



POLLINATORS IN TROPICAL ECOSYSTEMS OF SOUTHERN INDIA WITH EMPHASIS ON THE NATIVE POLLINATORS *APIS CERANA INDICA* AND *TETRAGONULA IRIDIPENNIS*[#]

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ABSTRACT

Ecosystems are rapidly urbanizing at the global and regional scales, particularly in the tropics, which has deleterious effect on hymenopteran pollinators. Based on the literature spanning multiple disciplines including ecology, pollination, agriculture, agroecology and entomology, this review deliberates on the pollinators and their global decline. Also, it turns the focus on honey bees and their role in agroecosystem. Relevant information from melissopalynology is brought together and the gaps and directions of future research on conservation and management of honey bees in tropical peninsular India are discussed. Focus is on the two species of the hived native *Apis cerana indica* F., and *Tetragonula iridipennis* Smith (Hymenoptera: Apidae), as these play a major role in transforming existing agricultural landscapes into agroecosystems, benefitting the farmers and maintaining ecological balance in tropical peninsular India. This review brings to the fore the fact that there is a tangible gap in reports and long-term studies of many native pollinators and in particular the two hived honey bees. Most studies present in a thorough manner visual observations of pollinators (bees) on plants but rarely combine them with quantifying the resources gathered from the plants, especially pollen. This combined approach is especially important to understand the hymenopteran pollinators from the purview of the pollination service they provide. It can be concluded that there is a pressing requirement for long-term observations along these lines with quantifiable pollen and vegetation data to arrive at meaningful plant-pollinator networks that are essential for conservation and management of the native Asiatic honey bees as pollinators.

Key words: Hymenoptera, Apidae, pollinators, agroecosystems, pollinator decline, pollen, melissopalynology, transformation, landscapes, pollination service, management of honey bees, conservation

Pollinators, including insects, bats, and birds, key for ecosystem functioning and global food security, are in dramatic decline over the past decades (Rhodes, 2018). Even if the extent of this decline is a much-debated topic because of the lack of uniform, long-term observations at the global scale there are estimates that should serve as a wakeup call. For example, there is an estimate of a “dramatic decline in average airborne insect biomass of 76% (up to 82% in midsummer) in just 27 years for protected nature areas” in Germany, which considerably exceeds the estimated decline of other animals (Hallmann et al., 2017). Similarly, in the UK and The Netherlands, over 60% decreases in bees and hover flies have been estimated since 1980 (Potts et al., 2010). As many as 200,000 pollinators serve to fertilize around 308,000 species of flowering plants (Rhodes, 2018). Globally, 87 major food crops depend on animal pollination, accounting for 35% of

the world’s food production (van der Sluijs and Vaage, 2016). Worldwide, an estimated 35% of crop production is dependent on insect pollination (Klein et al., 2007). Such dependence on animal pollination, especially insect pollination, underscores the key concern on the decline of pollinators. In tropical peninsular India too, much of the crop production – subsistence and commercial - depend even more on pollinators which is why we focus on this region and in particular on two of its native hymenopterans *Apis cerana indica* F., and *Tetragonula iridipennis* Smith because of their relevance and potential to transform existing agricultural landscapes into agroecosystems. With insect pollination as the focus, this review is written in the framework of ongoing studies including a pilot project aimed at Protection of pollinators and agroecological transitions in the Pondicherry region (POLLIN).

[#]Note: Scientific names given for plants and insects wherever possible, but where the publications have not provided them, it is preferred to retain their common names.

The importance of cross pollination, and specifically by insects, has been stressed since long. Charles Darwin found that the products of cross pollination resulted in more numerous, larger, heavier, more vigorous and fertile offspring, even in species that normally self-pollinate, attributing this result to ‘hybrid vigour’ (Darwin, 1876). Pollinators recognize flowers mostly by olfaction, followed by vision even if nocturnal pollination in several angiosperm families is well established. In turn, plants sometimes offer attractive, but non-rewarding structures to attract pollinators (Borges et al, 2003, 2016) - a fascinating subject beyond the purview of this paper. “Regardless of the type of pollinator, they become dusted with pollen when actively feeding on the nectar and/or pollen of a flower. Pollinators that do not actively feed on nectar, pollen, or plant exudates also become ‘dusted’ with pollen by walking around or in the flowers in search of food, mates, prey, shelter, etc. Thus, pollen is a natural marker on and or in any pollinator” says Jones (2014) in a stand-alone manuscript that provides a “detailed, step by step acetolysis technique” to recover that natural marker from any pollinator.

A great decline in pollinating entomofauna is reported worldwide, especially since the advent of industrial agriculture (van der Sluijs and Vaage, 2016). Globally, pollinator limitation has emerged as a potential risk to crop production and socio-economic stability too (Basu et al., 2011). Ollerton (2015) summarizes the evidence base for this decline, categorized taxonomically and geographically. Wild bees, honey bees, hoverflies, moths and butterflies, wasps, birds and mammals in Europe, North America, Tibet, China, Japan, South and Central America are included in this summary. There are some syntheses for Australia too (Klein et al., 2007). Although there has been a marked increase and interest in the scientific community on this topic in recent years, this has not yet caught popular media attention to the extent that (anthropogenic) climate change has. There is very little synthesis carried out in India (Pannure, 2016). A frequent emphasis has been on highlighting the threat, specifically, to native pollinating Hymenoptera in the areas where *Apis mellifera* L. has been introduced on an industrial scale (Anonymous, Status of pollinators in North America 2007; Allen-Wardell et al., 1998; Biesmeijer et al., 2006; Klein et al., 2007; Potts et al., 2010; Nicholls and Altieri, 2013). From an ecological point of view, Rhodes (2018), in a comprehensive review shows that it is most probable that the decline of pollinating Hymenoptera will be an unavoidable

ecological calamity that cannot be ignored. The review underlines the need for more empirical longer-term studies and data that are both more ‘geographically encompassing and species-inclusive’.

Many drivers, such as population crisis, urbanization and industrialization, deforestation, habitat degradation, poor agricultural practices like mono cropping, applying more pesticides, excessive chemicals and manuring could be the causes of global pollinator decline (Fitch et al., 2019). A recent assessment of pollinator decline for six regions and a global median underlines eight major drivers with land cover and configuration topping the list (Dicks et al., 2021). This paper also highlights as knowledge gap research in Africa, linking human wellbeing and pollinator decline. This could be the case for the Indian subcontinent as well. As several drivers of pollinator decline identified in this paper are likely linked with climate change, this review recommends that a focus on how to mitigate and adapt to it should be central to pollinator research and conservation strategies. These conclusions agree with those of Rhodes (2018), referred earlier. In an earlier paper Solomon Raju et al. (2003) had highlighted another of these eight drivers – the extensive use of genetically modified transgenic crops and other applications like chemicals in agriculture associated with long-term adverse impacts on biodiversity and particularly pollinators, the main risk being ‘gene pollution’.

Honey bees are considered to be the most important among the pollinators of agricultural and horticultural crops and there are several reviews of the same (Nicholls and Altieri, 2013; Yousuf et al., 2020). The value of the honey bee as a pollinator is far greater than its value as a honey producer. Of all the insects, honey bees in hives are the most amenable for crop pollination and can be reared in sufficient numbers and placed in orchards as required for effective pollination. It has been found (Abrol, 2011) that the use of hive bees results in a manifold increase in yields and an improvement in the quality of produce: world honey production is worth around £380,000,000, but the value of insect pollinated agriculture is worth somewhere in the region of £800,000,000,000; this includes the contribution of all insect pollinators, not just honey bees. The term ‘honey bee’ is used widely in both the popular and in serious academic writing referring to *Apis mellifera*, the industrially managed and introduced species. The economic activity of producing honey and bottling it for human use occurs nearly all over the world and the fact that beekeeping has been a part of the social and

scientific consciousness in Europe for several centuries now (Maeterlink, 1901) implies that *A. mellifera* is the most studied pollinating hymenopteran. In addition to *A. mellifera*, nine other different pollinating hymenopteran species, also popularly referred as ‘honey bees’ are recognized, all of them native to Asia, eight belonging to the genus *Apis* (Apidae), the ninth being the stingless bee *Tetragonula iridipennis* (Hymenoptera: Apidae) (Guerin, 2020). Three species of *Apis*, viz., *A. cerana indica*, *A. florea* F., and *A. dorsata* F., and *Tetragonula iridipennis* are the native species of honey bees common in southern India (Ramachandran, 1939; Xavier et al., 2014). Honey bee in this review refers to any and/ or all of this larger subset of corbiculate hymenopteran taxa.

Experimentation on introduction of the exotic *Apis mellifera* in several parts of India dates back to the 1880s (Ramachandran, 1939). In the 1920s and 1930s, large consignments of *A. mellifera* were imported into India, but these first efforts at scientific beekeeping proved unsuccessful. Similarly, the efforts made by private and government agencies in Uttar Pradesh, Punjab, Jammu & Kashmir met the same fate. Later, intensive efforts by the scientists of Punjab Agricultural University (PAU), Ludhiana in 1962 yielded results (Goyal, 1990; Rao and Rao, 1993). In southern India, although *A. mellifera* is still present and continues to be introduced by the government agencies (State Agriculture Departments, National Bank for Agriculture and Rural Development- NABARD), beekeeping with *A. cerana* is more widespread. Beekeeping with the stingless bee *T. iridipennis* is a traditional practice in many parts of Kerala. Wild or feral colonies of all four native species continue to be present in both urban and rural settings and in forests, but as landscapes transform, even these ‘generalist’ species are losing their habitats rapidly.

It is in a broad global and regional context that this review first briefly addresses the pollinators and their global decline and then turn the focus on honey bees and their role in agroecosystems. It also brings together relevant information from melissopalynology and discuss the gaps and directions of future research on conservation and management of honey bees in tropical peninsular India. The focus of this review is on *A. cerana indica* and *T. iridipennis* because of their current relevance and potential to transform existing agricultural landscapes into agroecosystems incidentally benefitting farmers and maintaining ecological balance. This review also highlights the specificity of southern India and contrasts this region

with other places where the introduction of *A. mellifera* has been successful (Koetz, 2013). This review is written within the framework of ongoing studies in the Pondicherry region, that although subject to heavy degradation, shows considerable resilience of the forest patches to anthropogenic pressure (Navya et al., 2017) and hence prompted the ongoing pilot project and a PhD work on pollinators in this landscape and their impact the agrarian system.

Bees in agroecosystems

Pannure (2016) evaluated pollinator decline in India using the TNAU Agritech portal (Tamil Nadu Agricultural University). There is very little integrated information in the public domain on this topic. This portal, with an entire section on “bee flora and pollination of crops” is a ready reckoner that estimates yield increases as high as 112% in *Medicago sativa* (Leguminosae) fields, and 17-19% in *Gossypium* spp. (Malvaceae) due to pollination by bees. The number of colonies/ ha for pollination is given (3 to 9 colonies/ ha) but the portal is ambiguous about the bee species referred to, as common names (Italian bee and the Indian honey bee) or *indica* (*sic*) and *A. mellifera* (*sic*) are all provided. The total acreage of bee-dependent crops in India is c. 50 m ha, but bee colonies are insufficient with only 1.2 million out of the 150 million required, i.e. <1% of the requirement. This underlines the wide scope for expansion of beekeeping for pollination in India. Table 1 lists 41 crops benefited by bee pollination in India, as inferred by us from selected publications, emphasizing the pollinator(s) observed on these crops and clearly underscoring the importance of *A. cerana* and *T. iridipennis* in pollination services.

The agrarian community of India is highly dependent on the production of vegetables such as *Cucumis sativus* (Cucurbitaceae), *Solanum melongena*, *Lycopersicon esculentum*, *Capsicum annuum* (Solanaceae), and *Allium cepa* (Amaryllidaceae) (Table 1). Approximately 70% of the tropical vegetable crop species produced are dependent on the activity of Apidae, which optimize the yield of most of these commodities (Roubik, 1983; Klein et al., 2007). Species of the Apidae are considered the best pollinators due to their speed of work, longer working time, large populations, migratory behaviour and their floral fidelity. Indirect benefits through pollination of certain crops such as coffee with Apidae population have increased the fruit set up to 83% (Deodikar and Suryanarayana, 1973). Among the other native Apidae, the major forage plants of *A. florea* in many parts of tropical peninsular India (Sambasiva

Table 1. Key crops that benefit from bee pollination

No.	Family	Botanical name	Common name	Pollinator(s) observed
Cereals and pulses				
1	Poaceae	<i>Triticum aestivum</i> L.	Wheat	(a)*
		<i>Oryza sativa</i> L.	Rice	(b)**
2	Leguminosae	<i>Vigna radiata</i> (L.) R. Wilczek	Mung Bean	(c)•
Oil seeds				
3	Asteraceae	<i>Helianthus annuus</i> L.	Sunflower	(a)*, (f)*
4	Pedaliaceae	<i>Sesamum indicum</i> L.	Gingelly	(b)**; (d)*; (g)•
5	Leguminosae	<i>Arachis hypogaea</i> L.	Groundnut	(c)•
Vegetable crops				
6	Amaranthaceae	<i>Amaranthus</i> sp.	Amaranthus	(d)
7	Amaryllidaceae	<i>Allium cepa</i> L.	Onion	(a)*
8	Leguminosae	<i>Cyamopsis dentata</i> (N.E.Br.) Torre	Cluster bean	(a)*
9	Cucurbitaceae	<i>Cucumis melo</i> L.	Muskmelon	(a)*
		<i>C. sativus</i> L.	Cucumber	(a)*
		<i>Cucurbita pepo</i> L.	Pumpkin	(a)*
		<i>Benincasa hispida</i> (Thunb.) Cogn.	Ash gourd	(d)*
		<i>Sechium edule</i> (Jacq.) Sw.	Chayote	(j)*
		<i>Trichosanthes cucumerina</i> L.	Snake gourd	(d)*
10	Malvaceae	<i>Abelmoschus esculentus</i> (L.) Moench	Okra	(b)**; (c)•
11	Solanaceae	<i>Solanum melongena</i> L.	Brinjal	(a)*
		<i>Capsicum annuum</i> L.	Chilli	(b)**
		<i>Lycopersicon esculentum</i> Mill.	Tomato	(b)**
12	Moringaceae	<i>Moringa oleifera</i> Lam.	Drumstick	(a)*
Fruit crops				
13	Anacardiaceae	<i>Mangifera indica</i> L.	Mango	(a)*
14	Lythraceae	<i>Punica granatum</i> L.	Pomegranate	(a)*
15	Cucurbitaceae	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	Watermelon	(a)*
16	Rutaceae	<i>Citrus aurantiifolia</i> (Christm.) Swingle	lime	(a)*
		<i>C. aurantium</i> L.	Orange	(a)*
		<i>C. limon</i> (L.) Osbeck	Lemon	(b)**; (h)*; (e)•; (g)•
17	Musaceae	<i>Musa</i> sp	Banana	(b)**; (d)**
18	Myrtaceae	<i>Psidium guajava</i> L.	Guava	(b)**
19	Rosaceae	<i>Malus pumila</i> Mill.	Apple	(i)•
20	Moraceae	<i>Artocarpus heterophyllus</i> Lam.	Jack Fruit	(b)**
Flower crops				
21	Rosaceae	<i>Rosa damascene</i> Herrm.	Rose	(a)*
Plantation crops				
22	Arecaceae	<i>Cocos nucifera</i> L.	Coconut	(b)**; (d)*
		<i>Borassus flabellifer</i> L.	Palmyra palm	(c)•
23	Rubiaceae	<i>Coffea benghalensis</i> B. Heyne ex Schult.	Coffee	(b)**; (d)*
24	Myrtaceae	<i>Eucalyptus</i> spp.	Eucalyptus	(c)•; (d)**
Medicinal plants				
25	Meliaceae	<i>Azadirachta indica</i> A.Juss	Neem	(e)•; (d)*; (k)**•
26	Phyllanthaceae	<i>Phyllanthus emblica</i> L.	Indian Gooseberry	(e)•
27	Rutaceae	<i>Murraya koenigii</i> (L.) Spreng.	Curry tree	(e)•
28	Lamiaceae	<i>Ocimum tenuiflorum</i> L.	Thulsi	(e)•; (d)*
Cash crops				
29	Anacardiaceae	<i>Anacardium occidentale</i> L.	Cashew nut	(b)**
30	Malvaceae	<i>Gossypium hirsutum</i> L.	Cotton	(d)*

Pollinator(s) (**Apis cerana*; **Tetragonula iridipennis*; • Honey bees) observed and reported by: Bhalchandra et al. (2014) (a); Singh et al. (2016) (b); Chaudhary (2001) (c); Gowda et al. (2020) (d); TNAU Agri-Tech portal (2021) (e); Slaa et al. (2006) (f); Kumar et al., (2015) (g); Abrol (2012) (h); Dulta and Verma (1987) (i); Mukherjee et al., 2019 (j) and Sundararaju (2011) (k), help illustrate the importance of the focal bee species of this review, in pollinating a wide range of plants.

Rao et al., 2015; Vidhya et al., 2019) were trees such as *Pongamia* (Leguminosae), *Azadirachta indica*, *Citrus* sp., and *Albizia* sp. (Leguminosae). *Anacardium occidentale* was visited for nectar collection alone (Sundararaju, 2011) by all three native *Apis* spp. (*A. florea*, *A. cerana indica* and *A. dorsata*) while the stingless bee (*T. iridipennis*) collected both nectar and pollen grains. In addition to the focal bee species (Table 1), Sundararaju (2011) found that four other bee species from coastal Tamil Nadu: *Ceratina (Pithitis) binghami* (Hymenoptera: Apidae), *C. smaragdula* (Hymenoptera: Apidae), *Braunsapis* sp (Hymenoptera: Apidae) and *Pseudapis oxybeloides* (Hymenoptera: Halictidae), also visited the flowers of this important cash crop (cashew) and were found carrying pollen grains on their legs and body hairs.

Apis cerana are desirable pollinators for a range of crops and specifically crops such as *Sesamum indicum* (Pedaliaceae) and *Helianthus annuus* (Asteraceae). Managed populations of *A. cerana* maintained in hives start foraging early in the morning until late in the evening for long time durations proving their efficiency in pollination. *Apis cerana* are more effective in pollination only when the colony occurs close to a crop field. They spend more time foraging, with high flight time, to the floral source (Abrol, 2012). Numerous agricultural and medicinal plants are visited by *T. iridipennis* (Roopa et al., 2017), which is also an established pollinator of vegetable crops such as *Sechium edule* (Cucurbitaceae) and is considered a critical pollinator, influencing positively the fruit-to-flower ratio (Mukherjee et al., 2019) (Table 1). While conventionally the Apidae are always correlated with pollination services, a study in New Jersey, USA found that native bees alone provide sufficient pollination at > 90% of farms, since the total pollen deposit in flowers was strongly, significantly correlated with native bee visits and not with the introduced *Apis mellifera* visits (Winfrey et al., 2007). At the time of this study, honey bees were undergoing extensive die-offs because of 'colony collapse disorder' (Stokstad, 2007 a, b) and in New Jersey native bees had the potential to buffer the drop in agricultural productivity.

In contrast, in a region such as India with a native population of diverse Apidae, in Aurangabad district, where *A. mellifera* is an introduced species, only a few *A. cerana* were observed, while *A. florea* and *A. dorsata* were more abundant (Waykar and Baviskar, 2015). Given the close proximity in size of *A. cerana* and *A. mellifera*, it seems that the former faces the

brunt of competition from the introduction of the latter. Interactions between the Apidae and flowering plants are excellent examples to understand co-evolution and mutualism. There is a need to understand bee –plant relationships to study food preferences of the Apidae and pollination (Shubharani et al., 2013). Bees are also site-specific and repeat their foraging paths (Janzen, 1971) because of which pollination by Apidae were considered to be the most important component of increasing the crop yields in agriculture.

Apis cerana

Smith and Hagen (1996) studied the distribution of the cavity-nesting *A. cerana* that extends from Iran to China and from Japan to southern Indonesia. In this extensive distribution, *A. cerana* occupies a wide range of habitats, such as rock crevices, tree hollows, gulleys. It has also been introduced into Australia, although not to the same extent as *A. mellifera* has been, where it is considered alien and invasive (Clarke et al., 2021). Unravelling the genetic diversity of *A. cerana*, an indigenous strain, is essential since it would unveil some useful elements on breeding strategies to honey bee farmers. Molecular genomics of colonies of *A. cerana* from 10 localities of Nilgiri Biosphere reserve revealed the taxonomy of two subspecies of *A. cerana*: *A. cerana cerana* (the black strain) and *A. cerana indica* (the yellow strain). The results suggested that mobile beekeeping has resulted in genetic recombination of different strains of the same species (Chalapathy et al., 2014).

Among the Asian honey bee taxa, *A. cerana* is a medium-sized honey bee (11.46± 0.091 to 12.74± 0.070 mm (Baskaran and Thiyagesan, 2013), smaller than the giant Asian honey bees *A. dorsata* and the Himalayan honey bee *A. laboriosa* Smith (Hymenoptera: Apidae)), larger than the dwarf Asian honey bees (*A. florea*). *Apis cerana indica* is the only *Apis* that has been domesticated in India (Ramachandran, 1939). In China and India, while almost all *A. mellifera* are managed and all *A. dorsata* run wild, it is difficult to distinguish between wild and managed *A. cerana* with any degree of certainty (Senapathi et al., 2021). Both *A. cerana* and *A. mellifera* look similar to an unaided eye. But, *A. cerana* is striped in the abdomen with evenly spaced black bands spreading left to right on the abdomen. However, colouration is highly variable in nature, and the most reliable morphological characteristic that distinguishes *A. cerana* is the extension of the radial vein on the hind wing, which is prominently absent in *A. mellifera* (Ruttner, 1988). Both *A. cerana* and *A.*

mellifera have pollen baskets on their hindlegs which allow the bees to transport pollen from flower to the hive which is composed of honey combs for storing nectar and pollen.

Foraging range of *A. cerana* varies in different locations, but generally it will occur within a maximum of 1500-2000 m (Dhaliwali and Sharma, 1974). It has a very wide range pollination of crop plants (Table 1), likely due to its long glossa which allows access to a wide range of plants (Deodikar, 1960). On a single foraging trip, *A. cerana* tend to collect either pollen or nectar (not both); on any given day, during daylight hours, they tend to forage on the same species (Corlett, 2011). Foraging time often depends on weather parameters, available floral resources and competition with other honey bee species. Some studies suggest that the introduction of honey bees (*Apis* spp.) may also have negative impacts, such as competition with the native pollinators for available floral resources, competition for nesting sites, co-introduction of nesting enemies, especially pathogens that infect the native organisms, disruption of pollination services of native plants and pollinating exotic weeds. Thus the ecological impacts of cavity occupancy by introduced honey bees (*Apis* spp.) gone feral is a subject that needs a complete review by itself (Goulson, 2003; Saunders et al., 2021).

Tetragonula iridipennis

Stingless bees (Apidae: Meliponinae) consist of two genera- *Melipona* and *Trigona*. Meliponinae includes eight genera, having 15 subgenera and 500 species (Grüter, 2020; Slaa et al., 2006), and *Melipona* includes 40 species, all of which remain restricted to the Neotropics (Camargo et al., 1988), amongst which *Melipona iridipennis* Smith is the most common species found in India. This species was subsequently renamed, initially as *Trigona iridipennis* and finally *Tetragonula iridipennis*. It was first described from Ceylon (presently Sri Lanka) by Smith (1954). Later, the same species was reported from India (Sakagami, 1978; Swaminathan, 2000; Danaraddi et al., 2009). These bees are commonly known as dammar bees in India (Rasmussen, 2013). Apart from *T. iridipennis*, seven other stingless bee species were also reported from India with their abundance in southern part of India (Rasmussen, 2013). This species is characterized by wings with brilliant iridescence (Swaminathan, 2000). Its body length is 3.5-4.0 mm, with stingers much reduced. This stingless, small honey bee species uses its mandibles as the organ of defence to protect their nests from the intruders.

Tetragonula iridipennis has the ability to visit a wide range of flowers and plant species, especially of the understory herbs (Table 1). It uses a field-based communication mechanism to a specific food location. Field-based communication mechanisms include scent trailing, food-site marking, and potentially aerial odour trails (Grüter, 2020). The members live in permanent eusocial colonies usually of thousands of female workers, a reproductive queen, and male drones. The nesting sites of this bee are tree trunks and wall cavities (Danaraddi et al., 2009). Majority of the nests occur in cavities of live trees (Roubik, 1983). The combs of *T. iridipennis* are made of a dark 'cerumen', a mixture of wax and resin which is the material used to build brood, honey and pollen pots. They are efficient pollinators because of their small size and their ability to forage the flowers of different sizes and shapes as listed in Table 1. Earlier studies on stingless bees were conducted on biology, nesting behaviour, morphometric characters, foraging behaviour and melissopalynology (Batista et al., 2003; Roubik, 2006). Vijayakumar and Jeyaraj (2016) have studied its distribution in southern India. However exclusive studies on species diversity of *Tetragonula* in different parts of India are lacking.

Melissopalynology

Studies conducted in Melissopalynology in India have generally been focused on *A. cerana* (Fatima and Ramanujam, 1989; Garg and Nair, 1993; Jhansi et al., 1994; Chakraborti and Bhattacharya, 2015) although there has been considerable interest in *T. iridipennis* too recently (Ponnuchamy, 2014; Vijayakumar and Jeyaraj, 2016; Bisui et al., 2019). Pollen data, be it from honey or from bee-loads is quantifiable and such an approach can contribute better to understanding the true impact of pollinators especially in agroecosystems, as also the surrounding vegetated lands, for example addressing questions such as specific crops that are visited, in connection with determining the possibility of pollen transport and potential cross pollination with related wild plants in the surrounding environment.

Pollen from honey samples collected by *A. cerana* from some districts of Andhra Pradesh in the southern part of India, showed that the honeys originate from two discrete floristic regimes: deciduous forests (Visakhapatnam and East Godavari) and agricultural tracts (Guntur) (Jhansi et al., 1994). The East Godavari district honey was unifloral and the remaining samples were multifloral which in turn shows that *A. cerana* adapts to different floral regimes. Similar studies were

carried out in Dharmapuri, Tamil Nadu (Agashe and Mary Scinthia, 1995) and in Hyderabad, Telangana (Fatima and Ramanujam, 1989). Another study in the Pondicherry region focussing on understanding the foraging behavior of *A. cerana* using classical melissopalynology (pollen from honey) over a three-year period used a statistical approach to show that pollen spectra were equally comparable between locations and also between months and years. This study demonstrated the complexity of ecological/environmental phenomena involved in the process of foraging by bees in a heterogeneous and complex landscape (Ponnuchamy et al., 2014). Foraging preferences of *A. cerana* in Madurai district, Tamil Nadu during summer in relation to seasonal and diurnal variations and flower availability revealed that specific groups of worker bees responded differently to the weather parameters. Among all the factors examined, wind velocity bore a negative impact on the foraging activity of bees (Hemalatha et al., 2018)

In Bankura District of West Bengal, *T. iridipennis* foraged on diverse angiosperm flora supporting the broad polylectic foraging of the bee species, and most of the visited plants were trees with flowers coloured yellow, white, and cream; these bees were considered small-sized by Layek and Karmakar (2018). Pollen loads of *T. iridipennis* revealed that the bee preferred trees with small sized flowers as a source of pollen and also that pollen diversity was higher in rural areas in comparison with urban areas (Bisui et al., 2019). Pollen loads from *T. iridipennis* hives nesting in wall crevices (Hyderabad) revealed that a major part of the pollen came from *Prosopis juliflora* followed by *Peltophorum pterocarpum* (Leguminosae) and *Cocos nucifera* (Ramanujam et al., 1993).

CONCLUSIONS

Most studies present in a thorough manner visual observations of pollinators (bees) on plants but rarely combine them with quantifying the resources gathered from the plants, especially pollen. This combined approach is especially important to understand the honey bees from the purview of the pollination service they provide. Pollen collection by *T. iridipennis* can also be considered antagonistic for the plant and partly beneficial for both the bee and the plant, especially on plants which produce flowers with small amount of pollen as most of the pollen meant for pollination is removed (Sambasiva Rao et al., 2015). Plants can mitigate the fitness costs associated with consumption

of their pollen by honey bees, by optimizing pollen release rates. Especially in buzz-pollinated plants, bees apply vibrations to remove pollen from anthers with small pores. These poricidal anthers potentially function as mechanism staggering pollen release (Kemp and Vallejo-Martin, 2021). Wild bees such as the carpenter bee (*Xylocopa* spp (Hymenoptera: Apidae)), blue banded bees (*Amegilla cingulata* (Hymenoptera: Apidae)) and other solitary bees also play a major role in pollination of tropical dry forests. Carpenter bees are more effective pollinators in crops like Solanaceae (tomatoes (*Solanum lycopersicum*) and brinjal (*Solanum melongena*)), that require buzz pollination as do Legumes (eg., *Cassia*). Usually, carpenter bees nest in tunnels bored into wood or hollow stems (bamboo) (Kevan et al., 1990). We found *T. iridipennis* nesting on *Mangifera indica* (Anacardiaceae) and *Ficus benghalensis* (Moraceae) trees in and around Pondicherry. They also inhabit the urban or built environment using niches like doors, windows, walls of the old buildings and also electric switch boxes.

A study on *Abelmoschus esculentus* (Malvaceae) crop ecosystem was conducted in Bangalore (Nandhini et al., 2018). Due to golden yellow flowers and nectaries, this plant is freely visited by honey bees, bumble bees, ants, butterflies and other insects during flowering period. The study revealed that *Apis* spp were the most dominant flower visitors (41.75%) followed by *Lasius niger* (Hymenoptera: Formicidae) (34.23%) and *Solenopsis invicta* (Hymenoptera: Formicidae) (24.02%). This is in agreement with the preliminary pollinator surveys conducted by us in the Pondicherry region on *Abelmoschus esculentus* crop ecosystem. The decline in wild bee faunal diversity has been strongly correlated to decline in wild flowers (Biesmeijer et al., 2006). When a patch of naturally occurring weeds within a managed farmland was removed, simultaneously that created a decrease in yield in the main crop sown within the same cropping season. Conversely, an increase in non-crop flowering species improves pollinator diversity. Field margins or bunds sown with a range of different annual and perennial flowering species result in variable improvements in the diversity and abundance of bees and other pollinators, depending on plant composition, seasonal flowering patterns and bee forage preferences (Carvell et al., 2007). There is also a long-standing theory that co-flowering plants may facilitate pollination rather than competing for it (Sletvold et al., 2016).

In the tropical peninsular Indian scenario, many

of the under-utilized common, mostly herbaceous, weedy plants that are edible, pan-tropical and flowering almost throughout the year, are important for both the pollinators to thrive and for the farmers in the agroecosystem (Sengupta, 2015). The persistence dynamics of most weed species in arable land are largely driven by insect pollination; the frequency of flower visited by insects is a good parameter for classifying a weed's pollination strategy (Loose et al., 2005; Lunau et al., 2006; Mahale, 2019). Pollinator declines can result in loss of pollination services which have important negative ecological and economic impacts that could significantly affect the maintenance of wild plant diversity, wider ecosystem stability, crop production, food security (Abrol, 2011). Annual mass flowering crops temporarily change the floral resource availability which in turn modifies the pollinator preferences and their stability in weed pollinator networks. (Schleuning et al., 2012; Mahale, 2019). Thomas et al. (2009) in the Nilgiri Biosphere Reserve, studied the diversity of social bees at 15 sites along with floristic analyses of local vegetation at each site. A Bee Importance Index (BII) was developed to obtain a measure of the bee diversity at each site. Seventy three plant species were identified as social bee plants and of them 45% were visited by one species of bee (*Apis cerana*), 37% by two bee species (*Apis cerana*, *Trigona* sp.) and 18% by more than two bee species (*Apis cerana*, *A. florea*, *A. dorsata*, *Trigona* sp.) indicating a certain degree of floral specialization among bees. Much value can be added to such studies by linking them with the analyses of the key resource gathered from the plants, pollen.

Along similar lines, Melissopalynology studies are found in various geographies of India and in different part of the world, but their main focus has been on characterizing the geographic origins as also some physiochemical parameters of honey, all targeting the honey market (Chakraborti and Bhattacharya, 2015). However, as a robust, quantifiable tool, palynology can be used much more effectively in understanding honey bee-plant relationship and can help demonstrate the complexity of ecological and environmental phenomena involved in the process of foraging by bees in heterogeneous and complex landscapes (Ponnuchamy et al., 2014). Given the direction of landcover and land use changes the world over, there is scope for further research from this angle too. Such a synthetic approach has been attempted in our ongoing studies, mentioned at the end of the Introduction. We analyse pollen loads as well as honeycombs: a) corbicular loads and comb samples from the hived bee *A. cerana* and b) pollen

collection from the pollen pots in the *T. iridipennis* hives. Plant flowering phenology and plant-pollinator surveys are conducted in parallel to pollen analyses. In the laboratory, the bee pollen loads were examined directly under the microscope and after chemical processing using acetolysis (Jones, 2014).

A comparison of observations from the ongoing studies and some published literature provided a set of 34 pollen/ plant taxa that are important for bee forage, especially the focal species of the review (Table 2). In the Pondicherry region nearly 22 have been stable for well over a decade and regionally, some taxa, over three decades (Ponnuchamy et al., 2014). Taxa such as *Antigonon leptopus* (Polygonaceae) and *Evolvulus alsinoides* (Convolvulaceae), though frequent in the field observations were not widely reported as bee or pollinator friendly; the former is an important nectar source and the latter preferred for the nutritive value of its pollen like other herbaceous plant species like *Euphorbia cyathophora* (Euphorbiaceae) and *Mimosa pudica* (Leguminosae) (Table 2). The list consists of a mix of the native TDEF vegetation and local crops and plantations. One extra regional study at sub temperate Bhimtal in Himachal highlighted common floral resources such as Asteraceae, Lamiaceae and Poaceae. In India, 41 key crops that depend on bees for pollination services have been listed from the literature already (Table 1). These results, particularly the overlap in the bee visited flora and the crops, further validate the win-win situation for agroecosystems that choose to diversify the available floral resources for the focal bee species of this review (*A. cerana* and *T. iridipennis*).

Observations of the authors on the field of *T. iridipennis* and *A. cerana* visiting plants such as *Cocos nucifera*, *Sesamum indicum*, *Talinum portulacifolium* (Talinaceae) were validated by the analyses of the pollen loads they carried. From the diversity of sites in and around Pondicherry, it is clear that several bees are generalist visitors to a range of available plants, though some loyalties to the plants that flower regularly throughout the year or mast flower seasonally are observed. *Cocos nucifera* is a steady source that flowers every month regularly and is available all through the year to the bees (Jay, 1974) and this is in agreement with our findings in the ongoing studies; in contrast, the focal bee species also utilize resources like *Syzygium cumini* (Myrtaceae) and *Peltophorum pterocarpum*, which mast flower (Table 2). At one of the study sites around Pondicherry, a farmer shared his observations of a marked decrease in fruit drop in his coconut trees

Table 2. Flora visited by the focal bee species- field and microscopic observations, ongoing study around Pondicherry and also those reported elsewhere

No.	Plant species/ pollen taxa	Where and when observed in the literature	
		Place	Year(s) of observation
1	<i>Lannea coromandelica</i> (Houtt.) Merr.*	Pondicherry	2007-2009
2	Phoenix*	Pondicherry	2007-2009
3	Casuarina**	Pondicherry	2007-2009
4	Commelina*	Pondicherry	2007-2009
5	<i>Fluggea leucopyrus</i> Willd.*	Pondicherry	2007-2009
6	<i>Leucaena leucocephala</i> (Lam.) de Wit.*	Pondicherry	2007-2009
7	<i>Peltophorum pterocarpum</i> DC.Backer ex K. Heyne.**	Pondicherry	2007-2009
8	Liliaceae*	Pondicherry	2007-2009
9	Boerhavia*	Pondicherry	2007-2009
10	<i>Sesamum indicum</i> L.**	Pondicherry	2007-2009
11	Ixora *	Pondicherry	2007-2009
12	<i>Dodonaea viscosa</i> (L.) Jacq.*	Pondicherry	2007-2009
13	<i>Tribulus terrestris</i> L.*	Pondicherry	2007-2009
14	<i>Borassus flabellifer</i> L.*	Pondicherry, Andhra Pradesh	2007-2009, 1982
15	Phyllanthus*	Pondicherry, Andhra Pradesh	2007-2009, 1982
16	<i>Cocos nucifera</i> L.**	Pondicherry, Karnataka, Andhra Pradesh	2007-2009, 2010-2012, 1982
17	<i>Syzygium cumini</i> (L.) Skeels**	Pondicherry, Karnataka, Andhra Pradesh	2007-2009, 2010-2012, 1982
18	<i>Mimosa pudica</i> L.*	Pondicherry, Karnataka	2007-2009, 2010-2012
19	Eucalyptus**	Pondicherry, Karnataka	2007-2009, 2010-2012
20	Asteraceae***	Pondicherry, Bhimtal, Karnataka, Madurai	2007-2009, 1994, 2010-2012, 2016-2017
21	Lamiaceae***	Pondicherry, Bhimtal, Karnataka, Madurai	2007-2009, 1994, 2010-2012, 2016-2017
22	Poaceae***	Pondicherry, Bhimtal	2007-2009, 1994
23	<i>Psidium guajava</i> L.**	Karnataka	2010-2012
24	Euphorbia*	Karnataka, Madurai	2010-2012, 2016-2017
25	Coffea**	Karnataka, Pondicherry	2010-2012
26	<i>Canthium coromandelicum</i> (Burm.f.) Alston*	Pondicherry	2003-2006
27	<i>Memecylon umbellatum</i> Burm.f.*	Pondicherry	2003-2007
28	<i>Solanum melongena</i> L.**	Coimbatore	2011-2013
29	<i>Solanum lycopersicum</i> L.**	Coimbatore	2011-2013
30	<i>Capsicum annum</i> L.**	Coimbatore	2011-2013
31	<i>Abelmoschus esculentus</i> (L.) Moench**	Coimbatore	2011-2013
32	<i>Momordica charantia</i> L.**	Coimbatore	2011-2013
33	<i>Trichosanthes cucumerina</i> L.**	Coimbatore	2011-2013
34	<i>Anacardium occidentale</i> L.**	Karnataka	2003-2008

TDEF vegetation (*); local crops and plantations (**); extra regional commonalities (***); first remain stable well over a decade in Pondicherry; the duration of observations varies between 1-5 years with most of them 2-3 years only highlighting the lack of long-term observations.

Out of 34 taxa observed in the ongoing studies the first 22 had been reported by Ponnuchamy et al (2014) from the same study area; 14-17 were recorded elsewhere earlier by Jhansi et al (1994); 16-21 & 23-25 by Subharani et al. (2013); 20-22 also by Garg (1996); 20-21 also by Hemalatha (2018) who recorded 24 as well. Nayak and Davidar (2010) report 26-27, two species that are characteristic of the Coromandel Coast while Davidar et al. (2010) report 28 to 33 from Coimbatore and Sundararaju (2011) 34 from Karnataka; 25 was reported in a review work by Deodikar and Suryanarayanan (1973)

within a few months of introducing both *A. cerana* and *T. iridipennis*. In the same site, where abundant pollinators' populations were observed, it was found that hedges and fences were planted with crop species like *Sesamum indicum* and weed plants like *Spermacoce hispida* (Rubiaceae), *Sida acuta* (Malvaceae), *Croton bonplandianus* (Euphorbiaceae) and *Tribulus terrestris* (Zygophyllaceae) were commonly reported.

Weeds have considerable value in supporting the lives of flower visiting insects, especially pollinators though it has been considered by some that weeds are predominantly self-pollinating (Sutherland et al., 2004). It has been observed in the ongoing studies that many weeds including the ones cited in Sengupta (2015), that occur in the vicinity of the crop lands and forested vegetation, do attract pollinators; these include common weedy plants such as *Tridax procumbens* (Asteraceae), *Asystasia gangetica* (Acanthaceae), *Tribulus terrestris* visited by many insect pollinators including the focal bees species of this review (Table 2). Therefore, it would be worthwhile to identify such plants in the surroundings of the landscapes to "trap" the pollinators inside in order to effectively reap the pollination services rendered by them. In urban settlements, road side plants, often considered weeds, attract pollinators like honey bees. Road side ornamental plants like *Turnera subulata* (Passifloraceae), *Tecoma stans* (Bignoniaceae), that are preferred by *A. cerana* and *T. iridipennis* can be planted and managed to enhance the populations of these bees.

In India, managed *Apis cerana* is a better pollinator than *A. mellifera* because of its longer foraging period (Sihag and Mishra, 1995). In Himachal Pradesh, Gupta et al., (1984) observed in *Plectranthus rugosus* (Lamiaceae) flowers that *A. cerana* foraged longer hours, starting early in the morning, than *A. mellifera*, though the latter was more efficient in gathering nectar. But it was found out in Fuzhou, China (Zhang et al., 2019) that *A. cerana* workers make more foraging trips, live longer and consume less sugar, partly due to smaller size, suggesting that *A. cerana* performs better than *A. mellifera* at the community level. This work also indicated that *A. cerana* is better adapted to scattered nectar sources than *A. mellifera*, which will starve at the same location. A study conducted in West Bengal (Bhattacharya et al., 2017) inferred that the age-old tradition of associating bees with honey and *Apis* seems to have strongly influenced the bee knowledge of the farming families whose knowledge on the other native bee species was limited. In India, the knowledge

of the right pollinators for most crops is not available. Little is known about the status of bee pollinators in the wild and their population dynamics, life history, habitat requirements, pollinator interactions with other elements of crop and crop associated biodiversity, the ecology of pollinators, or the ultimate consequences of their decline (Pannure, 2016).

The notion of scientific beekeeping in India goes back to at least the beginning of the 20th century (Ramachandran, 1939) and there has been a fascination with the idea that this can serve the farmers as an alternate source of easy income as honey is an important commercial product. However, since the floral sources in tropical peninsular India are generally available round the year, unlike in Europe, there is no necessity for the bees to store excess quantities of honey in their hives, and moreover, *A. cerana* doesn't store as much honey as does *A. mellifera* (Abrol, 2012). Our results highlight the role of the focal (native) honey bees (*A. cerana* and *T. iridipennis*) in pollination and suggest beekeeping with these species; the protection of their floral sources will sustain them in the ecosystem and consequently serve the agroecosystem. To accommodate the various pollinators, weeds, wild herbaceous plants, shrubs and trees, must be available which will allow the wild and managed pollinators to thrive well and adapt. This review senses a tangible gap in reports and long-term studies of many native pollinators and in particular the two hived Asiatic honey bees in South India. This review would like to put on record a pressing requirement for long-term observations comprising visual observations with quantifiable pollen and vegetation data to arrive at meaningful plant-pollinator networks.

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