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Beyond Bees: Non–Traditional Pollinators of Ecosystems

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Abstract: Bees are the premier pollinators in pollinator society. Bee pollination is the hotshot in pollination ecology. Bees are the most and maybe only efficient pollinators of angiosperms around the globe; however, the less-efficient or hilariously termed "accidental pollinators" are often consigned to oblivion. While bees are often hailed as the pre-eminent pollinators, there is a diverse array of other insects and animals that play crucial roles in the pollination of crops and wild plants. These group of pollinators often overlooked can be effective, efficient and only pollinators to some plants. Differentiating the myths from the facts on whether the animal is only a visitor that exploits the floral resources or is also bartering, by carrying out necessary pollination.

Keywords: Pollination, Non-bee pollinators, Non-traditional pollinators, Plant-Pollinator interaction

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Introduction

In pollination ecology, non-bee pollinators are often overlooked and underestimated. The buzzing of bees, fluttering of butterflies and flapping of birds; in pollination, is frequently hailed in the literature, however, other secondary pollinators are still under the shadow. All the available data relating on this phenomenon is stated as circumstantial, accidental or deceitful. Co-evolution suggests that the diversification of angiosperm started 100 million years ago (Benton *et al.*, 2022) and is been commonly thought to have stimulated by diversity of plant-pollinator interactions (Whittall and Hodges, 2007). The evolution of nectar in angiosperm is closely tied to plant-pollinator interactions and environmental factors. Nectar likely evolved from pollination drops in gymnosperms, transitioning to floral nectar as angiosperms developed closed carpels (Nepi *et al.*, 2012); as it has been reported that the early angiosperms only had pollen as a floral resource (Friis *et al.*, 2011). This shift may have been influenced by increasing temperatures and aridity during the cretaceous period (Nepi *et al.*, 2021). Nectar composition, particularly sugar

content has adapted over time to attract specific pollinators and deter nectar thieves (Hansan *et al.*, 2007). Recent research has revealed that nectar is more complex than merely a sugary liquid considered a simple food reward, containing nectarins and other secondary compounds that protect against microorganism and modulate pollinator behaviour (Nepi, 2017). Additionally, nectar-dwelling microorganisms, particularly yeasts, play a significant role in plant pollinator interactions, further complicating our understanding of nectar ecology and evolution (Nepi, 2017; Nepi *et al.*, 2021). Pollinator interactions depend on various factors; that are not determined on similar traits. If the traits are less beneficial the plants would evolve to acquire traits to enchant the potential pollinators and so if they cannot allure the most efficient ones than they will adapt traits more convenient and inviting for the potential pollinators. The purpose of this paper is to review the state of the knowledge on pollinators around the globe; relinquishing their role as the most or less efficient pollinators, summarize the various researches conducted on pollination ecology, recent advances and status of plant-pollinator interaction.

Methodology

A comprehensive literature review was undertaken to synthesize current knowledge on non-bee pollinators and their ecological and agricultural significance. Relevant publications were identified through comprehensive searches of international databases, including Web of Science, Scopus, PubMed, ScienceDirect, and Google Scholar. The search employed combinations of keywords such as "non-bee pollinators", "fly pollination", "moth pollination", "butterfly pollination", "ant pollination", "bird pollination", "bat pollination", "beetle pollination", "mammal pollination" and other related keywords. Studies were considered for inclusion if they: (i) reported empirical findings, reviews, or case studies addressing pollination by non-bee taxa; (ii) were published in peer-reviewed journals between 1900's to 2024 on the aspects of non-bee pollinators. Papers presenting relevant research identified based on the authors' knowledge were included as well. Data was organized thematically, grouping findings into major taxa. Where appropriate, results from multiple studies were compared to assess patterns in pollinator diversity, efficiency, and contribution to ecosystem services. The synthesized information was subsequently narrated according to their relative importance across ecosystems, and existing knowledge gaps.

Uncommon potential pollinators or hoodwinks?

The most underappreciated insects of order; Diptera or True Flies; including non-syrphid flies are significant flower visitors and pollinators with a diverse range of foraging behaviours and a crucial role in both natural and agricultural ecosystems (Cook *et al.*, 2020). Contrary to popular belief, flies are not just nuisances or decomposers; Flies can be as efficient as, or better than, bees for pollinating some crops (Ssymank *et al.*, 2008; Orford *et al.*, 2015).According to the study conducted by radar *et al.* (2020); Diptera was the second most flower visiting order (72%) after Hymenoptera in agricultural ecosystem; followed by Lepidoptera (54%) and Coleoptera (51%). The fly family Syrphidae (hoverflies) was the most frequent non-bee family, visiting over half of the crop species, followed by the blow flies, in the family Calliphoridae. The study also stated that, many non-bee insect pollinators, such as flies, beetles and butterflies are capable of large flight distances relative to most bees; such travel distance is essential for transgene flow (Raitif *et al.*,2019). Hoverflies' capacity to perceive floral electric fields has been revealed by recent studies, and this perception affects their foraging habits and propensity to return (Khan *et al.*,2021). They also provide dual benefits of pollination and pest control (Doyle *et al.*, 2020).

Nectar feeding in mosquitoes has received comparatively less attention. Mosquitoes are drawn to and feed on a range of plant nectar sources, including those found in flowers. Mosquitoes, particularly *Aedes* species, have been

identified as effective pollinators of certain orchids, notably *Platanthera obtusata* (Thien and Utech, 1970; Lahondère *et al.*, 2019). This mutualistic relationship is mediated by the orchid's nonanal-rich scent, which activates specific glomeruli in the mosquito's antennal lobe (Lahondère *et al.*, 2019). The ecological significance of mosquitoes beyond their role as disease vectors and emphasize the need for further research into mosquito-plant interactions, particularly nectar-feeding behaviors (Lahondère *et al.*, 2019; Peach, 2024). Understanding these relationships could have implications for vector control strategies and our broader comprehension of pollination ecology.

The relationship between plants and futile pollinators can vary from commensalism to animosity (Lau and Galloway 2004). Many studies have been conducted on efficient pollinators, however, low efficient ("ugly") pollinators are yet to be studied thoroughly. Negative interactions between efficient flower visitors and predators such as crab spiders, dragonflies, ambush bugs, bodyguard ants can affect pollination service; by plundering the floral reward chamber, which triggers the flower avoidance behaviour in pollinators (Romero *et al.* 2011) and creates "Landscape of fear" (Laundré *et al.*, 2010).

The role of ants as pollinators is highly variable. Ants do pollinate certain plants species (de Vega *et al.*, 2009) Ants outcompetes efficient pollinators, acts as a hooligan by being defensive and acts as a pollinator. A few more are suspected including a bizarre case of an orchid pollinated by pseudocopulation with a male ant (Peakall,1988). On first hand ants can be easily pictured as a pollinator because of its nearest relatives of the same order Hymenoptera such as bees and wasps, however, ant pollination is a less prevalent phenomenon. However, there are only a limited studies depicting ant pollination (less prevalent). Although ants are seen visiting flowers of variety of flowers and are generalists these encounters are frequently reported as bad for the blooms resulting in ineffective pollination (Gómez *et al.*, 1996; Beattie, 2007; Rico-Gray and Oliveira, 2007). Furthermore, pollen viability can deteriorate due to the antibiotic compound on the ant integuments (Beattie *et al.*, 1984; Dutton and Frederickson, 2012). Ants may also cause damage to reproductive structures of plants (Palmer *et al.*, 2006), avoidance or alternation of behaviour in efficient pollinators (Wcislo and Schatz, 2003; Sidhu & Wilson Rankin, 2016) causing negative impacts on plant reproduction (Carvalho *et al.*, 2024). However, ants may be an overshadowed pollinator of certain species (Tepedino *et al.*, 2011; Delnevo *et al.*, 2020; Natsume *et al.*, 2022). Plants adapting structures like extrafloral nectaries (EFN's) and Food bodies (FB's) is supposed to linked with two totally opposite ideologies of protectionist (presence of ants can frighten the less effective pollinators or herbivorous insects) and exploitationists (that points ants as the one that exploits the nectaries). It has also been stated by Wheeler (1910) that plants "have no more use of their ants than dogs do their fleas". However, certain studies suggests that plants consisting EFN's suffer less from herbivory (Rezende *et al.*, 2014).

The effect of ants on plant fitness is not constant over time, it fluctuates seasonally, resulting in increased rate of production of fruit in myrmecophilous plants (Monique *et al.*, 2022). Both plant and ant traits affect the pollination effectiveness. Ant protective mutualism or ant attendance can produce effects of different magnitudes and in different directions based on the pool of traits exhibited by the species involved in the interaction; both plant and ant traits affect the outcome (Leal *et al.*, 2023). Ants are responsible for seed-elaiosome mediated dispersal (myrmecochory) (Vander Wall *et al.*, 2005). There are many other structures evolved through time to form ant mutualism such as beltian bodies, mullerian and pearl bodies (FB's), providing structures such as domatium (Bronstein *et al.*, 2006); that attracts the ants by luring them in through rewards. Hence, it is difficult to label ants as if they are guards or backstabbers.

Thrips, small insects that have an ill repute, infamous due to their feeding habit on plant tissues (García-Fayos and Goldarazena, 2008) and spreading viral diseases to their host plants (Tayal *et al.*, 2023); have been found to play a significant role in pollination due to their thigmotactic behaviour (Terry, 2001; Williams *et al.*, 2001; Peñalver, 2012; Eliyahu *et al.*, 2015). Being small and less mobile takes away from the image of being an effective pollinator. Some species of thrips do act as a pest and damages the host plant however, on some occasions the non-pest species are framed as a pest merely due to their co-existence with the culprit species (Mound, 1997). Mound *et al*. (2022) stated that, definition of pest ranges from an organism that causes serious economic damage to an organism that is merely unwelcomed at a particular place; on a particular plant. Lewis (1976) stated that, "Several hundred species of thrips are pests" depends on how the word "pest" is interpreted. Sugiura (1996) even by named thrips as "supplemental pollinators" of *E. thunbergia*. The nature of pollination by thrips is still debated (Suetsugu *et al.*, 2018). In some host plant species thrips do acts as mutualists (Zhang *et al.*, 2021; Terry *et al.*, 2021). Similarly, the most effective recognised pollinators of oil palm plantation are *Elaeidobius kameronicus*, *Elaeidobius subvittus* and *Mystrops costaricensis* (Weevils: Coleoptera); native to west Africa; carries out Anthophilous oil palm pollination and were introduced to east Asia in the 1980s (Yousefi *et al.*, 2020). Hence, thrips and weevils may not be a generalized-pollinators; they are more obligate or specialized; "not for all" pollinator.

Pollination through snails and slugs, no matter how much the phenomenon seems ridiculous, backed by various researchers that the idea itself is vague, 'notorious and obscure' (Faegri and van der Pijl, 1979); Malacophily is a phenomenon that takes place in nature. Pollination by snails and slugs (Malacophily) is considered a rare (Abrol, 2012) and infrequent phenomenon. Malacophily is thought to be associated with the plant's prostrate habit and a floral arrangement where the stigma and anthers do not extend beyond the corolla (non-protruding stigmas and anthers) (Pammel and King, 1930) and so far it is recorded that nine species of plants pollinate through alacophily that are *Rohdea japonica* (sacred lily)*, Philodendron pinnatifidum* (Comb-Leaf Philodendron), *Alocasia odora* (Night scented lily), *Calla palustris* (Water arum), *Lemna minor* (Common duckweed)*, Chrysosplenium alternifolium* (Golden saxifrage)*, Phragmipedium caudatum* (Mandarin Orchid)*, Ipomoea pes-caprae* (Goat foot vine/ Beach morning glory) and *Volvulopsis nummularium* (Agracejo Glory)(Pammel and King, 1930; Atwood 1985; McGregor, 1976; Sarma *et al.*, 2007; Raju *et al.*, 2014). For *Volvulopsis nummularium*; on rainy days when anthesis was delayed by 30 mins and flower buds were open only partially, no bee activity was recorded. Snails were the one to pollinate the partially opened flowers during those days (Sarma *et al.*, 2007). Snails are usually active during night and on rainy days. Instead, multiple studies have actually refuted the occurrence of slug pollination in putatively slug-pollinated plant species (Kato, 1995; Vislobokov *et al.*, 2014; Vislobokov, 2017). Indeed, Faegri and van der Pijl (1979) noted that, even though malacophily is often postulated, even the textbook examples lack sufficient evidence. Herbivorous snails and slugs typically feed on soft vegetation (e.g. floral organs), and thus are more likely to impede pollination than enhance it (Suetsugu, 2019). Florivory by slugs can also reduce plant fitness both directly by destroying primary reproductive tissues (e.g. anthers, pistils or ovaries; McCall and Irwin, 2006). Since there are contradictory opinions on malacophily, the ambivalence can be resolved by conducting more accurate research in the future.

Lizards and geckos rarely visit and pollinates flowers, with few recent records that are mostly restricted and frequently recorded on island habitats (Olesen, 2003; Minnaar *et al.*, 2013; Hervías-Parejo *et al.*, 2020) and on inflorescence arrangement suitable for climbing visitors. The high densities that certain taxonomic groupings, like lizards, reach on isolated settings may be explained by the low species richness and,

consequently, a weak interspecific competition and low level of predation (density-compensation phenomenon; MacArthur *et al.* 1972). High densities of lizards on islands with scarce arthropod food, lead to trophic niche expansion into ecological release ('Ecological release'; Bolnick *et al.*, 2010); the term extended to 'interaction release' (Traveset *et al.*, 2015). Galápagos lava lizards, have been observed transporting pollen of various plant species across the islands (Hervías-Parejo, 2020). Also evident in the study made by Nelson (2010) on Canary Islands; Atlantic lizards acting as a pollinator on *Aeonium lancerottense*. As mentioned by Godínez-Álvarez (2004), many species of lizards are omnivorous and drives herbivory; consuming pollen, fruits and nectar and hence may be double mutualistic (Olesen, 2018; Gomes *et al.*,2014), helping in both pollination and seed dispersal. *Roussea simplex,* the sole member of the endemic family Rousseaceae from Mauritius; was once wide spread but is now critically endangered and has a gecko as its sole efficient pollinator (Hansen and Müller, 2009). However, the overall contribution of lizards to pollination may be relatively modest compared to insects and birds (Hervías-Parejo, 2020). Still the fact that lizards do play an important role in pollination and is not 'all bluff'; should be taken into consideration. Mutualistic plant-lizard interactions are prevalent and are studied majorly on biomes of islands, arid highlands, however, it is not still well studied across terrestrial mainland and pollination effectiveness by lizards is also poorly documented.

Bats are highly important pollinators for many night-blooming plant species (Fleming *et al.*, 2009). Pollination by birds and bats occurs in only 3 – 11 % of species (Devy and Davidar, 2003). Bat-pollinated plants are often highly specialized (Stewart *et al.*, 2022) and typically share little overlap with other pollinator groups (Trip and Manos, 2008). Previous research has shown that vertebrate-pollinated plants are more dependent on their pollinators than are insect-pollinated plants, especially in the tropics (Ratto *et al.*, 2018). Furthermore, bat-pollinated plants are more dependent on their pollinators than plants that are pollinated by other vertebrate groups, such as birds or rodents (Ratto *et al.*, 2018). The nectar-specialist species have long muzzles and tongues characteristic of nectarivores (Freeman, 1995), and forage almost exclusively on floral resources (Bumrungsri *et al.*, 2013). In contrast, the primarily frugivorous species have powerful jaws and well-developed molars (Francis, 2008) and while they mainly forage on fruits, they have also been observed foraging at flowers (Bumrungsri and Racey, 2007). Many of these bat-pollinated plant species such as Durian (*Durio zibethinus*), Banana (*Musa acuminata*), Indian trumpet flower (*Oroxylum indicum*), sator (*Parkia speciosa*), and mangrove apple (*Sonneratia spp.*) are ecologically and economically important (Kunz *et al.*, 2011; Stewart and Dudash, 2017; Stewart *et al.*, 2024). Despite their importance, bat pollinators are under studied, in part, because of the difficulty of studying these elusive, nocturnal, and volant animals (Kerth, 2022). Most research examining the effects of anthropogenic stressors on pollinators has focused on insects, but bats are affected by many of the same challenges. Research examining how bat pollinators respond to anthropogenic change is less comprehensive, but studies published to date have highlighted similar overall patterns. Habitat loss and degradation are some of the biggest threats to bats (Jung and Threlfall, 2016; Meyer *et al.*, 2016; Pereira, 2018; Frick *et al.*, 2020). Similarly, Regan *et al.* (2015) found that habitat loss due to agriculture is one of the main drivers of extinction among mammalian pollinators, most of which are bats, and that pollinating bat species tend to be more threatened than non-pollinating bat species. Moreover, flower-visiting bats exhibit dietary shifts in response to changes in landscape structure (Sritongchuay *et al.*, 2019) and climate change can affect the distributions of nectarivores bats and the plant species they pollinate, resulting in spatial mismatch between plants and pollinators (Zamora-Gutierrez *et al.*, 2021). Nonetheless, Leptonycteris nectar-feeding Bats are one of the efficient pollinators of agave spp. (Flores-Abreu *et*

al., 2019; Eguiarte *et al.*, 2021).

New observations (Kobayashi *et al.*, 2019, 2021b) indicate that non-flying mammals play an essential role as pollinators throughout Asia and beyond. Wiens and Rourke (1978) stated that plants suited for pollination by non-flying mammals (NPM) (including rats, marsupials, and primates) have robust, sturdy, dull-colored, cup-shaped flowers that are located at ground level; low shrubby plants with nocturnal anthesis (geoflorous). "Yeasty" or "nutty" odour emerging from the flowers is also a key contributor for attracting non-flying mammals (Rourke and Wiens, 1977). Coloured nectar, an unusual trait found in 67 taxa, is often associated with vertebrate pollination, insularity, and high altitudes (Hansen *et al.*, 2007). In recent advances, with the help of Environmental DNA (eDNA) metabarcoding; a recently developed molecular approach may provide an opportunity to rapidly detect the presence of all floral visitors and pollinators using deposited DNA during plant-pollinator interaction (Newton *et al.*, 2023) which may aid in plant-pollinator interaction studies.

From one of many non-flying pollinators; honey possum, Tarsipesspenserae, has been identified as a significant (Wiens, 1979) however, lesser effective pollinator of southwestern Australia, particularly for the *Banksia attenuata* plant (Wawrzyczek *et al.*, 2024). Other ground dwelling mammals such as rodents, elephant shrew and mongoose have been recognised as pollinators of Colchicaceae (Kleizen *et al.*, 2008), Cytinaceae (Johnson *et al.*, 2011), Ericaceae (Turner *et al.*,2011; Lombardi *et al.*, 2017), Fabaceae (Letten and Midgley, 2009)., Hyacinthaceae (Johnson *et al.*, 2001; Niedzwetzki-Taubert, 2022), Mystropetalaceae (Hobbhahn *et al.*, 2017; Steenhuisen and Hobbhahn, 2018), Orobanchaceae (Wester, 2011) and Proteaceae (Johnson and Pauw, 2014; Cárdenas *et al.*, 2017). Out of many less effective pollinators, mongoose and genets known for their carnivorous diet; have been observed visiting geoflorous flowers and feeding on nectar. They have been termed as pollinators however, more studies are needed to confidently discover their role in pollination (Steenhuisen *et al.*, 2015). *Callosciurus* squirrels and masked palm civets made sure of pollination success of *Mucuna spp.* (Kobayashi *et al.*, 2021a). Frugivorous- Carnivores such as Kinkajou (*Potos flavus*) and Binturong (*Arctictis binturong*) are seen visiting the flowers, foraging on nectar of *Protea* species, because of the sour milk like, cheesy odour emitted by the flowers (Kays,1999; Lambert *et al.*, 2014; Steenhuisen *et al.*, 2015). The role of kinkajous and binturongs as pollinators has not been extensively studied, but they are known to be important seed dispersers in Neotropical forests (Julien-Laferrière, 2001). White-nosed coati (*Nasua narica*) has also been said to pollinate *Ochroma pyramidale* (Bombacaceae) (Mora *et al.*, 2015). Till this date the role of these pollinators is considered as coincidental or is not taken into regard. Further research is needed to fully understand the pollination role of these species.

Conclusion

Bee pollination is indisputable and is the most efficient and ubiquitous way of pollination in agricultural practices. However, there is a dire need in shift of perspective with pollinators other than bee pollinators. These non-bee or secondary pollinators often exhibit unique adaptations and foraging behaviours that compliments the services provided by bee pollinators; ensuring a more robust and resilient pollination network. Pollination systems worldwide are under increasing threat from myriads of anthropogenic factors including habitat fragmentation, habitat loss, climate change, overuse of pesticides, Environmental contaminants like soil nitrogen and heavy metal pollution alters the pollination dynamics by altering the plant- pollinator interaction. Furthermore, the conservation of plant pollinator interaction is a pressing ecological and economic necessity. Hence, further research in recognising the role of secondary pollinators is indispensable, for mitigating the threats posed by

"Pollination crisis".

Ethical Statement

This is a review article hence no Ethical Approval needed.

Author Contributions

Each author has contributed equally to the study's planning, analysis, writing, and editing. All authors have read and agreed to the published version of the manuscript.

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Conflict of Interest

The authors declare no conflicts of interest.

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