatiles and acetoin (a compound involved in the chemical communication of several cockroach species), indicating that floral scent plays a crucial role in attracting them. Furthermore, it is suggested that plant-cockroach interactions are highly specialized and that the plant has evolved specific strategies to attract and reward its cockroach pollinators, possibly by exploiting the sensitivity of cockroaches to acetoin [21].

***Eucomis autumnalis* (Mill.) Chitt. and *Eucomis comosa* Houtt. ex. Wehrh.**

Eucomis spp. of the family Asparagaceae are commonly known as pineapple lilies. They are native to southern Africa and are grown as decorative plants all over the world. Their erect inflorescences (racemes) and coma (leaf-like tufts) at the tip, which resemble pineapples, are the features that distinguish them [22]. *Eucomis* has developed methods for attracting a variety of specialized pollinators, including insects and animals [23]. Among them, pompilid wasps are the primary pollinators of *E. autumnalis* and *E. comosa*, which produce hermaphrodite outcrossing flowers in their native environments. *E. autumnalis* and *E. comosa*, which are commonly found in Japanese parks and gardens, are identified by the color and morphology of their flowers, the form of their leaves, and the timing of their flowering periods [24]. *Blattella nipponica* cockroach species often visit *Eucomis* inflorescences, and observations over several years disclosed that these cockroaches visited both *E. autumnalis* and *E. comosa*, with pollen found attached to their bodies [25]. While other insects also visit the inflorescence, including ants, flies, and a scarab beetle, they do not appear to interact with the pollen. Despite their unspecialized floral structures and abundant nectar, which typically attracts wasps for pollination, the *Eucomis* flowers do not attract wasps or bees. The presence of *B. nipponica* cockroaches manifests a potential role in pollen transfer, indicating a novel pollination interaction in *ex-situ* setting and expanding the understanding of cockroach pollination in plant species [25].

***Mitrastemon yamamotoi* (Makino) Makino**

Mitrastemon yamamotoi is a holoparasitic plant belonging to the Mitrastemonaceae that remains entirely embedded within its host's tissues, except during the reproductive stage when its flowers emerge. The flowers of *Mitrastemon* species are

bisexual and protandrous, with collar-shaped perianth tubes [26]. The stamens are connate, forming a mitre-shaped androecium tube with a fertile zone of pollen-bearing locules and a sterile apical portion. The gynoecia are hypogynous and single-locular, with a thick, conical stigma. The plant produces a large amount of dilute nectar stored in upper-scale leaves as a pollinator reward [26]. Direct observations pinpoint the fact about the frequent visits of social wasps on *M. yamamotoi* flowers, crickets, cockroaches, flies, dung beetles, stag beetles, and ants [27]. Social wasps were recognized as the main diurnal visitors, sequentially visiting multiple plants and aggressively defending feeding territories. Other periodic visitors, such as flies and ants, also visited *M. yamamotoi* flowers, but pollen attachment to their bodies was found to be rare. Nocturnal visitors include various crane fly, *Orthoptera*, cockroach, beetle, centipede, and moth species, some of which visited multiple plants, touched anthers and stigmas, and carried pollen grains, facilitating pollination [27].

***Monotropastrum humile* (D. Don) H. Hara**

Monotropastrum humile, a non-photosynthetic plant belonging to the family Ericaceae, is found in East Asia, from the Himalayas to Japan. Its single flower blooms in Japan from March to August, coinciding with rising temperatures. Like other Monotropeae species, *M. humile* relies on external organic carbon sources for its growth [28]. The globular fruits of *M. humile* are approximately 12.5 mm wide, and each contains approximately 937 seeds embedded in the pulp. The seeds are small, have a hard testa, and lack elaiosomes for dispersal. Ripe fruits, lacking a distinctive scent, are dull white and inconspicuous against the forest litter where they fall to the ground [29]. The dull-white, fleshy fruits of *M. humile* have been reported to attract various arthropods. Among the arthropods, forest cockroaches (*B. nipponica*) were established as consistent visitors, consuming less juicy pulp containing numerous minute seeds, which were found to be intact and viable in their excreted frass. This suggests that *B. nipponica* can serve as the primary seed disperser for *M. humile*. Considering the modest species richness and cosmopolitan distribution of the cockroach order Blattodea, seed dispersal by cockroaches may be a widespread yet undocumented mechanism [29].

***Vincetoxicum hainanense* (Chun & Tsiang) Meve, H.H. Kong & Liedt**

Vincetoxicum hainanense, belonging to the family Apocynaceae, is an endangered vine species native to Hainan and Guangdong provinces in China and Cambodia. It typically grows as a twining vine, reaching a length of up to 3.9 meters and a width of 2.8 meters. It thrives in sandy soils near water sources, streams, and mixed evergreen and deciduous forests [30]. The small, pale green flowers of *V. hainanense* open at night and were evidenced to be self-compatible but not autogamous. Various insects, including beetles, flies, ants, and bush crickets, usually visit the flowers, but the most effective pollinator was found to be the cockroach, *Blattella bisignata*, which was the only visitor observed to carry pollen between plant species. Although ants and *Carabidae* are also occasional pollinators, the predominant pollinators for plants in this genus are typically flies, moths, and wasps. The role of cockroach pollination appears to be more significant than previously believed and warrants further investigation [31].

***Uvariopsis dioica* (Diels) Robyns & Ghesq**

Uvariopsis dioica is a small monoecious tree that reaches heights of up to 8 meters. It is found exclusively in Central African rainforests, and like most species in its genus, it exclusively bears flowers on its trunk (trunciflorous)^[32]. The flowers of the plant are unisexual and appear directly on the stem, primarily within the lowest 50 cm (occasionally reaching 1.5 to 2 meters) above the ground. This species is commonly found at low to moderate elevations on Mount Cameroon^[33]. Observations on pollination mechanisms manifested a diverse array of floral visitors, including ants, cockroaches, orthopterans, flesh flies, earwigs, and fruit flies. Despite the high abundance of visitors, their effectiveness in pollination was low, with rare occurrences of pollen grains on flowers and visitors. The pollination system of *U. dioica* involves *Orthoptera* and *Blattodea*, reminiscent of primitive flowers at the onset of angiosperm evolution, highlighting the reliance of this species on infrequent pollination events^[34].

***Uvaria elmeri* Merr**

Uvaria elmeri of the family Annonaceae is a woody climber exhibiting canopy foliage, with cauliflorous inflorescence blooming in the understory^[12]. The flowers are protogynous. The stolon is slender and elongated. The leaves are simple, alternate, and can be either glabrous or pubescent. The bisexual flowers, occasionally unisexual, are axillary, terminal, or leaf-opposed, occurring solitarily or in cymose fascicles. They are colored brown, purple, or yellow and are pedicellate or sessile. The petals are creamy-white or brown, spread horizontally downward, and emit an odor reminiscent of decayed wood or mushrooms^[12]. Insects visiting *U. elmeri* flowers include cockroaches, crickets, bugs, flies, ants, and stingless bees. The female flowers were mainly visited by drosophilid flies, myrmicine ants, cockroaches, and phorid flies, while the male flowers were primarily visited by cockroaches, crickets, and drosophilids. Cockroaches were nocturnal, and drosophilids were diurnal visitors. Cockroaches consume stigmatic exudate and pollen, removing most stamens during their visits, with some nymphs containing pollen in their guts. Pollen attachment was observed on cockroaches, drosophilids, and stingless bees, although most of the pollen collected by stingless bees was stored as food and not utilized for pollination^[12].

Conclusion

Cockroach-mediated pollination is acknowledged in 11 individual plant species worldwide. This put emphasis on the paramount function in which *Blattodea* species could take part as pollinators. This analysis undoubtedly call attention to the ecological connotation of cockroach pollination and establishes its distinct and essential plant-pollinator mechanism. One of the many methods that plants devote to effectually reproduce in multiple status quo is the peculiar way that this flora interacts with cockroaches. In addition to cultivating our awareness of plant-pollinator interactions, comprehending the processes behind this marvel also sheds light on ecological resilience and evolutionary adaptations. For a complete understanding of the sophistication of these atypical pollination tactics, further investigation into this pollination mechanism and its effect on plant reproductive success and ecosystem dynamics is authorized, as it can provide elaborate aspect on effective plant reproduction methods.

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