Foraging behaviour and niche differentiation in two South Asian bee species

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I certify that all material in this dissertation which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Abstract

Pollination across the tropics, including in South Asia, is dominated by social bees. I investigated the behaviour of two species: *Apis cerana* (Eastern honeybee) and *Tetragonula iridipennis* (Indian stingless bee) which co-exist in the same environment. The behaviour of these pollinators is somewhat understudied, and this work aims to fill some of the gaps in our knowledge Given the differences in size, colony organisation, and recruitment strategies, I hypothesised that there may be niche partitioning, perhaps mediated by spatial or temporal distribution. I analysed pollen from both species to assess their use of plant resources and found that the two species used different sources, and this is context-dependent. I performed an artificial feeder experiment to investigate the foraging distance of each species. The results indicate that *A.cerana* has a longer foraging range than *T. iridipennis* and may be a more efficient forager. Finally, I recorded the daily activity patterns of both species, which show similarities in general foraging activity. However, the results also show that the species may have different temporal patterns with regard to pollen foraging. Temperature also influences activity and pollen foraging in *A. cerana* but not in *T. iridipennis*. These behavioural differences may be mediating niche differentiation between the two species.

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Chapter One: Literature review

Introduction

Apis cerana and *Tetragonula iridipennis* are both key pollinators in the South Asian tropics, yet their behaviour remains critically under-studied. This literature review aims to assess the current state of knowledge on these two species, particularly regarding foraging behaviour and resource partitioning, and place this research within a broader context of tropical conservation and pollination ecology.

I start with a discussion of tropical conservation, including the concept of biodiversity hotspots, and emphasising knowledge gaps regarding insect conservation. I move on to discuss pollination ecology, examining major concepts and the effects of land use change and agriculture on pollinators and pollination services. The penultimate section will apply these themes to the particular case of the Western Ghats, a densely-populated biodiversity hotspot in which social bees dominate pollination, and human activity has shaped much of the landscape. Finally, I focus on the ecology and foraging behaviour of the two species, and the potential for resource partitioning or competition between them.

Tropical conservation ecology

Species diversity

The tropics harbour a large share of global biodiversity, both in terms of species richness and species endemism. It is estimated that over half of all species are found in the tropical rainforests[3,4]. In particular, plant diversity is exceptionally high in tropical regions, creating varied ecosystems in which a plethora of animal species can thrive[5,6]. Indeed, many vertebrate taxa, including birds, mammals, amphibians and reptiles are also highly diverse in these areas. Similarly, there is high diversity of invertebrates;[7,8] however, these tend to be understudied, despite accounting for at least 80% of all described species[9,10]. As Cardoso et al.[9] argue, the lack of data regarding invertebrate species is one of the major obstacles to their conservation.

As of 2015, the IUCN Red List of Species had assessed 61% of described vertebrates, but only 1.3% of invertebrates[11]. This data discrepancy between vertebrates and invertebrates cuts across all invertebrate taxa in tropical regions[12], but there have been attempts to assess particular insect groups or areas of forest to gauge levels of diversity[13]. However, within insects, the focus is generally on Lepidoptera and Odonata and many large groups including Hymenoptera are still massively underrepresented[9,14]. Indeed the Odonata were the first and currently sole insect order to be globally assessed, less than a decade ago[12].

Sampling in tropical regions can be problematic for many taxa as some areas have poor infrastructure and are less accessible.[10,15] Invertebrate species are often even harder to observe, and focus tends to be on those groups with wide distribution ranges and high dispersal[14]. Furthermore, more "charismatic" animals, for example birds and large mammals, have historically received a disproportionate level of attention from both conservation ecologists and funding bodies[15,16]. This is often defended by reliance on the concept of vertebrate “umbrella species”, usually birds or mammals. However, the presence of mammalian umbrella species does not always reflect higher overall species richness[17]. The concept has also been criticised for not taking into account the differences in ecological needs between large vertebrate species and the species under their “umbrella”[18,19]. This is particularly apparent when only area requirements are considered, as is often the case when using large mammals in protected areas as umbrella species for smaller mammals and invertebrates[19]. Sometimes insects, often butterflies, are themselves used as umbrellas, but this can also have limitations. Generally, umbrella species are more effective when more closely related to the species they are “sheltering”; for example in a study on endangered beetles in Sweden, in which the hermit beetle (*Osmoderma eremita*) was successfully used an indicator for other beetles[20]. However, the author adds the caveat that some species may be more sensitive to changes such as habitat fragmentation[20]. The conservation of vulnerable and under-studied species evidently cannot rely on those which receive the most attention.

From species to ecosystems

One way to promote invertebrate conservation in the face of data scarcity is to consider ecosystems and regions, as opposed to single species. The last few decades have certainly seen a shift in conservation discourse away from a focus on key species, and towards a more holistic approach. Furthermore, another limitation of the Red List of Species is that it is on a global scale, rather than a local one, thus perhaps not taking into account the particular idiosyncrasies of individual ecosystems[21].

When Norman Myers first coined the term "biodiversity hotspot" in 1988, it provided a framework for prioritising conservation efforts on areas which were both highly biodiverse and have already undergone significant habitat loss[3]. The map of the biodiversity hotspots (Figure 1) shows clearly that a significant amount of the world’s biodiversity is found in tropical regions (fifteen of the twenty-five original hotspots). Clearly, tropical ecosystems promote both plant and animal diversity. Conservation of a region or habitat should also be more cost-effective and conserve a wider range of biodiversity than investing the same funding in a few species. However, as Myers points out, the determination of biodiversity hotspots is based on plants and four vertebrate groups (amphibians, reptiles, birds and mammals). Although vertebrate are often poor proxies for invertebrates, plant diversity appears to be a good predictor of arthropod diversity, particularly in the case of herbivorous insects which specialise in a particular subset of plants[13,22].

Given that an estimated 30% of arthropod species regularly visit flowering plants, plant diversity will often underlie invertebrate diversity[23]. On the other hand, there has been criticism of biodiversity hotspots for treating all species equally and not assigning more value to those which are culturally significant, e.g. African mega-fauna[16]. It seems clear that the hotspot concept is not in itself a panacea.

Others have worked on a similar approach; in 1998, the WWF created a “Global 200” list of ecoregions most at risk[24]. Their aim is to represent all major habitat types and highlight the most globally important, assigning each with a conservation status. More recently, the IUCN has developed a Red List of Ecosystems and are currently aiming to assess all global ecosystems by 2025[25]. They identify key ecosystem types and focus on loss of biodiversity in each, acknowledging that the loss of ecological functions and ecosystem services are also important factors, but hugely complex to assess. Indeed, biodiversity itself is often a reasonable proxy for these more complicated interactions.

There has been criticism of this attempt; Boitani et al[26] argue that ecosystems cannot be assessed in the same way as species, partly because a species can be seen as a definable unit, whereas “ecosystem” is a more nebulous concept. Indeed, there is no standard list of ecosystems with which ecologists work. It is for this reason that we need to improve our understanding of ecosystems and the connections between biodiversity and habitat conditions.

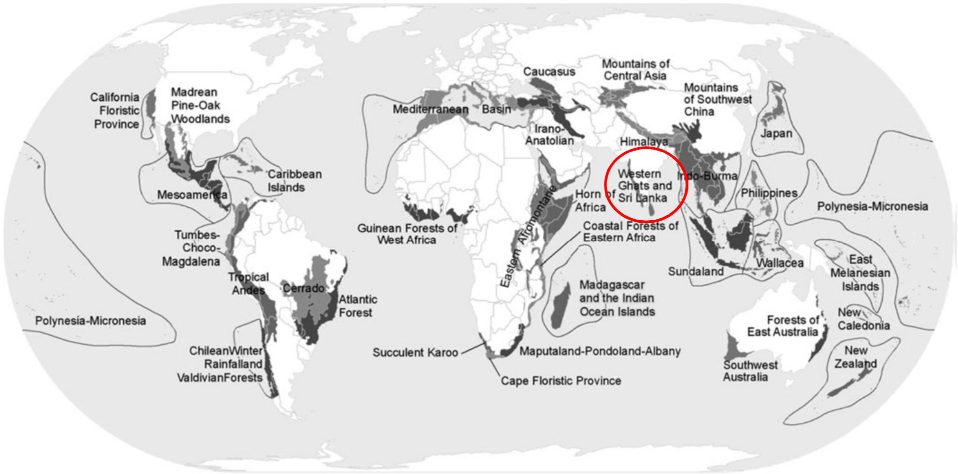


Figure 1.1 Map of the updated 35 global biodiversity hotspots, with the Western Ghats circled (modified from Mittermeier et al 2011[1]).

Deforestation and habitat fragmentation

There has been a concerted effort in recent years to understand the dynamics of ecosystems and the drivers of both species evolution and species loss. Given that two-thirds of the global population live in “biodiversity hotspot countries”, one might expect a conflict between human needs and those of other organisms[27]. Indeed, one of the most pressing issues in tropical conservation ecology is that of deforestation, driven largely by industrial logging and agricultural expansion[28,29]. Between 2000 and 2012, 2.3 million km^2 of forest was lost worldwide, largely in the tropics[30] and it is thought that agriculture causes around 75% of deforestation in developing countries[31]. Tropical forest conversion and degradation are known to cause overall levels of biodiversity, including among arthropods, to decrease[32]. Reforestation programmes could be beneficial, but new forests may not replace the value of natural forest to biodiversity[33]. It is therefore important to understand the impact of the loss of native forest on biodiversity and ecosystem functioning.

Tropical landscapes are often highly fragmented, with native forest patches scattered in matrices of human-modified habitats. In recent years, there has been much discussion of habitat fragmentation and its impact on populations and ecosystems, mostly focused on Neotropical mammals and plants[34]. However, protected areas in South and Southeast Asia may be the most affected by deforestation[29,35]. Furthermore, much of this work conflates habitat loss and habitat fragmentation; although they often co-occur, they should not be treated as equivalent[36]. In a recent review, Fahrig found only 17 empirical studies which try to assess fragmentation per se, none of which were carried out in tropical forests[37]. Although there is clear evidence for a negative effect of habitat loss on biodiversity, she found that when fragmentation itself is considered, the effects on diversity are often positive. For example, in a study on butterflies in a German agricultural landscape, there were more species found in many small patches than in larger patches of the same area[38]. This could be due to more ecosystems being represented in a larger variety of patches[37,38]. The value of small fragments partly depends on the nestedness of the species[39]. It is generally accepted that fragmentation is more detrimental for specialist than generalist species[40]; however, this would seem to depend on the specific location of fragments. On the other hand, small fragments are often more likely to be disturbed and it is important to ensure that they are not subject to degradation[41,39]. Furthermore, they may be subject to unavoidable edge effects[42].

Forest patches can vary widely in connectivity, and it is generally accepted that high connectivity is associated with population viability and thus biodiversity[43], which may be particularly important for species with specialised habitat needs[44]. In a fragmented landscape, connectivity can be improved via "habitat corridors" between patches. For this reason, there have been many studies on the effect of habitat corridors on the connectivity of animal populations. These show that corridors are generally beneficial, particularly for insects and birds; however, the extent of the benefit can vary between taxa[43] and there are potential negative effects, e.g. increased seed predation by small mammals[45]. One study on wooded corridors in tropical Costa Rica found that they facilitate pollinator (hummingbird) movement and thus increase pollination success of the native *Heliconia tortuosa*[46]. Several studies monitoring butterfly movement show that they use corridors to facilitate dispersal, including in agricultural landscapes[47,48]. Yet, such research has generally been limited to birds and mammals, with little attention given to any insects other than butterflies. Furthermore, experimental manipulations pose logistical and ethical challenges, and natural habitat corridors are often associated with other beneficial factors, such as patch size[43].

Evidence from tropical forest fragments also indicates that some vertebrate populations (birds, frogs and small mammals) are affected by characteristics of the surrounding non-habitat landscape, known as the matrix, whereas ant populations are not[49]. Once again, different taxa have very different habitat needs in terms of matrix quality. Geert et al show that flowering vegetative corridors may improve pollen dispersal of insect-pollinated *Primula vulgaris* in an agricultural landscape[50]. Most importantly, they found that dispersal was at its highest when the surrounding matrix was hospitable to insects (i.e. pasture land vs inhospitable arable land). This highlights the crucial differences between human-modified habitats, and the importance of a holistic view of the landscape[51]. In assessing the impact of deforestation and habitat modifications on tropical biodiversity, it is vital to ask: how hospitable is the human-modified matrix surrounding the forest patches?

The interplay between diversity and agriculture

It is important to consider the quality of the forest fragments themselves; the degradation of patches can be hugely detrimental to species diversity, having a greater impact than deforestation itself[41]. However, this section will focus on the land surrounding forest patches, which has often been converted to agriculture and may be as important for wildlife as the primary vegetation itself[52]. Many of these landscapes, including tropical forests, have been shaped by agriculture for centuries[53].

In the last few decades, conservation ecologists have started to recognise that the picture is more nuanced than a simple dichotomy between wildlife-rich “pristine” forest and sterile converted land[4]. Their focus has thus moved away solely protected areas to the whole landscape. Tropical agriculture varies in intensiveness; from agroforestry on the one hand to monoculture palm oil plantations on the other, and there appears to be a corresponding continuum of species richness[54]. Generally, it seems that biodiversity is most threatened by intensification, rather than land conversion *per se*[55].

Small-scale forest gardening of a variety of shrubs and trees, or agroforestry, is practised widely in the tropics and can harbour nearly as much plant and animal diversity as natural forest, although the species assemblage is often different[54,56,57]. As Bhagwat et al argue[54], agroforest fragments can increase the variety of available habitats in the landscape, provide corridors for wildlife, and help discourage local communities from depleting resources in protected areas. Canopy cover is an important factor in maintaining forest diversity; shade-coffee farms are known to have higher insect, bird and other vertebrate diversity than sun-coffee[4,58,59] and a review in 2016 found that increased shade is often associated with biodiversity in agroforestry systems[60]. Similarly, shade-cacao can retain high solitary bee and wasp diversity, although species composition may differ[61]. Practices like this are known as “land-sharing” – more extensive agriculture taking into account the needs of wildlife. However, some argue that land-sparing (creating larger reserves while intensifying existing agricultural land) is a better way to protect diversity; a study by Chandler et al. found that overall bird diversity was higher when farmers grew open canopy coffee while leaving an adjacent area of forest untouched[58].

There is continuing debate over the advantages of land-sharing versus land-sparing; in any case the merits of either may be species-specific[62,63]. However, it is clear that intensive monoculture plantations are generally detrimental to both vertebrate and invertebrate biodiversity[64]. One analysis of data collected in Southeast Asia shows that butterfly species richness decreases by 83% when primary forests are converted to oil palm plantations and by 79% when logged forests are converted[65]. Similarly, conversion of forest to rubber plantation decreases bird, bat and beetle diversity[66]. Bat and arthropod (including hymenopteran) diversity is also lower in monoculture oil palm plantations than polyculture, although butterfly diversity specifically does not differ[67–69]. However, as pointed out by Brockerhoff et al[70], grazed grasslands can be even less biodiverse than monoculture plantations[71].

Variation in agricultural management evidently influences local biodiversity, but this relationship works both ways; biodiversity can provide ecosystem services which increase the value of agricultural land. Animal pollination, which will be discussed in the next section, is one of the most well studied of these. A systematic review in 2014 found that atmospheric regulation, pest control and pollination are generally positively linked to species diversity. One study in China found that carbon storage, water yield and soil retention are all positively correlated with plant diversity[72]. However, water quality and pollination were not, indicating that a nuanced approach to management for ecosystem services is necessary. In shade coffee farms, vegetation complexity is good for climate regulation and nutrient cycling and usually increases arthropod diversity, which is associated with increased pollination and pest control[73]. Yet, in a minority of studies, pest species increased or pollinator species decreased with plant diversity. Furthermore, two studies in Borneo found that biodiverse forest fragments do not provide pest control or dung removal services for neighbouring oil palm plantations[74,75].

It has been argued that any perceived link between diversity and ecosystem services is due to the functional trait diversity of animal groups rather than their species richness or abundance *per se*[76]. However, this is currently understudied. Moreover, ecosystem service provision, like biodiversity itself, can be negatively affected by habitat fragmentation[77].

The way forward – reconciliation ecology

There is a limited amount of research on the benefits of reforestation, but one study in Ecuador found that species richness in Lepidoptera, Coleoptera and Hemiptera was lower in reforestations than native forest[78]. Furthermore, reforestation is often an expensive and gradual process and not always economically feasible. The conservation of tropical biodiversity requires another approach: “reconciliation ecology”, coined by Michael Rosenzweig, is based on modifying such existing anthropogenic landscapes to encourage diversity[79]. Based on the evidence presented above, we should keep in mind four key ideas. First, the landscape should be viewed holistically, not merely as forest patches in "sterile" agricultural land. In fact, a mosaic of different land use types may maintain the highest species richness. Second, different species, including those closely related, can have different or even opposing habitat requirements; this must be considered when managing land for biodiversity. Third, the provision of ecosystem services may be dependent on functional diversity; species' traits may therefore be more crucial than their taxonomy. Fourth, ecologists and farmers can work together; much traditional farming is small-scale polyculture which is generally beneficial for animal diversity[53]. As pointed out by Perfecto and Vandermeer, many small farmers' organisations recognise the need for wildlife conservation[4]. Furthermore, community-managed forests are less vulnerable to deforestation than protected areas[80].

In summary, the successful conservation of tropical invertebrates requires a deeper understanding of their relationship with landscape structure and agriculture. In the next section, this will be discussed regarding (mostly invertebrate) pollinators, which provide invaluable services to ecosystems and humans.

Pollination ecology

Pollination networks

To understand the links between biodiversity, pollination and agriculture, we must first appreciate the nature of plant-pollination interactions. They have evolved as mutualisms, although sometimes there is a conflict of interest, e.g.

nectar robbing (“cheating”) by pollinators can reduce plant pollination success[81]. Similarly, heterospecific pollen deposition is detrimental to plants, but not to their pollinators[82]. Nevertheless, the majority of interactions are mutually beneficial and the co-evolution of plants and animal pollinators has led to many plants being highly adapted to a specific pollinator functional group[83]. For instance, plants with long corolla tubes can be accessed only by species with long proboscises[84]. The existence of such pollination syndromes often allows us to predict pollinator groups based on floral traits[83], but the extent to which this holds true remains controversial[84].

Pollination networks comprise pollination interactions between plants and pollinators, with each species as a node in the network. They tend to be fairly generalised compared with other mutualisms[85], but there is a continuum of specialisation and some are very specialised indeed, e.g. *Ficus* spp. and some chalcid wasps[86]. When prioritising for conservation, this network structure itself is arguably as important as the species (or nodes) within it. Some theory predicts that more specialised networks are more vulnerable to disturbances as there is less redundancy; if one key pollinator declines, any plants dependent on it will be at risk[87]. On the other hand, losses of key players in generalised networks could cause an extinction cascade of interacting partners[87]. In general, pollination networks are asymmetric, in that specialist pollinators interact with generalist plants and vice versa, which may lead to high redundancy and thus stability[88]. The introduction of alien species (either plant or pollinator) can also impact on network stability[89].

Functional diversity appears to be an important factor in promoting network resilience to change; this increases when native plant diversity is high[90]. indeed network structure could be used as a proxy for determining the quality of a pollination service[90]. In the tropics, forest fragments keep networks stable by harbouring pollinators, with larger fragments holding more species[91,92].

In forest ecosystems, pollination networks are often influenced by canopy structure, with pollinator guilds varying widely from understorey shrubs to canopy trees. In general, floor species are pollinated by fewer species, perhaps because fewer pollinators are present in highly shaded areas[93]. Pollination networks are not static and can change over the course of a season or year. Sometimes these temporal changes are adaptive and indirectly confer stability on the network; for example, it has been suggested that plants which share pollinators may time their flowering to minimise competition[94].

Tropical pollination

Most in-depth or long term studies of pollination ecology are performed in temperate ecosystems[95]; however, there may be some key differences between temperate and tropical pollination networks which are obscured by this geographical research bias.

Firstly, it has traditionally been assumed that species interactions, including pollination, are more specialised in the tropics than at higher latitudes[82]. This is viewed as a function of the latitudinal diversity gradient; as diversity increases, mutualist specialisation also increases. When plant diversity is high, the chance of heterospecific pollen deposition is also high; thus, the more specialised the pollinator, the more effective the pollination. However, recent research suggests that tropical pollination networks are no more ecologically specialised than their temperate counterparts, in that the number of pollinators for each plant is similar[82,96]. Nevertheless, Moles and Ollerton go on to point out that tropical pollination may be more functionally specialised[96]; indeed, this may be more relevant to conservation of networks than simply the number of species. Indeed, Armbruster argues that we should consider “proportional” specialisation (with reference to the surrounding community) rather than comparing perhaps arbitrary species numbers[97]. It has also been argued that tropical plants are more specialised, but not their visitors[85]; however, this does not solve the problems of heterospecific pollen deposition or wasted pollen. Overall, the degree of specialisation in tropical pollination is still debated and much depends on the definition of the term “specialisation”.

Another key difference between tropical and temperate regions is the ratio of wild (native) pollinators to managed bees. Tropical plants (both crops and native vegetation) are more dependent on wild bees for pollination; keeping or transporting honeybee colonies can be problematic in these regions[98]. In the Neotropics, feral populations of Africanised honeybees (*Apis mellifera*) also play a key role[98]. On the other hand, managed bees perform a large proportion of pollination in Europe, and wild *A. mellifera* populations are relatively rare (perhaps extinct in many areas)[99].

Stingless bees (Apidae: Meliponini) are key pollinators in the tropics, particularly in South America[100]; they are highly successful in the Neotropics, perhaps due to their sociality, recruitment of foragers, and the ability of some species to buzz pollinate[101]. Furthermore, they are generalist pollinators and adaptable to new floral resources, and can also be domesticated[101]. They are thus thought to play a key role in tropical pollination networks; some evidence for this is presented in the following section.

Variations in climate, particularly rainfall patterns and temperature, produce differences in plant-pollinator interactions. For example, monsoons may lead to different foraging strategies to optimise pollen and nectar intake, leading to differences in the pollination network both temporally and spatially[102]. Bees in the Neotropics tend to be less florally constant than temperate bees, perhaps because tropical resources change more frequently[103]. Most tropical research is carried out in the Neotropics but a recent in-depth study of forests in East Asia emphasises the contrasts between pollinator communities in different climates[95]. In the temperate field sites, bumblebees dominated; small and solitary bees were more prevalent in the monsoon forests, while the rainforests favoured honeybees (especially *Apis dorsata*)[95].

Importance of insect pollination

Estimates vary but approximately 87% of all angiosperms (94% of tropical flowering plants)[104] and at least 35% of global crop production depends on animal pollination[104–106], mostly insects[107,108], and these proportions are even higher in tropical regions[104]. The contribution of insect pollination services to the global economy has been valued at over €150 billion *per annum*[87] and this is expected to rise with the increasing production of animal pollinated crops (these have risen by more than 300% in the last fifty years)[109]. With the global population at 7.5 billion and rising, food security is more crucial than ever. Despite this, and concerns over honeybee colony declines particularly in North America[110], wild pollinators are still underrepresented in conservation discourse[111]. The IUCN only formally assessed all of Europe’s 1,965 wild bee species as recently as 2015[112].

Managed bees

As mentioned above, managed populations of the Western honeybee (*A. mellifera*) are more prevalent in temperate regions than in the tropics. In South America, meliponine stingless bees are managed and the imported Africanised honeybee is mostly feral[99]. In Asia, both *A. mellifera and* the Eastern honeybee (*A. cerana*) are domesticated for pollination services and honey production, as is a species of stingless bee (*T. iridipennis*)[113]. Social bees are also more numerous than other bees making them more suitable for managed crop pollination[87]. In some areas, *A. mellifera* is replacing *A. cerana* as the honeybee of choice, partly because their colonies produce a higher honey yield[114].

At higher latitudes, *A. mellifera* is a key pollinator, and often crucial to crop pollination. Honeybee hives are regularly transported around Europe and America to provide pollination services. Almond production in America relies on transporting half of its honeybee hives to California to pollinate the trees during flowering season[87]. The bumblebees *Bombus terrestris* and *B. impatiens* are also commonly managed and transported for greenhouse pollination, particularly of buzz-pollinated crops (Solanaceae)[115]. Renting bees can be costly for farmers; besides, reliance on managed bees makes the pollination service vulnerable to any declines in a single species. Consequently, in recent years, there has been an increasing focus on the service provided by local native pollinators[87].

“Free” pollination services

There is a growing body of evidence showing that wild pollinators, especially wild bees, play a role in both temperate and tropical crop production, with the potential to contribute more to pollination. A recent synthesis of 29 studies across a range of biomes finds that wild bees are both valuable to crop productivity and benefit from proximity to natural or semi-natural habitat[116]. Two economically important American crops, apple and cotton, are pollinated more effectively when there are more and diverse wild bees[108,117]. This effect is not merely due to the number of bees present, as increasing honeybee numbers did not provide the same benefit[108,117]. Similarly, in Germany, wild bees outperform honeybees in pollinating cherry[118] and in Crete, watermelon pollination is just as efficient when performed by wild bees compared to honeybees[119]. In Mexico and Indonesia, wild bee diversity increases coffee yield[120,121]. A Costa Rican study found that coffee yields increased by 20% when wild bees were present (within 1 kilometre of a forest patch); this “free” service was valued at an estimated increased revenue of $60,000 per year per farm[122]. Tanzanian coffee also benefits from wild bee pollinators[123]. A large-scale study of 41 global crops, including in the tropics, shows that wild bee visits have a positive effect on pollination, which could not be reproduced by merely increasing honeybee populations[124].

There are several explanations for such effects. Firstly, wild bees may simply be more effective pollinators. They may be more likely to collect pollen than honeybees[108], as well as often having longer tongues; honeybees are also highly generalist, perhaps making conspecific pollen transfer less likely[87]. In this case, studies that use flower visitation as a proxy for pollination may even be underestimating the service provided by wild bees.

Another, compatible, explanation is based on the interactions between honeybees and wild bees in the crop. The presence of wild bees at an inflorescence may cause a honeybee to move on to another, increasing the amount of flowers visited[125]. This kind of interaction has been observed in sunflowers and suggests that the role of wild bees may actually be to increase honeybee efficiency[126].

As Geslin et al argue, it is not the mere species richness that is key for pollination services, but rather functional diversity, as in pollination networks in general[127]. Their study also found that functional diversity of insects in mango orchards increases with proximity to natural habitat[127]. Bee functional diversity also increases seed set in pumpkin (*Cucurbita moschata*) in Indonesia[128]. In Germany, bee diversity increases pollination of a variety of plants due to complementarity between bees; species differ in plant preferences and only bumblebees also pollinate in colder conditions[129], which was supported by observations in Israeli apple orchards[130]. A study in California found that honeybees and wild bees preferentially visit different sections of almond trees and wild bees were less affected by high wind speed than honeybees and so could continue pollinating on windy days[131]. Such networks should be more resilient to environmental or climatic change than a service dependent on a single species. Furthermore, wild bees could help buffer against fluctuations in honeybee populations and may themselves be less susceptible to disease[106].

There are several important caveats to this focus on conserving wild bees for pollination services. Firstly, it is dependent on the crop being considered and the landscape context; in some areas, it may not be cost-effective or even possible to encourage wild pollinators. For example, a study of rapeseed in Ethiopia found no link between pollination services and forest proximity, bee richness or abundance[132]. In such landscapes, wild bee abundance may already be so low that farmers are forced to supplement with honeybees.

We must also consider that crop pollination, although of quantifiable economic value, is not the only service wild bees can provide. Ideally, they can also help the conservation of native and threatened flora. There has been little research in this area but a two-year controlled experiment found that plant community species richness is positively affected by an increase in functional pollinator diversity[133]. Feral Africanised *A. mellifera* can help maintain the genetic diversity of remnant trees in highly disturbed forests in South America; however they could be detrimental to more specialised plants - collecting pollen or nectar without pollinating[134]. It is important to investigate whether other native species, e.g. Neotropical stingless bees, can provide similar conservation value, perhaps without the drawback of "cheating" the plant specialists. Furthermore, plants in highly species-rich habitats are already more pollen limited; heterospecific pollen deposition increases as plant density decreases[135]. Clearly this is more of an issue for plants unable to self-pollinate and thus dependent on animal pollination. This poses a risk to such species in biodiversity hotspots[136]. Lastly, some have also argued that there could be a trade-off between crop pollination services and the conservation of wild plants, due to competition for pollinators[137].

Pollinator declines

Over the last few decades, there have been numerous reports of pollinator declines across the world. Most of the research comes from Europe and the US, and is largely focused on the managed honeybee, which indeed suffered severe colony declines in the 2000s[88], but has started to increase again[138], (Bee Health in Europe 2013). Beekeeping is generally a less popular and lucrative profession thanks to a successful global honey trade[139]. Bumblebees are also well studied and have suffered declines in Europe and the US[88].

The first study to look at wild bee trends and pollination services in US was published only last year and found declines in species abundance over a five-year period; this was often lowest in the agricultural land where pollination services are most needed[140]. Likewise, the European Red List of Bees report found that 9% of wild bees are threatened with extinction[112]. There is a conspicuous lack of data on tropical wild bee populations and how they might be coping with the threats which are harming temperate honeybees and bumblebees[87]. However, there may be declines in stingless bees across the tropics and a few meliponine species are threatened with extinction[141]. There is also circumstantial evidence of pollinator declines; for example, in some areas of China, apple and pear flowers require pollination by hand[87]. The rest of this section will focus on the major drivers of pollinator declines, particularly in tropical ecosystems.

Land use change

Many studies on both temperate and tropical pollination systems, including a comprehensive review in 2013, show that proximity to natural habitat and landscape configuration are key factors in native pollinator diversity and also pollination services, which are negatively impacted by agricultural intensification [108,117,142,143]. The fragmentation and loss of natural habitat, e.g. temperate semi-natural grassland in Europe[112], or flowering forest trees in the tropics, is therefore a major driver of pollinator declines[86]. Plant and pollinators decrease in abundance and richness as habitat is lost and fragmented[144145] and plants suffer from extinction risk due in part to pollen limitation[146]. Habitat loss tends to lead to an increase in generalists at expense of specialists; and the remaining pollinators are often forced to generalise[144,147,148,149]. Species loss can cause a reorganisation (e.g. increasing modularity) of the entire pollination network, with knock-on effects on others[150]. Declines in bee diversity in Britain and the Netherlands have been particularly striking for flower and habitat specialists[151]. Similarly, in Brazil, generalist bees were less affected by forest loss than specialists[147]. Stingless and solitary bees are more dependent on forest fragments and plant diversity than feral *A. mellifera* (a generalist) in the Neotropics[152,153,154]. In these situations, generalist pollinators have the potential to provide “rescue” pollination services if necessary; for example, *Trigona spinipes*, a stingless bee which can disperse up to 200km (individual workers can fly over 8km) in a human-modified landscape[155].

Although some studies have suggested that tropical pollinators may be relatively resilient to land use change, e.g. a social stingless bee (*Partamona bilineata*) in Guatemala is not affected by landscape structure[100], this seems to vary with taxa and ecosystem. For example, in China rubber plantations are associated with a loss in wild bee diversity, but not hoverfly diversity[156]. In general, hoverflies are not as affected by matrix quality or distance to semi-natural habitat as bees are[157]. Similarly, in Indonesia cacao management intensity negatively affects species richness but in Ecuador has no effect[158]. However, proximity to natural forest was beneficial for the Ecuador pollinators[158] as it is for Indonesian social bees[159,160]. A synthesis of 23 studies across temperate and tropical crops actually suggests that social bees in tropical ecosystems may be the most vulnerable to decline due to habitat loss[161] and various studies suggest that solitary bees can cope better in disturbed sites[162,163]. Also, cavity-nesting bees require trees while open-nesting bees prefer open areas[147]; this may make cavity-nesting bees more vulnerable to forest loss. Indeed, species richness can be higher in disturbed forest than in untouched forest, perhaps due to a wider variety of nesting habitats available[147,164]. Much of the research on bees in tropical landscapes comes from agroforestry, particularly coffee production. Polyculture agroforests and high canopy cover are conducive to bee diversity[120,165], particularly that of social bees[166]. One study in Sulawesi found that eumenid wasps and solitary bees preferred intensification (maybe due to more ground nesting sites), while social bees were negatively affected[167]. Studies in Sulawesi found that of solitary bees and wasps, some species benefited from more intensive cacao agroforestry[61]. Social bees in Indonesian coffee agroforestry benefit from forest proximity[160]. However, another study in the same country found that solitary bee abundance benefited from agroforests rather than intensive land[168]. A study in Brazil found that solitary bees were unaffected, while solitary wasps were negatively affected[169]. Generalisations based on sociality may be misleading and not hold true globally; it appears that Mexican solitary bees prefer high canopy cover[166], while Indonesian solitary bees favour less shade[145,145]. In Tanzania, shaded coffee is favoured by wild bees, while *A. mellifera* dominated pollination of sun coffee[123]. It is vital to know which bees specifically are pollinating crops and actively manage the agroforest to maintain the right conditions these species, as they respond in different ways to land intensification[170]. In northern India, bee diversity is higher in less intensive farms, which harbour more rare species and wood-nesting bees, including *Tetragonula* spp. and *Xylocopa* spp.[171]. However, soil-nesting species benefit from intensification as they have basic habitat requirements.

Insect pollinated plants can benefit from organic, low-intensity farming in temperate ecosystems, due to higher pollinator abundance[172,173]. However, Brittain et al found no effect of organic farming versus conventional on pollinator diversity and abundance and pollination services[174]. They argue that the surrounding landscape is more of a factor in this case.

Plant diversity and type of floral resources appear to be important[145,175]; even flowering crops may not meet bees' specific nutritional needs, or provide sufficient nesting habitat[87]. Mass flowering crops may be good for some species, e.g. in temperate ecosystems, honeybees benefit from oilseed rape (*Brassica napus*)[117]. Coffee is also mass flowering, so a variety of flowering plants would provide bees with resources throughout the season[152]. Bee foraging distances can vary hugely with landscape factors and configuration[176]. It has been shown that bumblebees forage further for floral diversity, rather than plant density[177] and change their behaviour depending on nectar reward; after encountering “low quality” nectar, they fly further away in search of more rewarding nectar[178]. Bees specialised on pollen are particularly vulnerable, perhaps because of their specific nutritional requirements and the disparities in pollen quality among plants[175].

Mobility, i.e. ability to move between fragments, also appears to be a factor; this may help to explain why insect pollinated plants appear to be more affected by fragmentation and pollinator decline than bird pollinated plants[179]. Large bees can travel further and some temperate studies find small bees are more at risk from habitat loss, perhaps due to lower mobility and dispersal ability.[180,181]. Small Indonesian bees are more dependent on forest proximity than the larger species[168]. Habitat fragmentation caused an increase in intraspecific body size in *Andrena* (mining bees) in Germany[182], perhaps by selecting for larger foragers. However, in a study of Neotropical stingless bees, body size was not a factor in dispersal ability[183]. Yet, studies in New Zealand and South Africa found that large bees were actually be more vulnerable to habitat loss [127,142]. Overall, it seems that land use affects bees at different scales; Benjamin et al shows that in their study large bees are affected by mostly by the landscape scale level of agricultural land while small bees are only negatively affected at the farm scale[184]. They conclude that in some contexts pollination services could be most improved overall by focusing on local (farm scale) agricultural land use[184].

Much of the research suggests that landscape heterogeneity is beneficial to bee diversity; in Indonesia, for example, a combination of open land, agroforests and native forest patches is ideal[31,185]. Some have also argued that a resource-rich matrix around crops or native plants may be counter-productive, slowing pollinators down and reducing pollination of target species[186].

Agrochemicals

Neonicotinoids, the most frequently used class of insecticides globally, have been implicated in pollinator declines[187]. Most of the research is laboratory-based and conducted on honeybees, and sometimes bumblebees, in Europe and North America[187]. These studies generally show sub-lethal effects on individual foraging behaviour, longevity and cognition, with potential for colony-level impact[187]. However, it is hard to quantify these effects as a factor in population declines, partly because there have been very few long term studies on colony performance[187]. A recent study of populations of *A. mellifera, B. terrestris* and *Osmia bicornis* found some negative effects of neonicotinoids on reproduction in Hungary and the UK but not in Germany, where the pesticides appeared to have a positive effect on reproduction. These conflicting field results illustrate the difficulty in ascribing pollinator declines to agrochemicals.

This problem is exacerbated in the tropics, where there is a lack of field studies on pesticide impact. There is however some research on sublethal effects on stingless bees, as reviewed in Lima et al[141]; for example, neurological damage, e.g. impairment of mushroom bodies during development[141]. This may affect foraging behaviour. A study in India on agricultural intensification also found that pesticides lower the diversity of “wood-nesting” bees (including stingless bees)[171]. There is also concern that the smaller colony sizes of stingless bees may make them more vulnerable to loss of workers, compared with honeybees[188].

Disease

One of the current threats to *A. mellifera* populations is deformed wing virus (DWV), carried by *Varroa* mites[189]. DWV is much more prevalent in temperate colonies than in tropical ones despite Varroa infestation rates being similar[190]. This may be due to cold stress which reduces bee immunity or due to dry weather promoting viral transmission[190]. Africanised honeybees are more resistant to the mite, and it has been suggested that genetic flow between feral colonies and managed colonies in South America could help the managed colonies become more resistant[115]. *A. cerana* is also resistant to *Varroa,* due to its more efficient hygienic behaviour than *A. mellifera* (Lin et al 2016). However, it is highly vulnerable to Thai sacbrood virus (TSBV), which has decimated populations across Asia (Rao et al 2015).

Recent research has also shown that wild pollinators such as bumblebees are also at risk from DFV, as well as *Nosema ceranae*, a parasite of *Apis* spp.[191]; these diseases may be playing a role in bumblebee declines.

It is still unknown whether disease is causing declines of tropical native pollinators, such as stingless bees, as they has only recently gained attention. In 2016, Guzman-Novoa et al reported the first molecular detection of honeybee viruses (including DWV) in *Scaptotrigona* stingless bees, Mexico[192]. The first confirmation of brood disease in a stingless bee was this year in *Tetragonula carbonaria*, in Australia[193].

Invasive plants

The introduction of exotic plants has been posited as a threat to native pollinators worldwide, perhaps posing most of a risk to specialists. For example, *Rhododendron ponticum* invasive to Britain, produces nectar containing the secondary metabolite grayanotoxin I which can be toxic to both wild and managed bees[194,195]. However, it is not harmful to bumblebees, allowing them to potentially out-compete other species, thus disrupting the pollination network[195]. Similarly, exotic crops in Argentina alter the network by causing more heterospecific pollen deposition on native plants[196]. Declines in these native species may result in declines in their pollinator species, if they are dependent on them for floral resources. On the other hand, bee foraging behaviour is remarkably flexible and they may be able to adapt appropriately to invasive plants[197]. Indeed, there is not much evidence that invasive plants are a major factor in pollinator declines[198].

Climate change

Changes in climate can have direct impacts on pollination networks by interfering with plant phenology and pollinator behaviour. The effects on pollinators have mostly been studied in butterflies, whose geographic distributions have already changed in response to climate[88]. Such effects have been modelled by Memmott et al, who find that up to 50% of pollinator activity could potentially become temporally mismatched with their floral resources[199]. They note that pollination networks are fairly resilient to the loss of specialists, due to the high levels of asymmetry[200], yet pollination services are still likely to be degraded, and eventually generalist species may be affected[199]. In a temperate ecosystem, habitat loss and agricultural land cover interact with climate, making wild bees more vulnerable to high temperatures, perhaps because they are more exposed and they have fewer nesting sites, making weather a more important factor in survival.

Future

There are several crucial gaps in our understanding of pollination ecology, as research is mostly focused on Europe, North America and the Neotropics. More studies are needed on the ecology and behaviour of tropical bees, and this is what was the focus of the present study is. We also need more basic data on the abundance and distribution of tropical pollinators, particularly wild bees, in part so that potential population declines can be detected. In Europe, citizen science projects are being used to monitor abundance[87]; and collaborations such as the International Pollinators Initiative can help to collect abundance and diversity data[201]. Developments in molecular taxonomy and DNA barcoding could also allow more accurate species identification[87].

Understand both of these aspects it will become feasible to understand how these bees use the landscape and how are different species affected by habitat type and configuration. Future studies should distinguish between habitat size and habitat fragmentation and provide insight into pollinator movement[202,203]. The effect of urbanisation (increasing in many parts of the world) on pollinators should also be studied[87]. Stable isotope analysis can also be used to assess foraging habitats over the lifetime of a bee[204]. A deeper understanding of habitat needs could also allow us to use habitat as a proxy for the abundance of different taxa, e.g. presence of trees for cavity-nesting bees[205].

To gain knowledge of pollination networks at landscape level[143], measures of pollination success, rather than just floral visitation, should be applied, as argued by Delmas et al[135,206,207]. It will also take into account plant phenology and temporal variation in pollinator diversity and pollination networks; a changing climate makes this particularly important[144,208,209,210.] A variety of pollination syndromes is also an indicator of habitat quality[211].

It is furthermore important to investigate the precise connections between pollinator diversity and the pollination services they provide in the settings of tropical habitats[212]. This has so far been studied in detail for only some species (usually *A. mellifera* compared with wild bees) in the temperate regions.

Last, we need to understand physiological and colony-level effects of both agrochemicals and disease on native bees in the tropics.

Notwithstanding these knowledge gaps, there are interventions with the potential to help conserve pollinator diversity. Beekeeping practices could be improved; for example, a reduction in hive transportation could reduce the spread of disease. One way to achieve this is to encourage keeping of local bees (e.g. stingless bees in South America)[183153]. Similarly, we should be aware of the risks of moving new *A. mellifera* populations into the tropics[99]. Garibaldi et al argue for multi species management (including managed bees), to avoid reliance on a single species[213].

The active management of agricultural land, also known as ecological intensification, can help bee populations[214] and should be specific to pollinator, crop and landscape[215]. Pollination services are more efficient when bees have more habitat[216]; set-asides of natural habitat within the agricultural landscape are therefore beneficial, as are flowering margins with high species diversity, or allowing beneficial weeds to grow[87217,218219], bearing in mind the potential for pollinator limitation of the crop[220]. Models shows that pollination services are affected by the location of wild bee nesting sites; these can be optimised by giving them small habitats throughout[216221]. For example, nest boxes can be installed near crops to provide a home for solitary bees[222]. Agroforestry should be heterogenous with a high proportion of flowering plants and canopy cover. In Ecuadorian coffee farms, there are currently initiatives to grow more nectar and pollen rich plants[98]. Conservation of wild pollinators could be incentivised with compensation payouts.

However, such measures may not benefit already threatened species or species which cannot thrive in agricultural landscapes; we need to consider their needs as well[111223]. There may also be a trade-off between maximising pollination services and conserving wild plants[137]. Another model based on Indonesia suggest these two needs can be met in coffee agroforestry, when there are forest patches[224]. The preservation of native forest is clearly important; we need an approach combining this with agricultural management.

The Western Ghats – biodiversity hotspots

Biodiversity in the Western Ghats

The Western Ghats is a 1600km mountain range in the west of India, extending from Maharashtra in the north to Tamil Nadu in the southern tip of the country[225], with a total area of 180,000 km. The southern part of the range is generally wetter than the north and receives rain from both the southwest monsoon (June-September) and the northeast monsoon (October-December)[225]. There are two main types of tropical forest in the Western Ghats: montane rain forests at higher elevations and moist deciduous forests nearer sea level, which differ in composition and climate from north to south[2]. Differences in climate and seasonal variation are major drivers of plant biodiversity in Western Ghats rainforests[226]. The Western Ghats and Sri Lanka region is one of the original 24 biodiversity hotspots[227] and one of the eight "hottest" hotspots, defined by the amount of endemic plants and vertebrates and loss of vegetation[228].

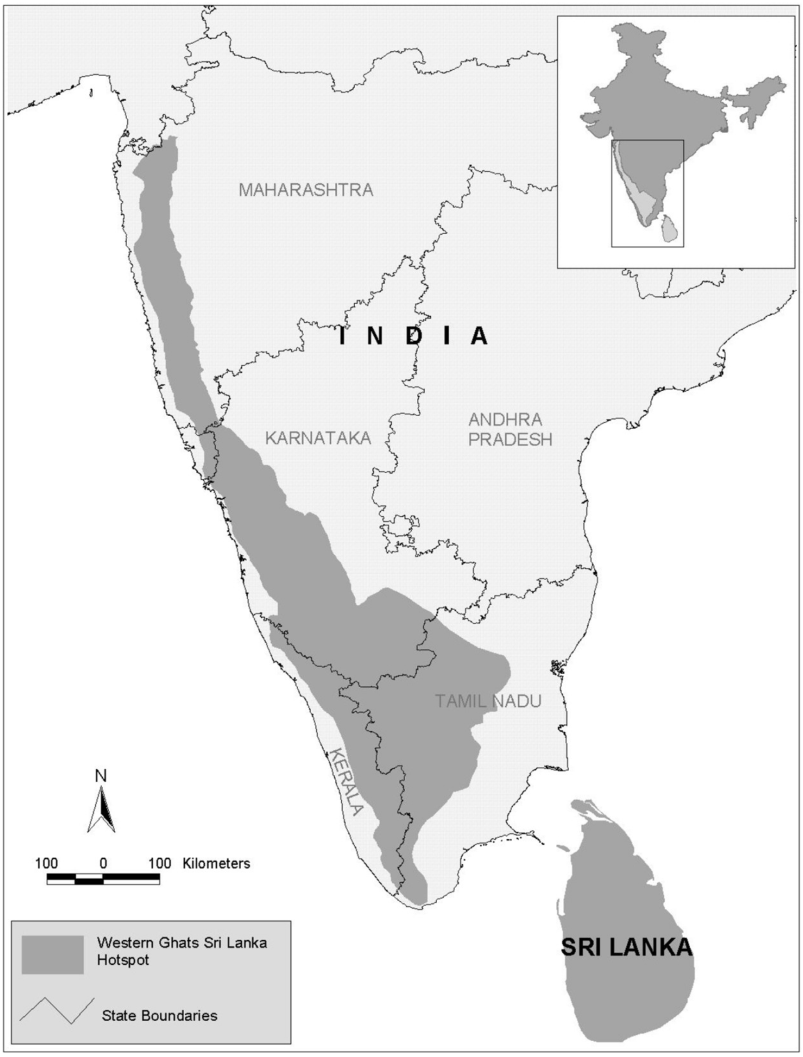


Figure 1.2 Map of the Western Ghats – Sri Lanka biodiversity hotspot. From Bawa et al 2007[2].

Anamalai Tiger Reserve, a protected area (PA) in the southern WG, is also listed as 32nd among worldwide protected areas, as defined by the "irreplaceability" of its biodiversity[229]. This is an assessment of the contribution an area makes to globa conservation.

The Western Ghats harbours 1500 endemic flowering plant species, 38% of the total in the area[2]; much of this diversity and endemism are found in the southern parts. 229 of these species are globally threatened and 39 are critically endangered [2]. There is also a high level of vertebrate diversity, especially for reptile and amphibian species, many of which are endemic to the region; 52 of these amphibians are threatened[230]. As in most of the world, studies on invertebrate diversity are limited to a few taxa, including butterflies, ants and odonates. There are 330 species of butterfly, but only 37 of these are endemic[230]. There are 223 species of odonate, of which 52% are endemic, and at least 140 species of ant[230]. Aquatic insects and molluscs may be at risk due to land use change, but generally little is known about the threats to invertebrate fauna in this region[230]. As Chitale et al argue, biodiversity hotspots in India are understudied compared to other areas[231].

Land use change

Around 9% of the Western Ghats is in 58 protected areas, but very little is known about the diversity and endemism of species in these sites, other than charismatic mammals and birds, e.g. tigers (*Panthera tigris*), gaur (*Bos* gaurus) or hornbills (*Buceros bicornis*) [2]. Furthermore, despite being under varying levels of protection, they are all subject to various hreats from human disturbance. For example, the Nilgiri Biosphere Reserve, set up with the aim for the conservation of unique biodiversity, is highly fragmented, partly due to the construction of roads and hydroelectric projects[232]. Hunting is very widely practised in protected areas, as is illegal logging, collection of fuelwood, and the extraction of non-timber forest products[2]. Other threats include livestock grazing, fire and tourism, which can all have a detrimental impact on wildlife and vegetation[2]. The size of the villages in or near PAs is positively associated with the amount of disturbance caused; a growing population is therefore an issue[233]. The Silent Valley National Park is one of the only remaining non-fragmented tropical montane rainforests in the Western Ghats and it is only 90km[2].

It is no surprise that human-wildlife conflict is pervasive in the Western Ghats: with its population of 60 million[234], it is the most densely populated biodiversity hotspot by a large margin; around 350 people / km^2, compared with 200 people / km^2 in the Philippines biodiversity hotspot[235]. Humans have lived in this area for over 12, 000 years and various forms of agriculture were practised here for over 2,000 years, often involving the slashing and burning of forests[236]. During this time, the landscape was under active management; agroforestry was widespread, and some sacred groves are up to 900 years old[237]. This long history of human disturbance may explain the relative resilience of Western Ghats diversity compared with other areas[238]; low-intensity agriculture could have helped to preserve forests and biodiversity together with human-made landscapes[239].

However, the 19th and 20th century saw an unprecedented rise in deforestation due to timber demands in the British Empire and the conversion of forest to commodity plantations, e.g. tea, coffee, rubber and pepper[240]. It is estimated that 40% of Western Ghats forest was lost during the 20th century, much of that to coffee plantations, and the remaining forest suffered increased fragmentation, with four times as many forest patches and the average area of each decreasing by 83%[241]. Natural habitat currently accounts for one-third of Western Ghats[242], but 14% of the “forest” area is actually anthropogenic landscape, including villages and agriculture[243]. Clear-felling of forests was banned in India in 1996, which helped to slow down deforestation; in the years 1990-2005, India actually saw an increase in countrywide forest cover[244] and deforestation in protected areas in Kerala (a state within the Western Ghats region) has ceased in the last decade[245].

Nevertheless, regional biodiversity is still threatened by human disturbance and land use change, particularly in the Northern Western Ghats[246]. Human-caused fires in the Western Ghats are increasing in frequency, and smaller fragments of forests are more vulnerable to being completely destroyed[237,247]. This poses a particular threat to rarer tree species, which may only be represented in a few fragments[248].

Furthermore, agriculture continues to become more intensive. The homegarden, particularly common in Kerala, is a form of agroforestry around a home, dominated by coconut but also containing plants for a variety of purposes, including medicine, timber and aesthetic value[249]. They are responsible for much of the agrobiodiversity: it is thought that there are 142 crop plant grown in Kerala, belonging to 43 families[250]. Yet, homegardens are becoming increasingly monocultural, concentrating on one or a few lucrative cash crops (often coconut or rubber) rather than traditional multi-storey intercropping (for example, coconut, cacao, black pepper and pineapple)[251]. Mohan et al found that high homegarden species richness tends to reduce its economic value[252]. Additionally, growing urbanisation (towns in Kerala increased over threefold from 2001 to 2011) is causing both a decline in homegarden ownership and vegetation diversity within them[249].

Coffee production has also become both more lucrative and more intensive; there has been a reduction in agroforest canopy cover and an increased use of agrochemicals, both of which increase yields[251,253]. Furthermore, the indigenous trees used for shaded coffee plantations are being replaced by *Grevillea robusta*, the Australian silver oak, an exotic species grown for timber[253], which also supports the cultivation of black pepper vines[254].

Similarly, there has been a reduction in intercropping with other crops, e.g. vanilla, areca and citrus[242].

The production of rice, a major crop in South India, has declined by 60% in Kerala in the last few decades[255], as it has fallen in market value. In some areas, such as the Wayanad district of Kerala, rice production is essentially limited to consumption by the paddy owners; most paddies have been converted to arecanut, banana or ginger production[253,256]. At the same time, rubber production has increased by over 600% in Kerala in the last few decades, and is the dominant crop, accounting for 5000km^2 [242]. Nevertheless, this rubber boom has been less dramatic than in many Southeast Asian countries[255,257].

Impacts on biodiversity

As discussed in the previous section, both forest fragmentation and the trend towards intensive and monocultural agriculture are generally detrimental to plant and animal diversity. Canopy cover is associated with vertebrate species richness, as supported by a review on 14 taxa, including birds, mammals, amphibians and reptiles; forest cover was associated with higher diversity for these groups, but interestingly not for invertebrates[242]. For example, one of the reviewed studies showed that cardamom plantations, characterised by native tree canopy, was similar to the forest in bird species diversity[258]. A recent study indicates that coffee agroforests harbour higher bird species richness than either rubber or areca plantations and this is mediated by canopy cover and density[259]. However, areca plantations can support high bird diversity when intercropped with other species, e.g. coconut, pepper or banana, and near or interspersed with native forest patches[239]. Furthermore, plant functional diversity can be maintained in low or moderate-intensity agroecosystems[260].

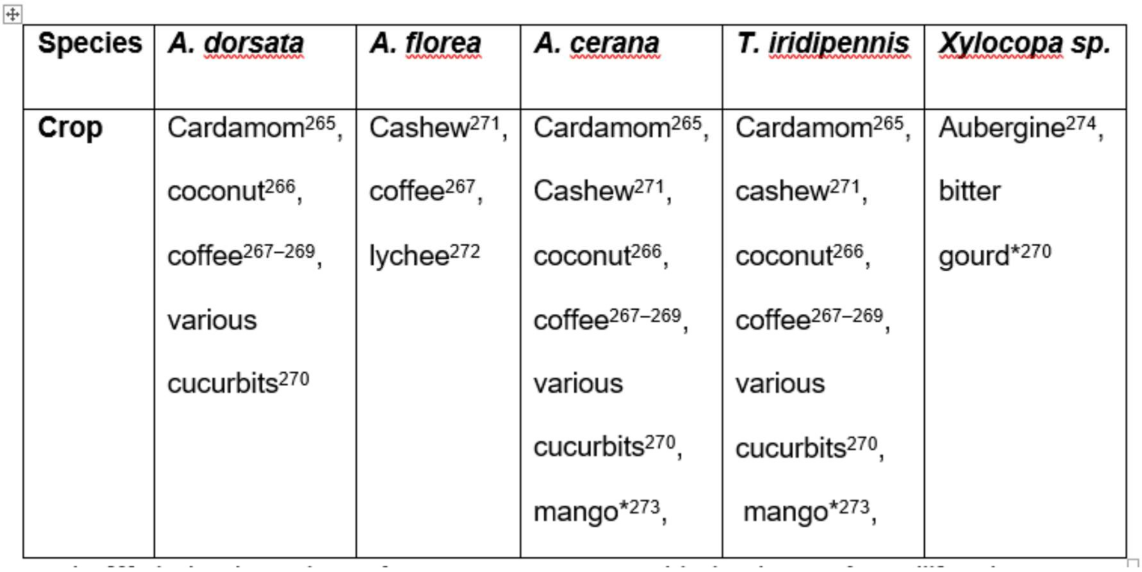
As elsewhere in the world, relatively little research has been conducted on the impact of land use change on invertebrates. One study indicates that soil invertebrate species richness is higher in forests than in monocultural plantations or annual crops; ants were actually more diverse in agroforest systems than in forests, supporting the idea that some taxonomic groups can actually benefit from the disturbance caused by low intensity agriculture[261]. The impact of land use change on pollinators and pollination services in the Western Ghats will be discussed later in this section.

Key pollinators

In the Neotropics, where most of the research on tropical pollination ecology is carried out, hymenopterans, lepidopterans and vertebrates all play key roles in pollination[262]. However, in the Asian tropics, pollination is dominated by bees, particularly the social species[262].

There are three native species of honeybee found in the Western Ghats region: *Apis florea, A. dorsata and A. cerana*. The dwarf honeybee, *A. florea,* and the giant honeybee, *A. dorsata*, are both open-nesting species and prone to migration, thus generally unsuitable for beekeeping[263]. *A. dorsata* also produces a lot more honey than *A. florea*; they are therefore the main target for honey hunters[264]. Honey hunting involves destroying the nests, threatening giant honey bee populations[265].

Beekeeping of the Asian honeybee, *A. cerana,* a cavity-nesting honeybee and sister species of *A. mellifera,* has been practised in India for millennia, with over a million hives in the country[266,267,268]. It continues to provide an income for many in the Western Ghats, which is one of the country's centres of beekeeping[268]. It is on average smaller than *A. mellifera*, although there is considerable size variation within its range across Asia and bees in south India are smaller than those in the north[267,269]. Worker cell size is larger in cold regions than in the tropics[264]. Indeed, northern *A. cerana* are comparable in size to *A. mellifera* in warm climates, e.g. Africa[267]. Wild *A. cerana* build nests with multiple combs, often close to the ground, in tree hollows (often coconut trunks), holes in rocks, or building cavities and likely to be found in both disturbed areas and native forest[264,267]. However, in parts of Asia in which they compete with other native cavity-nesting species, they are mainly found in disturbed or agricultural sites[267]. Wild colonies range from around 2000 to 34,000 bees[267] and seem to vary with geographical distribution (pers comm with Dr Hema Somanathan), and it is unknown how many exist in the Western Ghats. There are some aspects of *A. cerana* behaviour which distinguish it from *A. mellifera*. For example, it is generally more docile and less inclined to sting potential intruders to the nest[267].



Species	***A. dorsata***	***A. florea***	***A. cerana***	***T. iridipennis***	***Xylocopa sp.***
Crop	Cardamom[265], coconut[266], coffee[267–269], various cucurbits[270]	Cashew[271], coffee[267], lychee[272]	Cardamom[265], Cashew[271], coconut[266], coffee[267–269], various cucurbits[270], mango*[273],	Cardamom[265], cashew[271], coconut[266], coffee[267–269], various cucurbits[270], mango*[273],	Aubergine[274], bitter gourd*[270]

Table 1.1 Key crops in the Western Ghats pollinated by the major bee species.

However, there is a defensive mechanism against bee-hawking wasps and hornets, known as "bee-balling", in which around 30 worker bees surround the intruder, causing it to overheat and die[270]. Both species, and *A. dorsata,* perform bee-balling, but the Asian species are much more effective, probably because they are historically more exposed to such predators[270,271]. Similarly, the tropical environment has an impact on swarming behaviour; in the tropics, reproductive swarming of *A. cerana* is much more frequent than in temperate Asia or compared to *A. mellifera* and they also have high rates of non-reproductive absconding, e.g. due to external threats such as wasps or wax moths[267,272]. This could because the lack of true seasons and thus continuous abundance of resources enables colonies to easily find new sites. This frequent absconding could blur the distinctions between managed, feral, and completely wild populations[272]. *A. cerana* also has slightly different colony organisation to *A. mellifera*; workers have much higher levels of ovary activation (up to 5% of workers), even when queens are present, and are less responsive than *Am* workers to queen mandibular pheromones[273]. This may be an adaptation to a higher likelihood of queenlessness, caused by reproductive swarming[273]. However, worker reproduction is still policed (through oophagy) after the queen has left, although some eggs do survive, so it is unclear how adaptive this is[274]. *A. cerana* also seem to be more accepting of non-nestmate workers, including reproductive parasites in queenless nests[275,276].

A. mellifera, established in India in the mid-20th century, is also widely kept, with over 700, 000 managed hives, and has replaced *A. cerana* in much of Asia and parts of north India[277268]. One of the reasons for its success is that has a much higher honey yield than *A. cerana*, 37kg per year on average, compared with 7.9kg[268]; the smaller honey stores of *A. cerana* are connected with its higher likelihood of absconding[267]. Due to the more aggressive nature of *A. mellifera,* there have been fears that it would also replace wild *A. cerana* colonies, as it has done in parts of Japan[278]. However, there is no evidence of this in India, and *A. cerana* has the advantages of being more resistant to diseases caused by *Varroa destructor* and more adapted to the tropical climate of south India[279]. Furthermore, its readiness to swarm and abscond allows it to quickly inhabit new areas, making it more competitive in this sense than *A. mellifera*[267]. There have also been concerns about interbreeding between the two species, particularly as they use the same mating pheromones, and the potential for thelytoky (as in *A. mellifera capensis*), which could be detrimental to their long-term success[280]. However, experimental manipulations suggest that this may not be too much of a risk[281]. Furthermore, the timings of drone congregations are often different[277].

Stingless bees (Apidae: Meliponinae) are a subfamily of over 600 species, and many are important pollinators in tropical and subtropical regions across the globe[282,283]. In the wild, they usually nest in cavities close to the ground, in tree trunks, e.g. *Cycas sphaerica*[284], holes in the ground, or walls, and construct one or multiple small entrance tubes using plant resin and soil[285]. The internal structure of these nests varies between species and can either be combs or clusters of brood cells[286]. Like honeybees, they are eusocial, form perennial colonies of from 100 – 100,000 workers, and store honey (albeit in small amounts), making them suitable for domestication, also known as meliponiculture[287]. In India, there are thought to be eight species[288] but *T. iridipennis*, a "cluster builder" [286], is the most widespread and has been managed in India for centuries, if not millennia[288–290]. Both the honey it produces (around 600-700g per year per hive[291]) and the propolis from the nests are valuable as they are used in traditional folk medicine[292]. Research on propolis shows that it does have broad antimicrobial properties, making it an ideal material for nest construction[292]. Although they lack a functional sting, they can effectively defend a nest by using repellent resins at the entrance, guard bees, alarm pheromones and biting and chasing away intruders[293].

Aside from the social bees, there are other groups which contribute to the bee diversity of the Western Ghats. Carpenter bees, genus *Xylocopa*, are generally solitary and are important pollinators in the Indian tropics[294]. Additionally, some species can perform nocturnal pollination, enabling them to occupy a niche unavailable to other most bees[295,296]. *Xylocopa tranquebarica* is an obligately nocturnal bee and can navigate even on moonless nights[296]. It is also capable of buzz pollination, enabling it to pollinate crop species which honeybees cannot, e.g. Solanaceae such as aubergine[297].

Pollination in the Western Ghats

Research on pollination systems in the Western Ghats shows that social bees, including *A. cerana* and *T. iridipennis*, are major pollinators for both native plants and crops. Both species are generalist and polylectic, (e.g. in Kerala *A. cerana* collects at least 69 pollen types[298]), but individuals tend to be florally constant in the short term making them potentially highly efficient pollinators[299]. Their large colonies and effective recruitment also enable them to dominate floral resources.

The structure of pollination networks in forest ecosystems is partly mediated by canopy level; i.e. pollinator species diversity varies according to the height of trees or shrubs[300]. Upper storey trees and understorey plants tend to have different reproductive phenologies, which can impact on pollinator presence and theoretically can help to provide for pollinators over a long period of time[301]. For example, sequential blooms in plantations can support social bee colonies all year-round[265]. Furthermore, there is selection pressure on rare plants to flower early in the season, so they can be pollinated efficiently before the more abundant species flower[302]. Bhat and Murali argue that the pre-monsoon peak in flowering in many understorey species may be due to increased visibility of the flowers to pollinators, as leaves are absent[301]. Several pollinator studies have been conducted in medium altitude evergreen rainforests, in the Western Ghats, possibly the areas richest in biodiversity[303]. One study of the understorey shrub species in such a forest in Kakachi (Agasthyamalai hills), in the southern Western Ghats, shows that most of them are generalised to diverse pollinators, but honeybees (all three native species) are the most dominant floral visitors[304]. Another study found similar results and showed that social bees are especially attracted to mass flowering plants[305]. Also in Kakachi, Devy and Davidar found that *A. cerana* and *A. dorsata* were highly generalist and the main tree visitors overall (*A. florea* is apparently limited to the understorey, possibly because of its small size), but only visited species offering both pollen and nectar[303]. 75% of tree species were visited by one insect group, e.g. bees; this is more specialised than the trees in many other tropical forests. In a study of forests in the Nilgiri Biosphere Reserve, nearly half of the plant species had only one species of bee visitor, usually *A. cerana* or *Tetragonula* spp., while *A. florea* and *A. dorsata* tended to visit the more generalised plants[263]. There are far fewer social bee species in the Western Ghats than in the Neotropics, for instance, but the reasons for many of the differences in pollination ecology instance are still unclear.

There is a limited number of studies on the pollination ecology of specific native forest tree species in the Western Ghats. In the mass-flowering semelparous *Strobilanthes kunthianus*, in Kerala, *A. cerana* is the key pollinator[306]. It is possible that this species has outcompeted the wild bees. The congeneric *S. consanguinea* is also pollinated by *A. florea* and *Amegilla* sp.[307]. In an endangered medicinal plant, *Rauvolfia micrantha*, *A. cerana* and *T. iridipennis* are the only floral visitors which pollinate[308] and the critically endangered *Impatiens platyadena* is mainly pollinated by *A. cerana* and *A. dorsata*[309]. Meanwhile, *Canarium strictum*, a tall canopy tree found across Asia but declining in South India, is highly generalist, being pollinated by *A. dorsata, Xylocopa violacea,* the butterfly *Junonia* spp*.,* small flies, and a species of wasp[310]. However, the carpenter bee was the most frequent pollinator.

Pollinator limitation may be a contributing factor to the decline of some threatened plants in the Western Ghats; there is therefore potential for conservation via increasing pollinator abundance.

There have been several studies on the pollination of common crops grown within the Western Ghats region. Cardamom (*Elettaria cardamomum*) is grown in high-elevation hills of this area, usually in areca plantations, or under native forest canopy[311]. In a study of flowering cardamom plantations in three states of the Western Ghats (Karnataka, Kerala and Tamil Nadu) nearly 20 animal species visited the flowers[311]. However, only three of these were in fact pollinating (i.e. transferring pollen from anther to stigma): *A. cerana, T. iridipennis* and, less frequently, the solitary bee *Ceratina hieroglyphica*. At the Karnataka site, *T. iridipennis* was found to be almost twice as efficient as the honeybee; 83% of flowers it visited were pollinated, compared with 46.5% for *A. cerana*, perhaps because this bee also foraged for nectar. Furthermore more, visitation by *T. iridipennis* after *A. cerana* increased fruit set, indicating the importance of complementarity and functional diversity. At the other two sites, however, *A. cerana* was the principal pollinator; there were very few stingless bee visits[311], and in another study, *A. cerana* accounted for nearly 96% of visitors (although in this case *A. cerana* hives were kept nearby)[312]. The reason for the lack of *T. iridipennis* is unclear, but these results highlight the variability of pollination networks even for the same crop or between apparently similar ecosystems. Interestingly, a comparison of wild and cultivated cardamom shows that the wild plants tend to be pollinated by solitary bees (e.g. *Amegilla* sp. and *Megachile* sp.) and the crops by social bees, *A. cerana, A. dorsata*[313]. The social bees may be more attracted to the higher density and longer flowering of the cultivated cardamom. Unlike the crop, the wild cardamom was found in undisturbed forest, which may be more hospitable for solitary bees than the plantations. Several studies of coffee (*Coffea canephora*) agroforests in Kodagu, Karnataka, found that nearly 91-99% of all floral visitors were social bees[314–316]. Nearly 60% of these were *A. dorsata*, but *A. cerana* and *T. iridipennis* were also frequent visitors. The presence of these bees is shown to contribute to seed and fruit set, but the relative efficiency of each of the three species is unknown. In mango orchards in Maharashtra, *T. iridipennis* was found to be the most frequent flower visitor, with *A. cerana* and the blowfly *Chrysomya* sp. also visiting often, indicating that the stingless bee could be a key pollinator for mango[317]. However, the authors only counted insects per panicle, rather than the effectiveness of pollination. In bamboo, for example, *A. cerana* is a common visitor, but it is unclear whether it is a pollinator in Western Ghats species[318].

Pollinator declines

Pollinator species, including social bees, are thought to be in decline in India, as in most of the world. Domesticated *A. cerana* is in decline across Asia, including north India, by around 55% in the last decade, and is already regionally extinct in parts of Japan and China[115,319]. Populations may actually be increasing in south India, perhaps because of greater interest in beekeeping and the inability of *A. mellifera* to adapt to a tropical climate[319]. The data on abundance of wild *A.cerana* and other species, including *T. iridipennis*, is even more scarce, but circumstantial evidence suggests declines. Coffee and cardamom yields have declined in recent years in the Western Ghats, thought to be because of pollinator limitation[265]. In India as a whole the yield of many pollinator-dependent vegetables, e.g. cucurbit species, has decreased in recent years, while increasing for pollinator-independent crops[320]. Although figures are scarce, there are several ongoing threats to all bee pollinators in India (and the Western Ghats) which may be cause for concern.

Land use change

As in other tropical regions, landscape structure in the Western Ghats affects bee abundance and diversity and thus the pollination of crops and native plants. However, studies on the direct impact of land use change on pollinators in this region are limited. In coffee agroforests, visitation rate by the pollinator *A. dorsata* is negatively affected by distance to the nearest forest patch and smaller forest patches also harboured fewer *A. cerana* and *T. iridipennis*[316]. However, presence of the exotic *G. robusta* increases *A. dorsata* visitation to coffee, perhaps because of the absence of competing flowering plants. Solitary bees are not abundant in these coffee plantations; perhaps because the habitat is unsuitable for ground-nesting[315]. Overall, in these agroforests, decreased shade did not have a negative impact on pollination; the key is asynchronous flowering, which provides continuous floral resources and limits competition for pollinators. The pollination of *N. nimmoniana* was also compared in a disturbed site vs an undisturbed site; the former had lower bee abundance and diversity and *T.*

iridipennis was not present, as it was in the undisturbed site[321]. The authors suggest that solitary and stingless bees may be particularly vulnerable to habitat loss, notwithstanding the fact that *T. iridipennis* appears to be flexible in its nesting requirements[321,322].

Interesting, the boom in rubber production in Kerala in the 1970s saw a concomitant rise in beekeeping of *A. cerana*, due to the understanding that rubber is a valuable nectar source for this species[323]. This is an example of a positive effect of land use change on a managed pollinator; any potential trade-offs (for example, the impact on wild pollinators) have yet to be conclusively studied, but it is possible that other bees may also benefit from this nectar source.

Agrochemicals

Most research on the effects of agrochemicals on bees has been carried out in Europe and North America on *A. mellifera* and *Bombus* spp. However, studies on *A. cerana* show that neonicotinoids impair learning and foraging behaviour in *A. cerana*, potentially impacting on colony performance and survival[324,325]. Recent studies even suggest that *A. cerana* may be more vulnerable than *A. mellifera* to three of the most commonly used neonicotinoids: imidacloprid, clothianidin[326] and dinotefuran[327].

Diafenthiuron, used widely in cardamom plantations, is toxic to *A. cerana* and also has sublethal effects on homing and foraging[328]. However, *A. dorsata* and *T. iridipennis* are the most susceptible cardamom pollinator species[329]. To date, there has been no study of the mechanisms behind the effects of agrochemicals on *T. iridipennis*, but they may be similar to other stingless bees[141].

There has been a recent overall decline in pesticide use in Kerala but an increase in the highly toxic chemicals, which could be a cause for concern for pollinator species[330]. Analysis of honey from *A. mellifera*, *A. dorsata*, and *A.florea* shows that *A. mellifera* is exposed to more pesticides, probably because they forage more on cultivated plants[331]. Thus, encouraging native bees to pollinate crops could be problematic if they are sprayed with harmful insecticides.

Disease

A. cerana is vulnerable to Thai sacbrood virus, which wiped out around 90% of the colonies in southern India and many states in the north in the early 1990s[323]. This caused beekeepers in the south to start keeping *A. mellifera*; however, as discussed above, this species is vulnerable to *Varroa* infestations, which have limited its spread in the Western Ghats[268]. Furthermore, there is the possibility of pathogens spreading between the species, or into wild populations, but very little is known about the impact of disease on wild bees, or domesticated *T. iridipennis*.

Future

Clearly, most of the pollination services in the Western Ghats are provided by social bee species, with *A. cerana* and *T. iridipennis* as two of the key pollinators. However, honeybee hives require monetary investments by the farmers and might not be easily affordable, and over-reliance on a single species is risky. Moreover, functional diversity should be promoted[265], by encouraging traditional home-gardens and other biodiversity-friendly management, and perhaps restoring forest fragments where possible[332]. More research needs to be conducted on the behaviour of native wild bees and the pollination ecology of varied agricultural and natural ecosystems.

Apis cerana **and** ***Tetragonula iridipennis*****: niche partitioning**

In many environments, species are potential competitors for the same resources, and therefore avoid competition by using them differently, e.g. temporally or spatially. This niche (or resource) partitioning enables the species to co-exist. *A. cerana* and *T. iridipennis* are both generalist pollinators, as are most bees[84,333], and living in abundance in the same environment, hypothetically with access to the same resources. Consequently, there is potential for competition between the species, and perhaps a level of niche resource partitioning in order to reduce that competition, allowing the species to co-exist. Nesting resources can be subject to competition and/or partitioning, but this current study focuses on the partitioning of food resources and the potential interplay with foraging behaviour. Indeed, one of the major ways in which colony fitness can be directly affected is by competition for pollen or nectar. Interestingly, it is known that when pollen resources are scarce, honeybees increase their foraging efforts to provide for their brood; on the other hand, stingless bees respond by reducing their brood production[334]. However, the use of different plant types has not often been directly compared in *A. cerana* and *T. iridipennis*. In north India, pollen and nectar collection was compared and there was mostly overlap between plants used[290]. However, this is based on observations within a given area rather than total input to the colony; furthermore, data is not provided on frequency of visits. On the other hand, analysis of pollen collected by three Malaysian stingless bee species shows evidence of interspecific partitioning, despite being the same size and living in close proximity (within 250m) to each other[335]. Similarly, in both north India and Japan, *A. mellifera* and *A. cerana* differ significantly in pollen sources[336,337]. It should also be noted that partitioning can vary over time; mass flowering events can cause temporary convergence in pollen diet, while resource scarcity forces foragers further afield and leads to divergence[338].

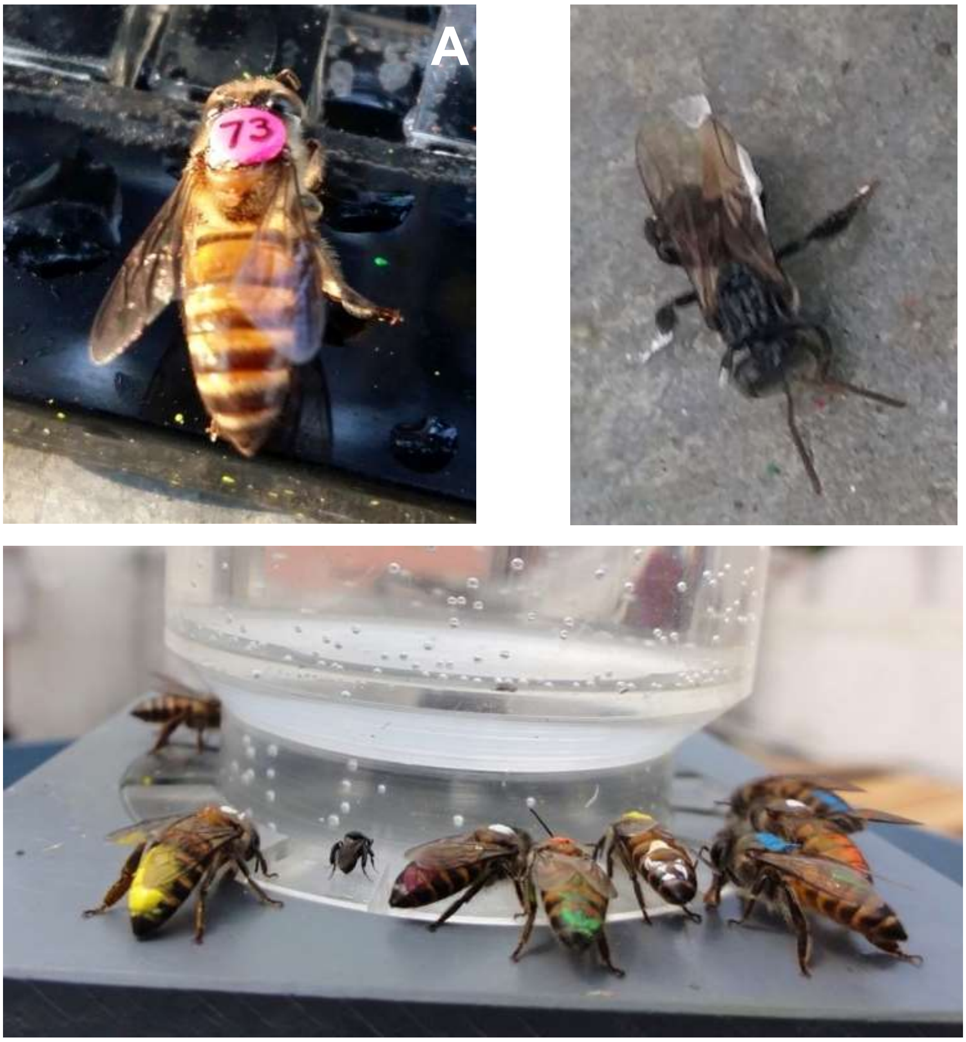


Figure 1.3 A: *A. cerana*; B: *T. iridipennis*. C: both species at an artificial feeder together, for size comparison.

There are several major ways in which sympatric social bees can partition such resources: temporal variation, differences in spatial distribution, innate preferences or resource requirements, and colony communication and recruitment strategies. I will discuss each of these as they relate to the differences between *A. cerana* and *T. iridipennis* and conclude with the scenario of direct competition in the form of interspecific interactions.

Temporal variation: diurnal activity patterns

Diurnal activity patterns are expected to vary somewhat between bee species, partly because of differential impacts of light intensity and temperature, and availability of floral resources[339,340]. For instance, smaller sized bees can generally forage at higher temperatures as they lose heat more easily[264]. Such temporal partitioning can also be a good mechanism for reducing competition. However, despite being crucial pollinators, there are very few studies on the overall colony activity of Asian bees.

Reddy observed *A. cerana* colony foraging over two years in Karnataka, finding that pollen foraging was highest in July (rainy season), perhaps due to the availability of particular floral resources, but nectar foraging was more common throughout the year[341]. A later study shows that foraging activity is highest in the morning; pollen foraging peaks at 08:00 and is very low after midday, while nectar foraging is high between 07:00 and 11:00 and then declines[342]. Similarly, Mattu and Verma examined the activity of *A. cerana* colonies in the Himalayas[343]. Overall foraging activity was higher in the summer and autumn and there was seasonal variation in diurnal activity patterns, perhaps because of climatic variation and differences in floral resources. Generally, pollen collection peaked in the morning (around 10:00) and nectar peaked later in the day; there were higher numbers of nectar foragers across all seasons. Clearly, honeybee activity varies between temperate and tropical ecosystems.

A study of *T. iridipennis* colonies in Kerala found that, like *A. cerana*, pollen foraging was at its peak in the rainy season (June and July)[344], which was supported by a study in Karnataka[345]. Saravanan and Alagar observed colonies of *T. iridipennis* in Tamil Nadu, finding that activity was highest in the morning, and had a second peak in the evening, with low activity between 13:00 and 15:00[346]. More nectar foraging was observed overall and was constant throughout the day, while pollen foraging peaked in the morning. Similarly, colonies in Kerala perform 90% of their pollen foraging between 05:00 and 09:00, while nectar collection continued throughout the day[287]. Various other studies have shown that pollen foraging peaks in the morning in related species, including *T. laeviceps*[338,347,348], and general foraging activity peaks in the morning in *T. iridipennis*[345,349]. However, Singh and Khan found that *T. iridipennis* colonies in north India had two peaks of pollen foraging activity: 8:00 and 16:00[350]. Generally, both *T. iridipennis* and *A. cerana* seem to focus on pollen foraging in the morning, perhaps due to higher pollen availability (most anthesis takes place in the morning), and nectar foraging later in the day, perhaps because it has become more concentrated.

Most research on foraging activity is carried out in specific crop plants; even so, there are few direct comparisons of these patterns in *A. cerana* and *T. iridipennis*, and only a couple of these in south India. In a cardamom plantation in Kerala, both species foraged from 06:00 to 13:00, and there was considerable overlap, but *T. iridipennis* peaked at 07:00 and 13:00 while *A. cerana* peaked at 08:00[312]. The authors suggest that nectar depletion over time accounts for these differences; larger bees require more nectar[312]. These two species were also most active in the morning when pollinating macadamia, but the peak activities of individual species are not mentioned[351]. In Australia, the stingless bee *T. carbonaria* foraged for macadamia pollen in the morning, focusing more on nectar later on; however, *A. mellifera* collected nectar generally at a constant rate throughout the day, without collecting much pollen at all[352]. In rambutan trees, *A. cerana* and *T. iridipennis* were similar in activity throughout the day (peak at 10:00-11:00), but the honeybee was much more abundant than the stingless bee in the early morning, perhaps to collect more pollen around the time of anthesis[353]. Similarly, in fennel *T. iridipennis* starts foraging later than the honeybee species[354], while in bitter gourd there may be considerable overlap[355]. However, in Mangalore gourd, *T. iridipennis* activity peaks around 11:30, with a sharp drop-off afterwards; *A. cerana* peaks two hours later. Finally, a study on aubergine pollination in Sri Lanka found that the foraging activity of *A. cerana* and *T. iridipennis* almost completely overlaps[356]. Aubergines are buzz-pollinated and *T. iridipennis* can only collect fallen pollen, so may benefit from other species' recent visits, including those of *A. cerana* which can damage the anther to extract pollen[356]. Furthermore, a comparison of *A. cerana* and *T. laeviceps* finds that the latter tends to visit pepper (*Capsicum annuum*) later in the day, perhaps because they can use the depleted resources[357].

Many of the studies on *A. cerana* pollinating activity are comparisons with other honeybees, particularly *A. mellifera*. In temperate Asia, they generally forage earlier in the morning and later in the evening than *A. mellifera* and the open-nesting species, perhaps because they are active at lower temperatures[264,358–360]. In one study in Kashmiri apple orchards, *A. cerana* also peaks in activity earlier than *A. mellifera*, perhaps as a competitive strategy[358].

Overall, there is clearly considerable overlap in diurnal activity between the two species, but the extent of this overlap may depend on the climate and the plants being visited. We need more direct comparisons of colony activity in the same environment to assess whether there is temporal partitioning.

Resource preference

Another way in which resource partitioning can occur is through divergence in floral preferences between the species. This can be relatively fixed, e.g. due to differences in visual ability, cognition or innate colour preferences. Or it can vary with colony cycle or season, caused by different nutritional needs, at the worker or the colony level, e.g. specific amino acid requirements.

Honeybees and stingless bees have very similar colour receptors and both show a marked preference for blue and blue-green flowers[361,362]. However, when this colour range was absent, a comparison of *A. cerana* and *A. mellifera* on flowering plants shows that related species can have different preferences, *A. cerana* preferring pink or white flowers, while *A. mellifera* prefers yellow[363]. This may be due to evolving in different environments; colours can be associated with resource richness. Neotropical stingless bee species also vary in their colour preferences[364] but both of these studies were on experienced bees, so do not necessarily reflect innate preferences. Although *A. cerana* and *T. iridipennis* are both present in the Asian tropics, the differences in size and physiology make it likely that their vision would also differ to a certain extent. For example, bee size is usually correlated with visual sensitivity and larger stingless bees are able to forage at lower light levels than smaller species in Costa Rica[365]. This may impact on diurnal activity patterns. Another study compared *A. mellifera* and the Neotropical stingless bee *Melipona quadrifasciata*, finding that the latter is better at discriminating colours in the blue-green region than *A. mellifera*, which is better at discriminating other colours[366]. These species evolved and/or were domesticated in different environments; such findings are possibly not transferable to sympatric species. Unfortunately, the study of stingless bee vision is very recent[364] and there are no direct comparisons of this trait in *A. cerana* and *T. iridipennis*.

Likewise, their nutritional requirements have not been directly compared, but there are likely to be species differences. It is expected that both species would show a preference for nectar high in sugar content, but they may differ in their behavioural response to this reward[367]. *A. mellifera*, for instance, carries the same quantity of nectar regardless of concentration, while the Neotropical stingless bee *M. compressipes* carries more when it is concentrated, and *M. fuliginosa* carries more when it is dilute[368]. This behaviour affects the time spent at each flower, and therefore the amount of flowers visited. Furthermore, although bees acquire most of their protein from pollen (for brood), the presence of amino acids in nectar can influence flower choice. For example, nectar containing glycine is attractive to *A. mellifera*[369] but repellent to *Melipona* spp.[370]*.* Meanwhile, *T. hockingsi* seems indifferent to nectar with amino acids[371]. Pollen quality also affects honeybee foraging; they tend to prefer pollen with higher levels of essential amino acids[372]. This is assumed to also apply to stingless bees, but there have been no similar studies on them.

Spatial variation: landscape distribution

The distribution of bees in a landscape is mediated mainly by size (which affects foraging distance and height) and navigational ability. These are likely to be key factors in resource partitioning between *A. cerana* and the smaller *T. iridipennis*.

Size also influences the altitude at which bees live and forage; in the tropical highlands, *A. cerana* is the dominant pollinator, while *T. iridipennis* is only found below 1500m[262]. However, in areas where both bees are present, foraging range is a key mechanism of resource partitioning. It is well established that bee foraging ranges vary with size; larger bees can fly further. In a review of both homing experiments and feeder training experiments, Greenleaf et al found that maximum foraging distance was correlated with size in a range of social and solitary species[373]. Within the Neotropical Meliponinae, foraging range also increases with species size[374]. *A. cerana* generally forages up to around 1km from the nest[262,264], does not follow an artificial feeder further than around 1.5km[375], but has been known to fly up to 4km[376]. This is much shorter than *A. mellifera*, which regularly travels over 2km and can travel up to 15km[377], although in the Neotropics feral *A. mellifera* generally travels up to 1km[378]. The Neotropical stingless bee *Melipona mandacaia* can follow a feeder up to 2.1km[379]. However, the smaller *T. carbonaria*, a close relative of *T. iridipennis*, generally forages around 300m from the nest, with a maximum of around 700m, based on homing experiments[380]. Given that *T. iridipennis* is slightly smaller than *T. carbonaria*[288,380], it is expected to have a more restricted flight range. This limits *T. iridipennis* to nearby resources, while *A. cerana* can forage further afield to find preferred plants. If preferred resources are limited, this could cause competition and resource partitioning[381]. This is corroborated by pollen analysis in Sri Lanka; the smallest bee (*T. iridipennis*) collected the richest diversity of pollen, while the largest (*A. dorsata*) visited half as many species. *A. florea* and *A. cerana* showed intermediate levels of pollen diversity. Additionally, smaller bees can access resources provided by smaller flowers and may also be able to nectar rob plants which larger bees cannot, a behaviour common in *Tetragonula* spp.[382].

Species often partition resources by forest canopy height, which can be influenced by size. For example, in a Malaysian rainforest, the largest bee (*Apis koschevnikovi*) visited the canopy feeders while some of the smaller stingless bees preferred the understorey[383]. However, stingless bees are also known to pollinate canopy trees[262]. In a study on the yellow flame tree (*Peltophorum pteroca*) in Malaysia, honeybees (including *A. cerana*) were more likely to forage at the top than the bottom, but *Tetragonula* spp. foraged at all levels[384]. There is no clear trend for stratified foraging and it may depend on specific flowering phenologies.

Lastly, the navigational ability of bees affects their distribution in a landscape. As central-place foragers, bees can navigate both to a food source and back to their nest, using memorised visual landmarks as reference points[385]. Both honeybees and stingless bees measure distance travelled by optic flow; the more visual information flowing past, the greater the distance estimated by the bee[386–388], and in honeybees the perception itself has been shown to affect gene expression[389]. The two species may regularly fly at different heights, which alters the amount of optic flow being processed and thus distance estimation; the impact that this may have in practice is unknown[390,391]. Indeed, navigation has only recently been studied in stingless bees but there may be subtle differences in the way they “view” the landscape. Leonhardt et al found that *T. carbonaria* has greater homing success in relatively homogenous forest environments than in macadamia plantations which have obvious large visual landmarks, which are believed to be key to honeybee navigation[385]. The authors speculate that stingless bees may include olfactory cues in their map of the landscape, noting that they can find specific resin sources based on volatile production[392]. Landscape fragmentation may affect species in different ways; for instance, pollination studies in an Amazonian rainforest suggest that stingless bees fail to cross open land, while *A. mellifera* is seemingly unaffected by habitat structure[134]. In general, landscape structure is known to affect bee species at different scales, due to different habitat requirements and foraging ranges[393]. However, the behavioural and cognitive mechanisms behind this have not been investigated in these two species.

Communication and recruitment strategies

Social bees dominate pollination networks in many landscapes because of their large colonies and ability to recruit nestmates to floral resources. *A. cerana* has larger colonies than *T. iridipennis*, making it generally more competitive when mass recruiting foragers. Furthermore, honeybees have a highly developed, precise and efficient recruitment system. The waggle dance, performed by a returning forager, conveys both distance and direction of a floral resource to potential foragers, using the solar azimuth as a reference point. Waggle dances can also communicate information about the quality of the food source[394]. Moreover, the dance can be modified in response to toxic nectar; if alternative sources are available, bees will alter their dances to discourage foragers from following them[395]. The existence of distinct dialects among different *Apis* species remains debateable[396,397], but *A. cerana* can successfully decode and apply *A. mellifera* dances[398].

Far less is known about the mechanisms of stingless bee recruitment, but there is evidence that olfaction plays a key role in many species. Some stingless bees such as *Melipona panamica* simply scent-mark the food source, while others such as *Scaptotrigona* spp. leave a continuous scent trail on the vegetation between the source and the nest[399]. Some, such as *Trigona hyalinata*, leave a short trail in the direction of the food source[399]. These methods can effectively convey both distance and direction of the food source and have all been shown to increase the recruitment of nestmates[399]. Flaig et al recently found that *Partamona orizabaensis* can mass recruit bees to a specific food source without scent marking it or any substrate[400]. They speculate on the possibility of an aerial "odour tunnel" left when a bee flies back to the nest. Stingless bees may also have intranidal mechanisms of recruitment. For example, food exchange (trophallactic contact) or body and antennal contacts between the returning bee and other foragers can play a role, perhaps through transferring scents, but it is unclear whether they merely trigger foraging or convey location information[399]. They can also run around excitedly and produce buzzing sounds[399]. Finally, some species, such as *Trigona corvina*, lead new recruits in the direction of the food source by performing 'piloting flights'[399401].

Recruitment in stingless bees has mainly been studied in the Neotropical species and the recruitment mechanism of *T. iridipennis* has not been studied. Von Frisch reported *T. iridipennis* foragers running around the hive "excitedly", but it is unknown whether this is a recruitment mechanism[402]. The congeneric *T. carbonaria* can communicate direction of a food source but apparently not distance[403]. How this information is conveyed is still unknown, but they do not use scent trails; they may mark the food source and/or the food scent could be transferred during body contacts[403]. Yet, given the variation in communication techniques among even closely related species, this may not apply to *T. iridipennis.*

There are potential drawbacks to the (putative) recruitment systems of both species. Some stingless bees are able to follow the scent markings of heterospecifics; this could cause increased competition between species[404]. *T. iridipennis* is the only stingless bee in the Western Ghats so this should not be an issue, unless other social bees can also detect their scents. On the other hand, one of the idiosyncrasies of honeybee dance communication is its dependence on the solar azimuth. Around midday, this becomes harder to bees to gauge and they generally dance less[264]. This presumed decline in recruitment might at least temporarily impede the competitiveness of *A. cerana*. Furthermore, scent marking bypasses the problem of bee perception; honeybee waggle dances convey distance as perceived by optic flow[386,387], thus the information may vary depending on the landscape structure[405].

Interspecific interactions

Despite potential temporal and spatial partitioning, it is likely that abundant sympatric bees will often interact at the same plant or even the same flower. Some stingless bees such as *Trigona* spp. are known to out-compete others by aggressively defending food sources in groups[406]. In a Malaysian rainforest, Nagamitsu and Inoue found a dominance hierarchy of stingless bee species and a trade-off between searching ability and successful defence of a resource[383].

T. iridipennis also shows high levels of aggression towards sympatric honeybees. Koeniger and Vorwohl investigated competition at artificial feeders between *T. iridipennis, A. florea, A. cerana* and *A. dorsata* in Sri Lanka[381]. Generally, smaller species would be aggressive towards larger ones, and *A. cerana* also displayed intraspecific aggression between colonies. *T. iridipennis* won contests against *A. cerana* alone; overall, in varying combinations of species, *T. iridipennis* was the most successful in controlling the feeder. This high level of aggression can help to compensate for a short foraging range.

In a more natural setting, however, aggressive interactions between bee species may not be common. In a study on macadamia pollination, Heard observed no aggressive interactions between *A. mellifera* and *T. carbonaria*[352]. This may be because the abundance of food in a macadamia orchard averts direct competition. Or it could be because *T. carbonaria* has not evolved to react to *A. mellifera*'s presence; aggression is thought to be triggered by a bee's cuticular profile. Chaudhary and Kumar did not observe aggression between *T. iridipennis* and *A. cerana* in a cardamom plantation in Kerala; again, there is no need to defend individual flowers when resources are plentiful.

Summary and aims

This review of the literature highlights the scarcity of knowledge regarding pollination ecology in tropical regions, particularly in the Asian tropics. *A. cerana* and *T. iridipennis* are key pollinators in South India, yet very little is known regarding their foraging behaviour or potential niche partitioning between them. Given the current lack of data, I developed straightforward experiments and observations to attempt to investigate their foraging behaviour. These were also designed to be logistically possible in the time available, and suitable for the climatic conditions of South India. Thus, there are three major questions of my thesis, and three types of experiment/observation with which to answer them.

First, is there resource partitioning between the species; specifically, do they utilise different pollen sources?

Second, is there variation in their spatial distribution; specifically, how far does each bee forage in a given environment?

Third, is there temporal variation between them; specifically, do they vary in diurnal foraging activity patterns?

These questions are answered respectively by: collection of pollen from both species; training each species to an artificial feeder; and direct observations of activity at the hive.

Chapter Two: Methods

Study species

All hives of *Apis cerana* Fabricius and *Tetragonula iridipennis* Moure (formerly also referred to as *Trigona iridipennis*) were hired from a local (Kadakkal) beekeeper (Figure 2.1).

Locations

Three field sites in Kerala were used (Figure 2.2): peri-urban part of the city Trivandrum (IISER city campus (Malayil building), Trivandrum – 8° 32.639'N latitude; 76° 55.336'E longitude); paddy field (near Kadakkal – 8° 51.411'N latitude; 76° 56.566'E longitude); rubber plantation (Kadakkal – 8° 50.167'N latitude; 76° 54.381'E longitude). The sites were chosen as there were logistically convenient and access was granted by landowners. They also represent typical areas of human activity in Kerala that alter the landscape, reducing natural forest and increasing fragmentation, and where humans impact significantly on the plant communities that are suitable as food sources for bees.

Figure 2.1 Hives of the study species. Top: *T. iridipennis* hive. Bottom: *A. cerana* hive.

Figure 2.2. Study locations. A: City (peri-urban area of Trivandrum), hives were housed on the roof and on the ground of a 3-storey building. B: Rubber plantation (hive is in the right corner of the picture). C: Paddy field (hive was located at the edge of the paddy).

Pollen collection

Pollen was collected from *A.cerana* in all three sites from a total of eight hives, using pollen traps for between 0.5-2 hours per day. Collections were made between December 2015 and February 2016 (dry season) and between April and July 2016 (end of dry season and transition to wet season). It was not possible to develop a similar method of pollen trapping *for T. iridipennis* as their activity was severely disrupted when attaching any artificial device to the nest entrance. Therefore, to establish a proxy for pollen utilisation by foraging *T. iridipennis*, pollen was collected by removing stores of two separate hives, one in a rubber plantation (February 2016) and the other in the city (July 2016). Given the lack of knowledge of pollen-storing behaviour, consumption and division of labour in *T. iridipennis*, I did not attempt to make a comparison with stored A. cerana pollen.

Pollen was frozen or stored in alcohol. A total of 216 slides were prepared using detergent to reduce clumping, and basic fuscin gel to stain the pollen. Slides were analysed using a Leica phase-contrast microscope LM1000. For frozen pollen, each pollen load was sampled, while alcohol-stored pollen was sampled as a whole and pollen grains were counted in a subset of microscope images.

Artificial feeder training

Artificial feeder training was performed for both species in the rubber plantation (December 2015) and for *A. cerana* in the paddy field (April 2016). Due to unexpected weather patterns with early onset of the monsoon, it was not possible to also conduct experiments with *T. iridipennis* in the paddy field. Both bee species were trained to an artificial feeder containing 30% sucrose solution, placed 1m from the hive. *A. cerana* foragers were captured from the feeder and marked with a small number tag at this initial distance (100 for each habitat). *T. iridipennis* were not tagged, due to their small size. The feeder was then placed at increasing distances from the hive, up to 210m. For both species, I recorded the time taken for 15 bees to feed simultaneously at each distance, defining this as the point when the hive successfully exploited the feeder. If this target was not reached and the number of bees feeding simultaneously had not increased for 30 minutes, I increased the distance in order to ascertain a maximum distance at which the bees would give up. I increased the distance after 15 *T. iridipennis* bees were feeding simultaneously. For *A. cerana*, I also recorded the visits of the individually marked bees. I waited until the time when 15 foragers were feeding simultaneously and 20 marked bees had visited at least twice, before removing the feeder and placing it at the next distance. This was in order to gain an idea of the taken taken for individual bees between hive and feeder at each distance, which was not possible in *T. iridipennis* as they could not be individually marker. To change the position of the feeders, the feeder was removed and cleaned, and the observer retreated to wait until the bees cleared the area. The feeder was then positioned at the next distance. Bees are known to remain faithful to successfully visited patches[407,408] while they are still profitable. The distance between hive and food source influences a honeybee's evaluation of the source's profitability; i.e. an increased distance will reduce the reward to energy expended ratio[402]. Therefore, I analysed the latency to fully exploit the feeder at each distance with two types of measurements, as explained above, to detect any reduction in attractiveness due to the distance and/or the limit of a species' foraging range[373]. For *A. cerana,* the whole experiment lasted two days (reaching maximum distance on the second day) in the plantation and one day in the paddy field. For *T. iridipennis*, it lasted one day in the plantation, reaching maximum distance on the same day.

In the paddy field, it was necessary to place the feeder on a path on the edge of the field (up to 50m), after which the feeder was placed in the middle of the field (and more in line with the hive).

Activity recording

Observations were made over a period of 5 weeks (on 29 days for *A. cerana* and 35 days for *T. iridipennis*) in the urban site in June 2016, the end of the dry season. Five hives of *A. cerana* and eight hives of *T.iridipennis* were observed for 5 minutes every hour, with assistance from 1-3 other students, so many hives were observed simultaneously. Observations were made from 6:00 to 18:00, but due to a logistical mistake, no observations of *T. iridipennis* were made between 08:00-09:00. Therefore data were included in the GLM for a time period between 9:00 and 17:00.

All exits, pollen forager entries and non-pollen forager entries were counted. Weather data were also gathered from local meteorological weather station (temperature (°C), UV index, cloud cover (%), humidity (%) and wind (km/h)). Most observations were made on the roof of the three-storey building, but 2 hives of *A. cerana* and 4 hives of *T. iridipennis* were at ground level, in order to detect any confounding effects of the height of the hive location on the bees' activity.

Observations were also made from videos of two *A. cerana* hive entrances located on the roof top of the building that were recorded between 18th February and 7th March (mid dry season) from 06:00 to 18:00, for a total of 9 days. These videos were also analysed in another longitudinal study that extracted data for a group individually-marked pollen and nectar foragers[409], but I utilised the raw video material separately to extract data on hive activity across the day. I sampled five minutes in the middle of each hour of the day, counting the number of exits, pollen forager entries and non-pollen forager entries (presumably nectar foragers according to Ramesh et al[409] who captured returning bees with and without pollen and found that those without pollen never carried water and those with pollen never carried nectar).

Statistical analysis

Statistical tests were performed using IBM SPSS Statistics 24. Chi squared tests were performed on pollen frequencies within species, to determine if one pollen type was favoured. Pollen frequencies were not quantitatively compared between species, as methods of sampling were too disparate. Feeder training data was analysed using a general linear model (GLM), with species or location as a fixed factor, distance as a covariate, and time as a dependent variable. A GLM was also constructed with the activity data, using overall activity (exits) and pollen foraging as dependent variables; species, hive and location (ground or roof) as fixed factors; and time of day and weather conditions (temperature, humidity, cloud cover, UV index, wind speed and rainfall) as covariates. An interaction between species and hive was specified to account for the fact that hive is nested within species. Separate GLMs were constructed for each species (with the above variables to same) to determine the effects of location and temperature on each. Another GLM was used for *A. cerana* to compare seasons, using overall activity (exits) and pollen foraging as dependent variables; season, hive and location (ground or roof) as fixed factors; and time of day and weather conditions (temperature, humidity, wind speed and rainfall) as covariates.

Figure 2.3
A: Pollen collection at *A. cerana* hive entrance.
B: Pollen collection from *T. iridipennis* hive.
C-D: *A. cerana* feeder training in the rubber plantation.

Chapter Three: Results

Pollen analysis

Bees visited 20 different plants for pollen collection (12 by *A. cerana*; 13 by *T. iridipennis)*. Of these, only 5 were shared. 8 were unique to *T. iridipennis* and 7 to *A. cerana*. A breakdown of samples by species and site is given in Table 3.1. Of the twenty pollen morphotypes, only one has been conclusively identified: Morphotype 1 (coconut: *Cocos nucifera*): see Figure 3.1. The identification of the other morphotypes requires the help of an experienced palynologist and has yet to be accomplished.

A. cerana collected significantly higher amounts of coconut (*Cocos nucifera*, Figure 3.1) pollen than all other types combined in all locations. City: 83.88% (x^2 = 459(1), p<0.05); Plantation: 90.57% (x^2 = 1,875(1), p<0.05); Paddy: 99.94% (x^2 = 3,662(1), p<0.05).

At the plantation site, *T. iridipennis* collected mostly coconut pollen: 66.7% (x^2 = 8,438(1), p<0.05). However, in the city, morphotype 11 (Figure 3.2, as yet unidentified) was primarily collected: 58.88% (x^2 = 506.3(1), p<0.05) and 8.09% coconut.

The relative overall percentages of each pollen type in the five groups are shown in Figure 3.2. The species are not statistically compared as the sampling methods are too disparate.

	Total	**Unique to site**
A. cerana city	8	4
A. cerana plantation	7	3
A. cerana paddy	2	0
T. iridipennis city	10	3
T. iridipennis plantation	9	3

Table 3.1 Pollen types for each group: total number and number unique to site (within the species).

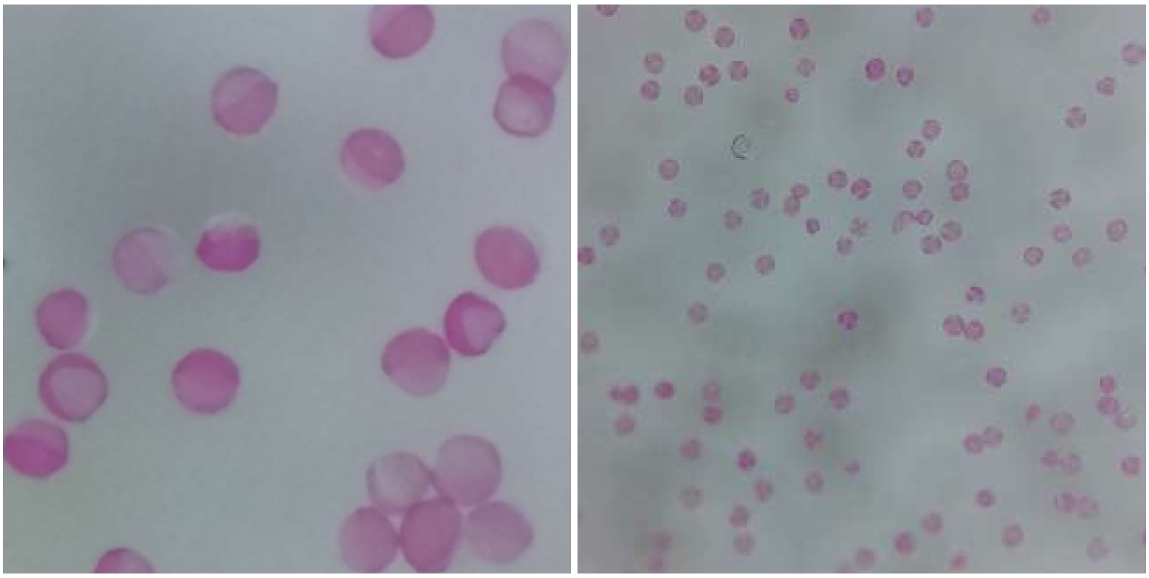


Figure 3.1 Images of slides with pollen samples. Left: pollen morphotype 1 (Coconut), Right: pollen morphotype 11 (unidentified). Pollen samples were stained with basic fuscin gel.

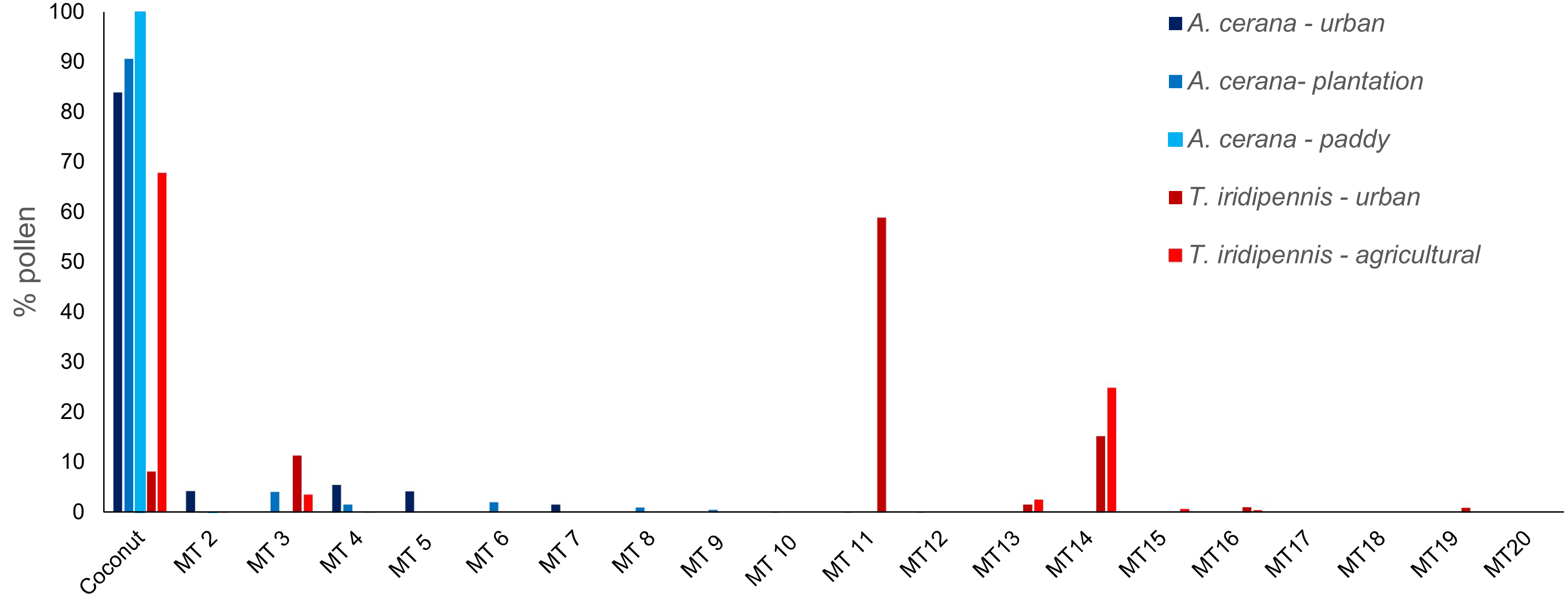


Figure 3.2. Overall percentages of each pollen morphotype, sampled from pollen sacs of returning A. cerana foragers or from pollen stores of T. irridipennis hives.

Artificial feeder training

Species comparison

T. iridipennis followed the feeder to a maximum of 130m but beyond 70m there were visits from only 4 bees simultaneously or fewer. *A. cerana* continued following until the end of the plantation (210m). A comparison of time taken for each species to exploit the feeder (15 bees feeding simultaneously) is shown in Figure 3.3. The time taken for *A. cerana* was constant across all distances up to 70m ($F=0.012_{1,5}$, $p=0.916$, $R^2 = 0.02$), while *T. iridipennis* was slower at all distances and slowed down as the distance increased: there was a significant interaction between species and distance as an effect on time taken ($F=6.516_{3,1}$, $p=0.029$, $R^2 = 0.808$).

Habitat comparison

In the paddy field, *A. cerana* went to a maximum distance of 70m, but with only 10 bees visiting simultaneously at this distance. 50m was the maximum at which 15 bees fed simultaneously. A comparison of *A. cerana* in the plantation and the paddy field is shown in Figure 3.5. At every distance, *A. cerana* is slower in the paddy field: there is a significant interaction between location and distance as an effect on time ($F=6.881_{1,3}$, $p=0.03$, $R^2 = 0.798$). When the full distance is analysed for the rubber plantation, *A. cerana* time taken is significantly affected by distance ($F=17.525_{1,3}$, $p=0.003$, $R^2 = 0.687$).

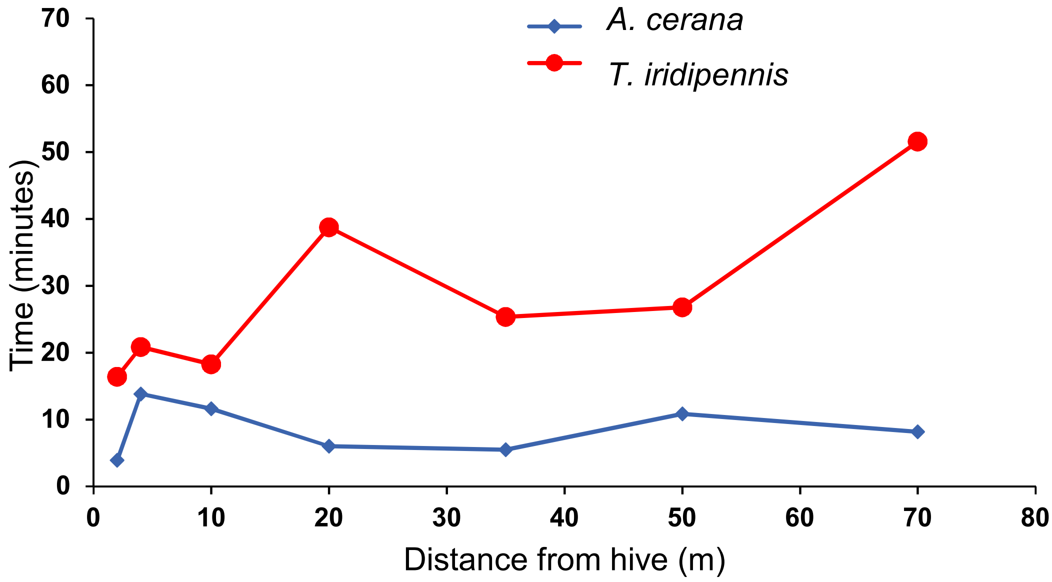


Figure 3.4 Species comparison: *A. cerana* v *T. iridipennis*. Time taken to "exploit the feeder" (15 bees to feed simultaneously) vs distance

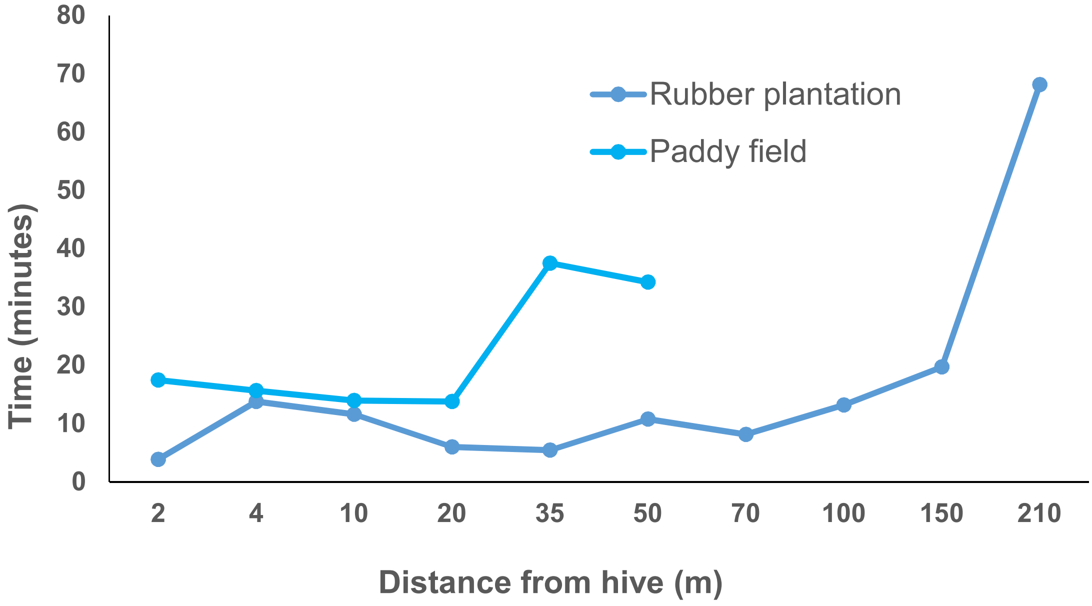


Figure 3.5 Location comparison: rubber plantation v paddy field. Time taken to "exploit the feeder" (15 bees to feed simultaneously) vs distance from hive.

<u>*A. cerana* marked bees</u>

None of the marked bees visited at every distance in the rubber plantation, and most visited at only three or fewer. Table 3.2 shows the number of marked bees which visited the feeder at *x* number of distances (total bees = 99). Of the 42 bees which visited only once, most of those visits were either close to the hive or at the furthest distances (Table 3.3.)

No of distances	9	8	7	6	5	4	3	2	1
No of bees	2	0	5	9	5	8	14	14	42

Table 3.2 Number of distances in the rubber plantation visited by marked bees.

Distance	2m	4m	10m	20m	35m	50m	70m	100m	150m	210m
No of unique visits	9	7	3	2	2	0	1	1	8	9

Table 3.3 Number of unique marked bees at each distance in the rubber plantation.

As expected, the average time between visits (for marked bees) increases with distance (Figure 3.5).

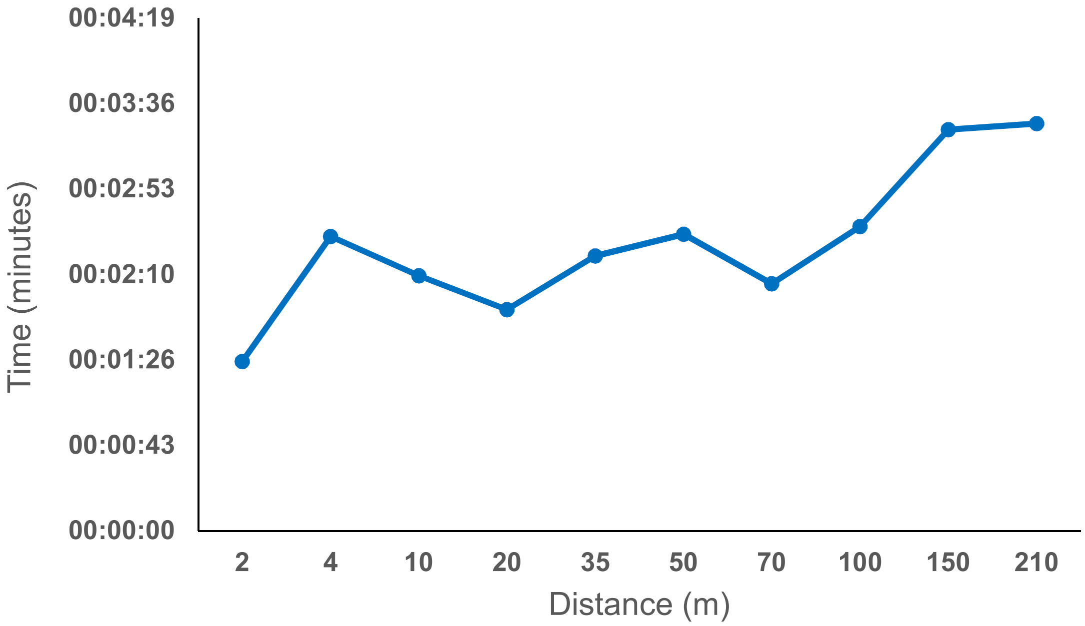


Figure 3.5 Time between first and second feeder visit for *A. cerana* marked bees in the rubber plantation.

Diurnal activity patterns

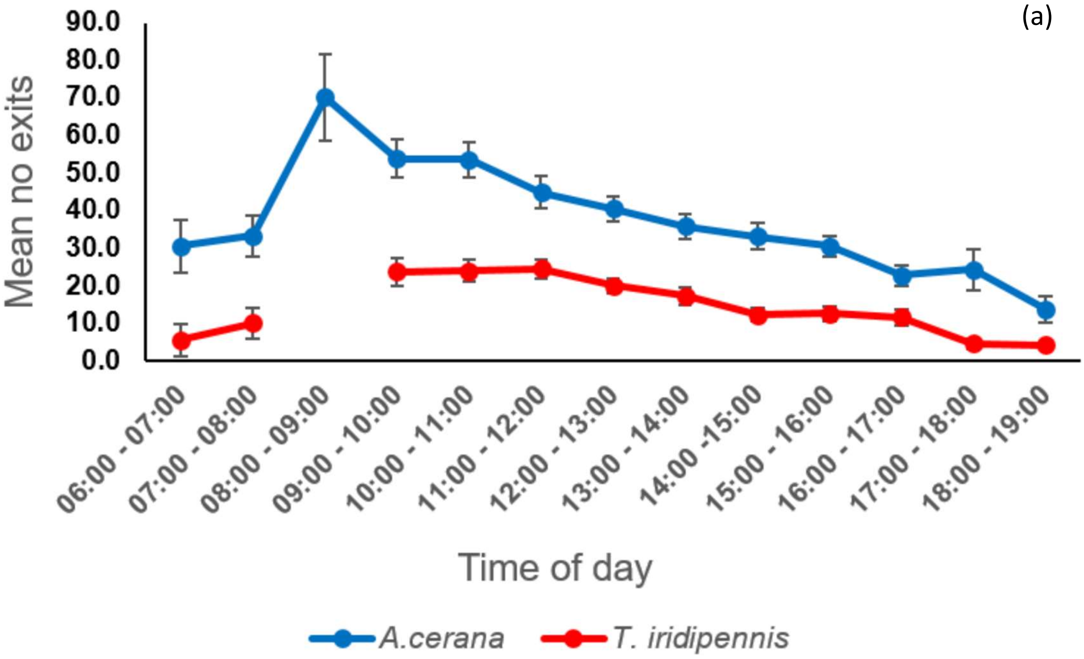
Species comparison

The overall activity pattern through the day (number of exits) was similar in both species (Figure 3.6a). Generally, activity increases from 06:00 and remained high (there is a peak in *A. cerana* from 08:00-09:00) until 10:00-11:00, after which it declined throughout the rest of the day. Pollen foraging (as a proportion of hourly entries) also peaked in the morning and declined throughout the day for both species (Figure 3.6b); however, *T. iridipennis* showed high activity from 07:00-08:00, while *A. cerana* peaks between 08:00-09:00. *T. iridipennis* also collects pollen more in the afternoon than *A. cerana*.

The statistical analysis revealed that there is a significant effect of species on both overall activity ($F=45.971_{22,1}$, $p<0.001$, $R^2=0.335$) and proportion of foraging devoted to pollen ($F=11.893_{22,1}$, $p=0.001$, $R^2=0.221$). Furthermore, there is a significant interaction between species and time category for both variables (activity: $F=29.761_{22,1}$, $p=<0.001$, $R^2=0.335$; pollen: $F=30.877_{22,1}$, $p<0.001$, $R^2=0.221$).

Temperature has a significant effect on activity and pollen foraging of *A. cerana* (activity: $F=14.526_{12,1}$, $p<0.001$, $R^2=0.282$; pollen: $F=11.525_{12,1}$, $p=0.001$, $R^2=0.362$), but not *T. iridipennis* (activity: $F=3.537_{16,1}$, $p=0.061$, $R^2=0.283$; pollen: $F=0.033_{16,1}$, $p=0.857$, $R^2=0.166$) (Figure 3.7). Activity of *A. cerana* appears to peak at 25°C, then decline until 30°C when it increases again. Pollen foraging peaked at 26° then declines with increasing temperature.

Hives located on the roof showed reduced overall activity in both *A. cerana* ($F_{5,1}=11.156$, $p=0.001$, $R^2=0.282$), and *T. iridipennis* ($F_{7,1}=24.215$, $p<0.001$, $R^2=0.283$) (Figure 3.8). In *T. iridipennis*, the proportion of pollen foraging increased on the roof ($F_{7,1}$=5.486, *p*=0.004, R^2=0.166), while there was no effect of location on *A. cerana* pollen foraging ($F_{5,1}$=0.603, *p*=0.438, R^2=0.362).



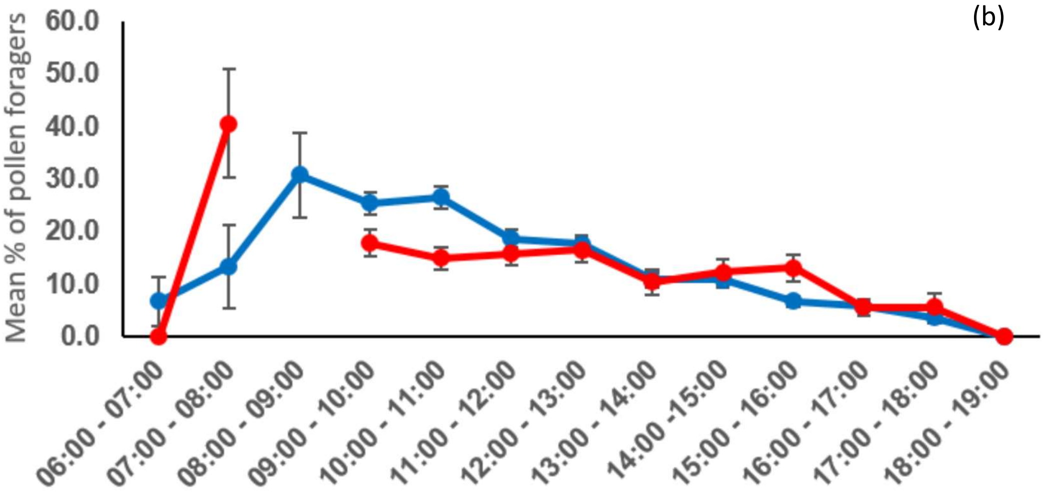


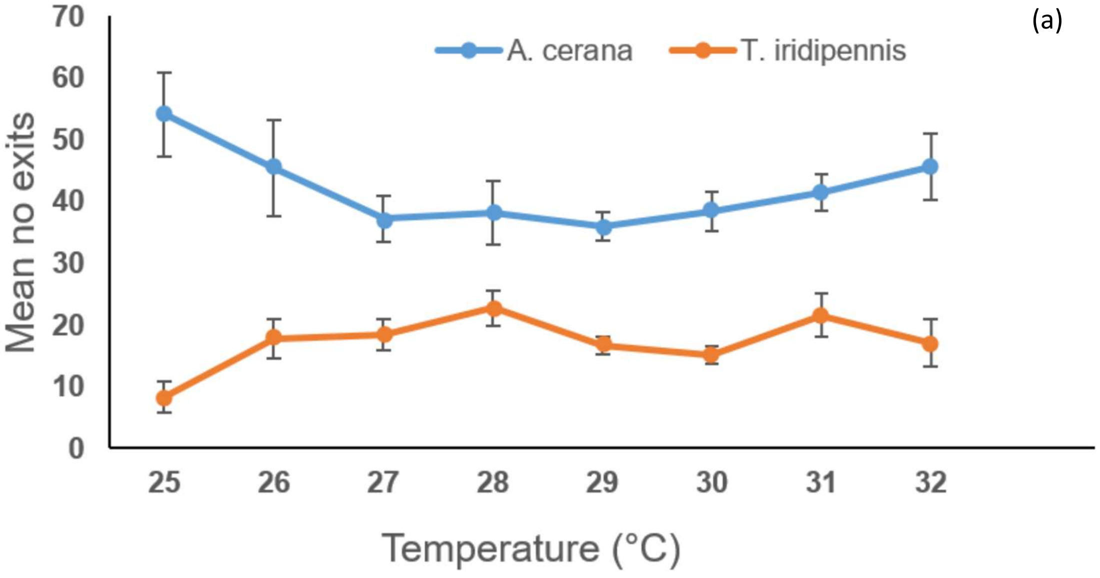
Figure 3.6 Species comparison for activity and pollen foraging throughout the day.

A. cerana: 29 days, 5 hives.

T. iridipennis: 35 days, 8 hives.

(a) Mean no of exits (with s.e.m.) at each time.

(b) Mean % of pollen foragers (with s.e.m.) at each time.



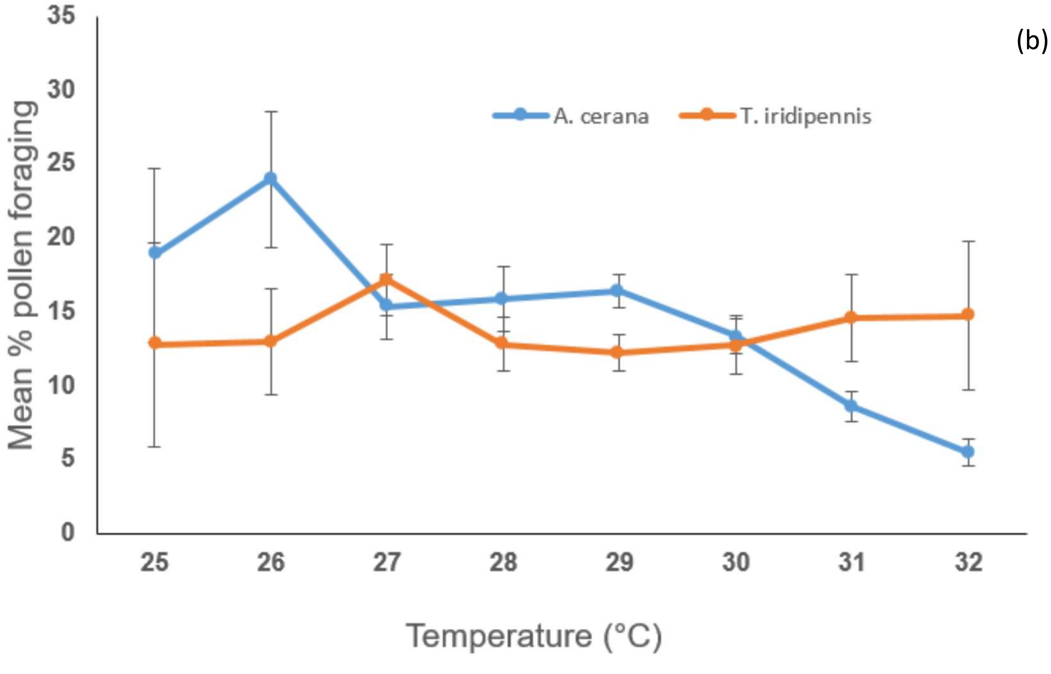


Figure 3.7 Species comparison for activity and pollen foraging, against temperature.

A. cerana: 29 days, 5 hives.

T. iridipennis: 35 days, 8 hives.

(a) Mean no of exits (with s.e.m.) at each time.

(b) Mean % of pollen foragers (with s.e.m.) at each time.

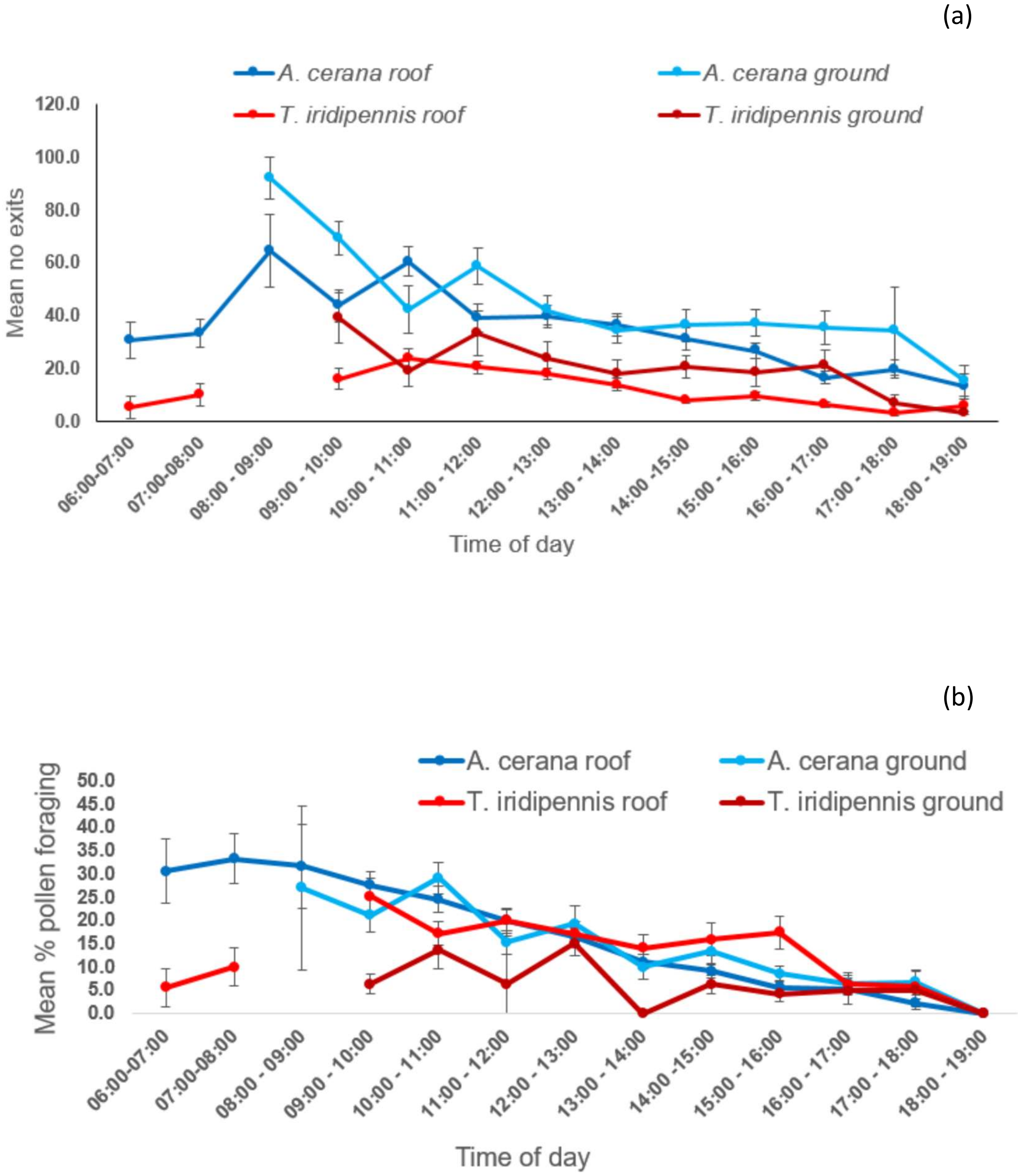


Figure 3.8 Location comparison of daily activity for both species for activity and pollen foraging.

A. cerana roof: 5 hives, 28 days

A. cerana ground: 4 hives, 18 days

T. iridipennis roof: 2 hives, 14 days

T. iridipennis ground: 8 hives, 33 days

(a) Mean no of exits (with s.e.m.) at each time.

(b) Mean % of pollen foragers (with s.e.m.) at each time.

Seasonal comparison

The activity pattern of *A. cerana* in the dry season shows highest foraging activity in the morning which declines almost to zero around 13:00, and increases slightly in the afternoon (Figure 3.7a). Pollen foraging peaks between 09:00-12:00 and declines sharply (Figure 3.7b). When comparing the data collected in the middle of the dry season and at the end until the start of pre-monsoon rains, there is a significant effect of season on the activity ($F=5.194_{13,1}$, $p=0.023$, $R^2=0.259$) and pollen foraging ($F_{13,1}=6.687$, $p=0.01$, $R^2=0.366$) of *A. cerana.* There is also a significant interaction between season and time of day on overall activity ($F_{13,1}=7.285$, $p=0.007$, $R^2=0.259$) but not on pollen foraging ($F_{13,1}=3.21$, $p=0.074$, $R^2=0.366$). This seems not to be explained by temperature, rainfall or humidity levels.

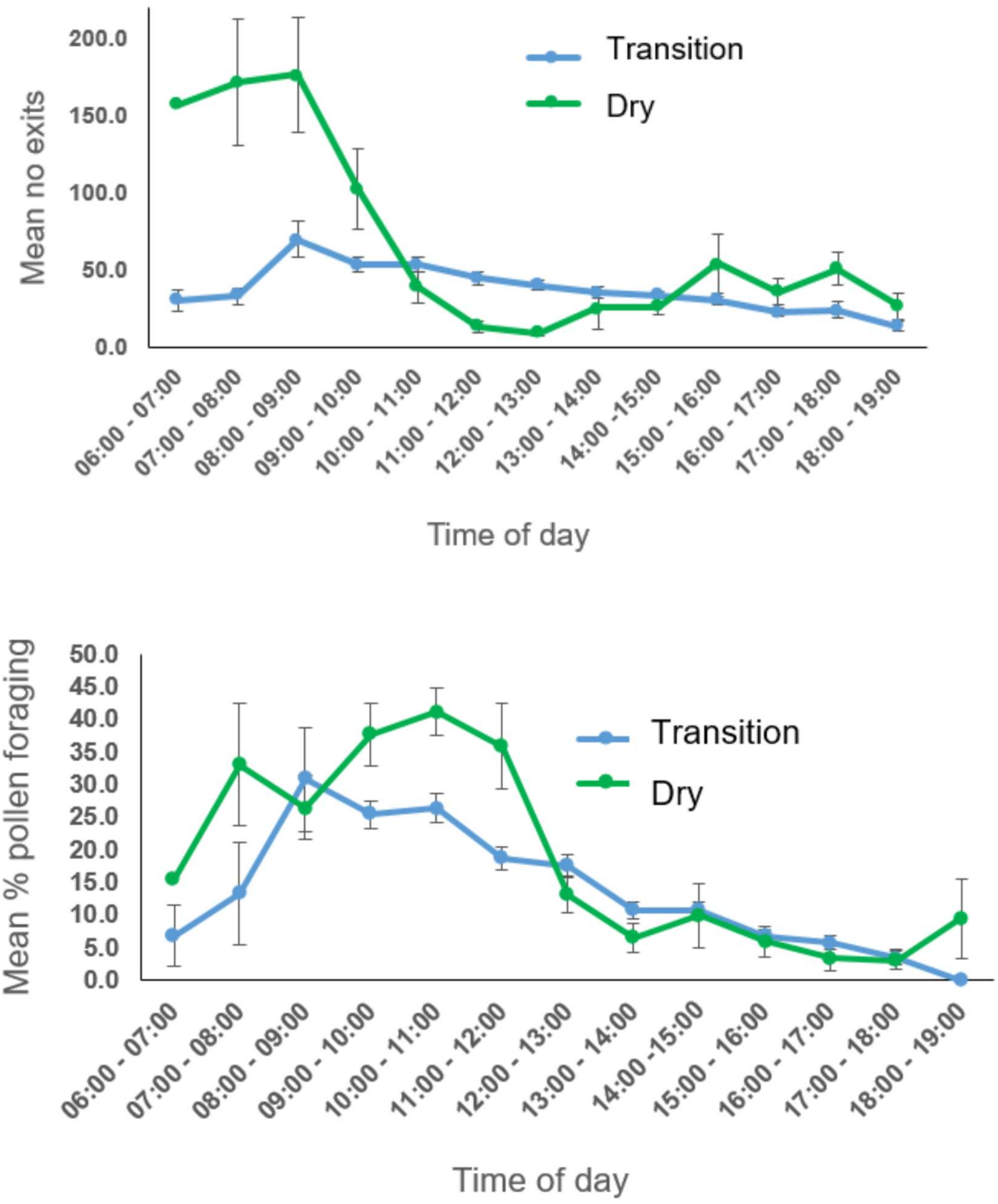


Figure 3.9 Season comparison (transition v dry) of *A. cerana* in the city.

A. cerana transition: 5 hives, 29 days

A. cerana dry: 2 hives, 9 days

(a) Mean no of exits (with s.e.m.) at each time.

(b) Mean % of pollen foragers (with s.e.m.) at each time.

Chapter Four: Discussion and conclusion

Pollen resource partitioning

The collection of pollen from differing plant species is one way in which bee species can partition resources, and has been shown even for highly related bees nesting in the same location[335]. This study indicates the potential for pollen resource partitioning between *A. cerana* and *T. iridipennis* in the Western Ghats region. In the agricultural landscape, both species collected mostly coconut pollen (*T. iridipennis* to a lesser extent), but in the urban setting, *T. iridipennis* relied less on coconut pollen, favouring morphotype (MT) 11.

There are several, mutually inclusive, explanations for this difference. Firstly, it may be that coconut is the preferred pollen for both species and its abundance near the rubber plantation negates the need to find alternative sources. It may be less abundant in the city, but *A. cerana* has a larger foraging range (as discussed in previous literature and below), allowing it to seek out coconut further away. *A. cerana* may also have exhausted the supplies of coconut pollen nearby. *T. iridipennis* is meanwhile forced to supplement with less desirable pollen closer to the hive. This explanation is partially supported by the fact that there were multiple coconut trees close to the hives in the rubber plantation, but not in the city. Although coconut trees are extremely common in Trivandrum, they are more spread out and there are few within close proximity to the urban hives. Indeed, waggle dance analysis of an *A. cerana* hive at this site shows that most pollen collection is carried out between 120 and 480m[410].

However, this is also the case in the rubber plantation so by itself may not explain the difference between species in only the city.

Second, *A. cerana* and *T. iridipennis* may have differing pollen preferences; *A. cerana* may prefer coconut while *T. iridipennis* prefers another species, which is only available in the city, as indeed MT11 appears to be (at least it wasn't found in that area of the agricultural landscape). It may be an horticultural plant, found in urban gardens. As both bees were found to collect the MT11 pollen, the plant is presumably not specialised to smaller bees, i.e. *T. iridipennis*.

Third, both species may prefer (or be indifferent to) MT11; but if the plant is limited in numbers, *T. iridipennis* may have been able to outcompete *A. cerana* by aggressively guarding the flowers. Trivandrum has lower floral density than the rubber plantation; the relatively limited resources available may be worth defending. As discussed in the literature, *T. iridipennis* can successfully defend a resource against larger, less aggressive bee species[383]. I also observed some aggressive interactions at artificial feeders, for instance *T. iridipennis* biting the wings of *A. cerana* immobilising the larger bee for some time.

Finally, there may be an effect of height on the foraging and search strategy of each species; if *T. iridipennis* flies at a different height it may more encounter different pollen sources. Eltz et al suggest this as a potential explanation for the partitioning they found among stingless bee species in Malaysia[335].

Overall, only ¼ of pollen types were shared between the species and the above explanations can also apply to the 13 pollen types which were collected only by one of the species. Some of the plants may be specialised to small bees like *T. iridipennis* or far enough away to only be reached by *A. cerana*.

There has been little research directly comparing pollen collection by these two species; the study in north India did not find evidence for resource partitioning, but it was based on observing visitations to plants in a given area, rather than overall pollen intake[290]. Furthermore, this present study indicates that it may vary with location; in some contexts, partitioning may be minor, while in others it may be substantial. Even within the agricultural landscape, *A. cerana* showed differences in pollen collection between the rubber plantation and the paddy field. In the paddy field, the amount of non-coconut pollen collected in negligible, while it is around 10% in the plantation. This reflects the fact that, unlike the rubber plantation, the paddy field itself provides few floral resources, and coconut trees are found along much of the perimeter. There may also be limitations on *A. cerana* foraging in or across the paddy field; these will be discussed below.

Sampling pollen is one of the simplest ways in which to detect differences in utilisation of floral resources. However, there are several key limitations to this approach. Possibly the most crucial is the difference in sampling methods; the pollen collected from *A. cerana* by stripping it from the legs of returning foragers represents their intake for a specific time period. Collecting pollen from stores is more difficult to interpret functionally because here for instance it is unknown for how long *T. iridipennis* usually stores pollen. Furthermore, it is difficult to randomly sample pollen stores. Sampling more than one *T. iridipennis* colony would be useful, but each time the colony is destroyed. Unfortunately, it turned out that *T. iridipennis* are very sensitive to interference near their hive entrance, and it would require further development of suitable traps and long-term multi-step habituation, which could not be accomplished within the time period for field studies in India for the present work. To gain further insights in resource utilisation, this would be however a useful way forward.

Without mapping the proximity of pollen sources and thus the availability of pollen types, it is not possible to determine whether any preferences arise exclusively from pollen properties. Whilst many plants are abundant and may flower for more than few days, staggered across individual plants or flower several times during the year, like coconut, seasonal availability of pollen resources should also be considered. Here we collected *T. iridipennis* samples in the middle of the dry season in the rubber plantation (February), but the city sample was taken in the wet season (July). Thus, the availability of pollen resources is likely to vary across the year, and choices are made between simultaneously flowering plants. Depending on their abundance and properties, a number of factors may impact on the evaluation of the pollen rewards and influence the decisions of individual foragers[411]. It would also be useful to understand whether nectar foraging is done at the same time as pollen foraging, and might thus also influence the forager's choice of flower patch to visit. In *A. cerana* a study conducted in parallel found that pollen foragers did not carry nectar in their crops when returning to the hive[409], thus suggesting that at least in this species these two foraging activities are temporally segregated. Indeed, pollen foragers can intersperse foraging trips with nectar foraging[409]. This question is yet to be investigated in *T. iridipennis*. Finally, flower visitation rates and the knowledge of how far foragers can travel (see discussion below) may also provide complementary data on both pollen and nectar preference, at least between specified plants.

Despite the discussed methodological shortcomings in the present study, the results demonstrate that both species are flexible in their pollen collection and, at least in some contexts, there is resource partitioning. Potential reasons for this remain unclear, but will be discussed further below.

Spatial partitioning

Within the rubber plantation, the species differed hugely in their response to the artificial feeder training (Figure 3.3). At all distances, *T. iridipennis* was slower to exploit the feeder. This is probably partly an effect of colony size; *T. iridipennis* colonies are smaller than those of *A. cerana* and (as shown in the activity data) there are fewer foragers. This may make recruitment slower, as there are fewer foragers allocated to each resource. Furthermore, their navigation (for instance if they navigate partly by odour[392]) may affect the speed at which foragers can find the feeder. Additionally, their method of recruitment (which is currently unknown) may also be less effective than the honeybee waggle dance. Leaving an odour trail, for instance, may be time-consuming; following the trail may also be less direct than following dance directions[400]. If recruitment is based just on an odour left at the feeder, as in *M. panamica*[399], or intranidal body contacts[399], then this may be even slower to follow.

T. iridipennis stopped visiting completely after 130m, while *A. cerana* carried on until the plantation ended (210m) and is likely to have continued further if possible (waggle dances show that occasionally they foraged up to 2km for pollen and up to 1km for nectar in this environment[410]). Moreover, in previous studies which applied feeder training, *A. cerana* followed the feeder up to 1.5km[375] but it has been reported that it can fly up to 4km[376]. Still, this is a direct comparison of the two species in the same location and supports the idea that flight range is very much associated with bee size[373]. Furthermore, a recruitment system based on odour (either trail or location scent-marked) may be increasingly ineffective at longer distances. The closely related *T. carbonaria* in Australia can travel up to 700m but generally forages around half that distance[380].

As predicted, the range of *T. iridipennis* was more restricted, most likely due to its smaller size. However, its foraging range could well be beyond 130m, as it cannot be excluded that rich selection of foraging sources closeby could contribute to the decision to give up the feeder when it was too far. Homing experiments in which bees are displaced at increasing distances and their return is recorded would help to determine this species' maximum flight range. Furthermore, the maximum foraging range may also vary in different environments; in the rubber plantation, there may have been other floral resources closer to the hive which were more profitable or cost less energy to visit than the feeder. *T. iridipennis* may fly further in resource-poor contexts.

The fact that context influences flight range is supported by the fact that *A. cerana* did not follow the feeder beyond 70m in the paddy field (the paddy field and plantation sites potentially providing different resources). As Jha and Kremen point out, foraging range is highly flexible between landscapes; they found that bumblebees (*B. vosnesenskii*) travel further for plant species diversity (perhaps optimising their nutritional intake)[177]. Furthermore, as shown above, *A. cerana* and *T. iridipennis* often visit different plant species; this could also contribute to differences in motivation to visit the experimental feeder.

In the rubber plantation, there does appear to be other nectar sources available even when the feeder is close to the hive; many (marked) *A. cerana* foragers visited only when the feeder was at the near distances and then gave up, presumably due to lack of interest. Alternatively, the colony intake of nectar at this point may have been high enough for some of the foragers to stop collecting. Recording the activity at the hive in parallel could help to provide answers to these questions, as such visual observations at the hive would demonstrate whether any of the previous visitors to the feeder continues being active as a forager and go to other locations.

The vegetation structure changes considerably around 120m, with the rubber trees becoming less regular and the undergrowth denser and less maintained. *A. cerana* slowed down considerably between 150m and 210m, which may be partly due to this change in structure. The average time between 1st and 2nd visits for marked also increases sharply at 100m onwards. They may have found it more difficult to relocate the feeder in this cluttered environment, and/or found alternative resources while searching. At 150m and 210m, there are also more new visitors than at intermediate distances; this may be because the previous visitors decided to switch to other resources nearby.

Interestingly, in the paddy field, *A. cerana* stopped visiting the feeder completely after only 70m. The reason for this may simply be more resource richness nearer the hive in the paddy field. Yet waggle dances of bees in the paddy field indicate that most foraging is between 100m and 700m, which is shorter than in the plantation, but still often much longer than they followed the feeder[410]. Motivation to follow the feeder may also vary with season; the plantation experiment was performed at the beginning of the dry season (December), while the paddy field experiment was nearer the end of the dry season (April), when alternative sources of nectar could be more plentiful. However, there may be also an explanation related to landscape structure; up to 50m, the feeder had been on a path on the edge of the paddy field (it was not possible to place the feeder in the field at short distances). Because the path bended, at 70m the feeder was moved to a position in the field. The huge decline in bee visits occurred between 50m and 70m, which coincided with this move into the field. It is possible that the bees preferred to navigate along the more structured path. Indeed, when the feeder was placed at 50m in the field, bees continued to visit but it took them twice as long to reach 15 bees as it did on the path. When the feeder was placed at the same distance on the path, several hours later, bees arrived almost immediately. The displacement of the feeder away from familiar landmarks (i.e. the path vegetation) may influence navigation. Honeybees are known to navigate at least partially using known landmarks[385]. Some have postulated that the interpretation of optic flow data may vary with landscape structure[405]. However, these results should be interpreted with caution; perhaps they had found temporarily profitable food sources around the same time as the feeder was moved. Furthermore, waggle dance analysis of bees in the same location shows that they do regularly cross the paddy field to forage[410]. In any case, whether it is due to resource availability or landscape structure, location appears to have an impact on the distance to which *A. cerana* will follow an artificial feeder.

Unfortunately, it was not possible to repeat this experiment over multiple days or with multiple hives and it is unknown how *T. iridipennis* would have responded to the feeder in the paddy field environment. Furthermore, both species were trained to the same concentration of sucrose solution. It is more than possible that the species have different nectar preferences or behavioural responses to the same concentration, as is the case for different *Melipona* species[368]. In spite of these limitations, the data suggest that the species may differ in their distribution within a given landscape, and this may contribute to the resource partitioning discussed above; if *T. iridipennis* is limited in flight range, it will forage on plants closer to the hive. Equally, if the two species differ in pollen and/or nectar preferences, this will inevitably affect the spatial distribution of their foragers.

Temporal partitioning

In the transition to the wet season, both species show high levels of overall activity and pollen foraging in the morning, which then declines throughout the day (Figure 3.4). The majority of foraging is not for pollen and can be assumed to be mostly nectar foraging (although some may be water-collecting, a behaviour seen in *A. mellifera*[412]. However, the exact patterns of activity differ somewhat between species.

The present data on *A. cerana* support previous research that reported their foraging patterns; several studies show that foraging activity is highest in the morning and declines after midday[342,343], the present data shows a peak between 08:00 and 09:00. Exact pollen foraging peaks appear to differ with location but are all in the morning. For example, in Bengaluru, Karnataka, it peaks at 08:00[342], while in the Himalayas it peaks at 10:00[343]. This data shows a peak between 08:00-09:00. This variation in pollen foraging is to be expected given the difference in floral resources between locations. Furthermore, Trivandrum is much more similar in climate to Bengaluru than to the Himalayas so the patterns are expected to be similar.

The data on *T. iridipennis* is a little more conflicted. Some studies show activity peaks only in the morning; in Dharwad, Karnataka, the peak is from 10:00-12:00[345]; in Orissa it is at 11:00[348]. However, in Tamil Nadu, there are two peaks: the main one between 08:00 and 12:00, with a lesser peak from 15:00-18:00[346].

However, this study was conducted in the dry season. The current data shows highest activity between 07:00 and 12:00 but the exact peak is unclear, given the lack of observations between 08:00 and 09:00. Most studies show pollen foraging of *T. iridipennis* peaks in the morning[287,346]: in Kerala, colonies collect 90% of their daily pollen between 05:00 and 09:00[287]. However, colonies in north India have two peaks of pollen foraging: 08:00 and 16:00[350]. This data indicates a peak between 07:00 and 08:00, but again this is uncertain.

The data indicates that the species differ significantly in both overall activity pattern and pollen foraging pattern between 09:00 – 17:00. *A. cerana* activity is highest between 10:00 and 11:00, with a pollen peak at the same time, while *T. iridipennis* peaks between 11:00 and 12:00, with a pollen peak between 12:00 and 13:00. Furthermore, 09:00 to 11:00, *A. cerana* pollen foraging is higher, while from 13:00 onwards *T. iridipennis* pollen foraging is consistently higher.

Coconut anthesis is in the morning[413] and available as mass bloom on individual trees, thus an early arrival is clearly beneficial to collect pollen in abundance. The early peak seen in *A. cerana* pollen foraging could reflect the potential competition for shared resources, such as coconut. They might be compensating for *A. cerana's* ability to fly further and to mobilise larger numbers of foragers.

Temperature has a significant effect on both the activity and pollen foraging of *A. cerana* but not that of *T. iridipennis*, even when time of day is accounted for. In *A. cerana*, activity appears to increase with temperature (between 24° and 32°C) but most striking is the peak in activity at 25°C. Pollen foraging, on the other hand, shows a clear peak at 26°C. Pollen availability (i.e. production by plants) may vary with temperature; this might be expected to also impact on *T. iridipennis*. Or it may be that nectar collection is preferred at higher temperatures; perhaps the nectar is more concentrated.

The location of the hives (ground vs roof) has an effect on overall activity in both species. At almost all time points, both species are more active when on the ground level than on the roof. Ascending from ground level to foraging resources at various heights might be energetically more convinient and bees might prefer to fly upwards rather than downwards from the rooftop to trees and shrubs on the ground. It would be interesting to collect pollen samples from foragers returning to their hives located on the ground level to detect potential differences in foraging. It is surprising that small bees like *T. iridipennis* are able to deal with the descent and ascent to the roof top, which is presumably much higher and more exposed to drag, lift and turbulence than when they forage on flowers in their natural habitats, high up in the forest trees. Accordingly overall activity was lower on the roof. However, interestingly, *T. iridipennis* pollen foraging activity was affected by location; colonies on the roof devoted more foragers to pollen collecting at all time points throughout the day. Perhaps an increase in the proportion of pollen foragers is an attempt to compensate for lower overall activity; this would suggest some pressure on *T. iridipennis* foragers to sustain minimal rates of pollen collection to sustain the colony’s brood, which seems less important for nectar collection, presumably as foragers may respond flexibly to difficult environmental conditions by feeding in the field and thus reduce the hive’s consumption of stored honey. Maia-Silva et al found that stingless bees downregulate brood production when pollen is scarce; it would be interesting to see if this is the case in *T. iridipennis* on the roof[334]. *A. cerana* does not increase its pollen foraging when located on the roof, but they might be much less limited in reaching pollen resources. This chimes with my earlier suggestion that pollen resources are limiting for *T. iridipennis* in this environment; they seem to be out-competed for coconut pollen, and must utilise other plants they can find nearby that might be less abundant in pollen or less frequent.

The comparison of *A. cerana* activity between seasons (transition to wet versus the middle of the dry season) shows some key differences which appear to be unrelated to temperature. Firstly, activity levels are much higher between 06:00 – 11:00 and then drop off sharply around midday. This could be an adaptation to even higher temperatures in the dry season which weren't encountered during the observations. Secondly, the proportion of foraging devoted to pollen is higher in the morning in the dry season and peaks a bit later. This could easily be due to seasonal variation in plant resources; collection of pollen from *A. cerana* in the dry season could help to confirm this hypothesis.

Conclusion and outlook

These data suggest that there is (pollen) resource partitioning between *A. cerana* and *T. iridipennis*, particularly in certain environments (e.g. the city of Trivandrum). The difference in foraging range, and thus spatial distribution, is likely to play a key role in such partitioning, but it remains unknown to what extent species preference is also a factor. A level of temporal variation between the species is also apparent, although it is unclear how exactly this may translate to partitioning. Activity observations in other landscape contexts, e.g. rubber plantations, although logistically more challenging, could shed light on this.

In general, more work needs to be conducted, especially on *T. iridipennis*, to understand the distribution of these species in the landscape and their plant visitation behaviour. In particular, homing experiments would be helpful to determine the maximum foraging range of *T. iridipennis*. Furthermore, experiments could be conducted to determine its system of recruitment[414]; this is invaluable for a deeper understanding of the foraging behaviour. Pollen analysis for both species in more "natural" environments (e.g. forest patches) may also provide an interesting comparison with the apparent reliance on coconut within man-made landscapes.

These data are therefore the first steps in a comparison of *A. cerana* and *T. iridipennis*, key pollinators in agricultural and natural ecosystems in South Asia. Further knowledge regarding their behaviour will provide invaluable insights into pollination ecology in this area and across the tropics.

Bibliography

1. Mittermeier, R., Turner, W., Larsen, F. & Brooks, T. Global biodiversity conservation: the critical role of hotspots. pp 3-22, *Biodiversity Hotspots.* (Springer, Berlin, Heidelberg, 2011) .
2. Bawa, K., Das, A., Krishnaswamy, J. & Karanth, K. CEPF Western Ghats and Sri Lanka ecosystem profile. *ATREE & Wildlife Conservation Society, Bengaluru, India* (2007).
3. Myers, N. Threatened biotas "hotspots" in tropical forests. *Environmentalist* 8(3) 187–208 (1988).
4. Perfecto, I. & Vandermeer, J. Biodiversity conservation in tropical agroecosystems. *Annals of the New York Academy of Sciences* 1134*,* 173-200 (2008).
5. Dirzo, R. & Raven, P. H. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28, 137–67 (2003).
6. Becerra, J. X. On the factors that promote the diversity of herbivorous insects and plants in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America* 112(19), 6098–6103 (2015).
7. Erwin, T. L. Tropical forests : their richness in coleoptera and other arthropod species. *The Coleopterists Bulletin* 36(1), 74–75 (1982).
8. Hill, J. L. & Hill, R. A. Why are tropical rain forests so species rich? Classifying, reviewing and evaluating theories. *Progress in Physical Geography: Earth and Environment* 25(3) 326–354 (2001).
9. Cardoso, P., Erwin, T. L., Borges, P. A. V & New, T. R. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 144(11), 2647–2655 (2011).
10. Beck, J. Ballesteros-Mejia, L. , Buchmann, C. M., Dengler, J. , Fritz, S. A., Gruber, B. , Hof, C. , Jansen, F. , Knapp, S. , Kreft, H. , Schneider, A. , Winter, M. & Dormann, C. F.. What's on the horizon for macroecology? *Ecography .* 35, 673–683 (2012).
11. IUCN. The IUCN Red List of Threatened Species. *The IUCN Red List* (2015). Available at: http://www.iucnredlist.org.
12. Clausnitzer, V. Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E., Bedjanič, M., Darwall, W.R., Dijkstra, K.D.B., Dow, R., Hawking, J. & Karube, H.. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. *Biological Conservation* 142(8), 1864–1869 (2009).
13. Basset, Y. Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J. & Tishechkin, A.K., Arthropod Diversity in a Tropical Forest. *Science* 338(6113), 1481–1484 (2012).
14. Cardoso, P., Borges, P. A. V, Triantis, K. A., Ferrández, M. A. & Martín, J. L. The underrepresentation and misrepresentation of invertebrates in the IUCN Red List. *Biological Conservation* 149(1), 147–148 (2012).
15. Ballesteros-Mejia, L., Kitching, I. J., Jetz, W., Nagel, P. & Beck, J. Mapping the biodiversity of tropical insects: species richness and inventory completeness of African sphingid moths. *Global Ecology and Biogeography* 22(5), 586–595 (2013).
16. Jepson, P. & Canney, S. Biodiversity hotspots: hot for what? *Global*

Ecology and Biogeography 10(3), 225–227 (2001).

17. Branton, M. & Richardson, J. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology* 25(1), (2011).
18. Cardoso, P., Borges, P. A. V, Triantis, K. A., Ferrández, M. A. & Martín, J. L. Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation* 144(10), 2432–2440 (2011).
19. Roberge, J-M. & Angelstam, P.E.R. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18(1), 76–85 (2004).
20. Ranius, T. Osmoderma eremita as an indicator of species richness of beetles in tree hollows. *Biodiversity and Conservation* 11(5), 931-941 (2002).
21. Bacchetta, G., Farris, E. & Pontecorvo, C. A new method to set conservation priorities in biodiversity hotspots. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology,.* 146(3), 638-648 (2011).
22. Zhang, K. Lin, S., Ji, Y., Yang, C., Wang, X., Yang, C., Wang, H., Jiang, H., Harrison, R.D. & Yu, D.W. Plant diversity accurately predicts insect diversity in two tropical landscapes. *Molecular Ecology* 25(17), 4407–4419 (2016).
23. Wardhaugh, C. W. How many species of arthropods visit flowers? *Arthropod-Plant Interactions* 9(6), 547–565 (2015).
24. Olson, D. & Dinerstein, E. The Global 200: a representation approach to conserving the Earth’s most biologically valuable ecoregions. *Conservation Biology* 12(3), 502-515.(1998).
25. Keith, D., Rodríguez, J.P., Rodríguez-Clark, K.M., Nicholson, E., Aapala, K., Alonso, A., Asmussen, M., Bachman, S., Basset, A., Barrow, E.G. and Benson, J.S., Scientific foundations for an IUCN Red List of Ecosystems. *PLoS ONE* 8(5), e62111 (2013).
26. Boitani, L., Mace, G. M. & Rondinini, C. Challenging the scientific foundations for an IUCN Red List of Ecosystems. *Conservation Letters* 8(2), 125–131 (2015).
27. Bhagwat, S. A., Dudley, N. & Harrop, S. R. Religious following in biodiversity hotspots: challenges and opportunities for conservation and development. *Conservation Letters* 4(3), 234–240 (2011).
28. Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T. and Malingreau, J.P. Determination of Deforestation Rates of the World’s Humid Tropical Forests. *Science.* 297(5583), 999–1002 (2002).
29. Laurance, W. Reflections on the tropical deforestation crisis. *Biological Conservation* 91(2-3), 109-117 (1999).
30. Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R. & Kommareddy, A. High-resolution global maps of 21st-century forest cover change.*Science* 342(6160), 850-853 (2013).
31. Toledo-Hernández, M., Denmead, L. H., Clough, Y., Raffiudin, R. & Tscharntke, T. Cultural homegarden management practices mediate arthropod communities in Indonesia. *Journal of Insect Conservation* 20(3), 373–382 (2016).
32. Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. Primary forests are irreplaceable for sustaining tropical

biodiversity. *Nature*, 478(7369), 378 (2011).33. Takano, K.T., Nakagawa, M., Itioka, T., Kishimoto-Yamada, K., Yamashita, S., Tanaka, H.O., Fukuda, D., Nagamasu, H., Ichikawa, M., Kato, Y. & Momose, K., 2014. The extent of biodiversity recovery during reforestation after swidden cultivation and the impacts of land-use changes on the biodiversity of a tropical rainforest. pp 27-49, *Social-Ecological Systems in Transition* (Springer, Japan, 2014),

34. Deikumah, J.P., Mcalpine, C.A. & Maron, M. Biogeographical and taxonomic biases in tropical forest fragmentation research. *Conservation Biology*, 28(6), 1522-1531 (2014)..
35. DeFries, R., Hansen, A., Newton, A. C. & Hansen, M. C. Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications* 15(1), 19–26 (2005).
36. Fahrig, L. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34(1), 487–515 (2003).
37. Fahrig, L. Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution and Systematics* 48, 1-23 (2017).
38. Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C.. Contribution of small habitat fragments to conservation of insect communities of grassland–cropland landscapes. *Ecological Applications*, 12(2), 354-363 (2002)..39. Hill, J.K., Gray, M.A., Khen, C.V., Benedick, S., Tawatao, N. & Hamer, K.C.Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582), 3265-3276.(2011).
40. Harrison, S. & Bruna, E. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*22(3) (1999).
41. Hill, J. & Curran, P. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *Journal of Biogeography* 30(9), 1391-1403 (2003).
42. Murcia, C. Edge effects in fragmented forests: impications for conservation. *Trends in Ecology & Evolution* 10(2), 58–62 (1995).
43. Beier, P. & Noss, R. F. Do habitat corridors provide connectivity? *Conservation Biology* 12(6), 1241–1252 (1998).
44. Brückmann, S. V., Krauss, J. & Steffan-Dewenter, I. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. *Journal ofApplied Ecology* 47(4), 799–809 (2010).
45. Haddad, N. M., Hudgens, B., Damschen, E.I., Levey, D.J., Orrock, J.L., Tewsbury, J.J., & Weldon, A.J. Assessing positive and negative ecological effects of corridors,

pp 475–504 in *Sources, Sinks and Sustainability*(Cambridge University Press, 2011).

46. Kormann, U. Scherber, C., Tscharntke, T., Klein, N., Larbig, M., Valente, J.J., Hadley, A.S. and Betts, M.G.Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. *Proceedings of the Royal Society of London B: Biological Sciences* 283(1823), 20152347(2016).
47. Sutcliffe, O.L. & Thomas, C.D. Open corridors appear to facilitate dispersal by ringlet butterflies (Aphantopus hyperantus) between woodland clearings. *Conservation Biology* 10(5), 1359-1365 (1996).
48. Delattre, T., Vernon, P. & Burel, F. An agri-environmental scheme enhances butterfly dispersal in European agricultural landscapes.

Agriculture, Ecosystems, & Environment 166, 102–109 (2013).

49. Gascon, C., Lovejoy, T.E., Bierregaard Jr, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M. & Borges, S.. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91(2-3), 223–229 (1999).
50. Geert, A. Van, Triest, L. & Rossum, F. Van. Does the surrounding matrix influence corridor effectiveness for pollen dispersal in farmland? *Perspectives in Plant Ecology, Evolution and Systematics* 16(4), 180-189. (2014).
51. Bennett, A. F., Radford, J. Q. & Haslem, A. Properties of land mosaics: Implications for nature conservation in agricultural environments. *Biological Conservation* 133(2), 250–264 (2006).
52. Fischer, J. & Lindenmayer, D. Landscape modification and habitat fragmentation: a synthesis. *Global ecology and biogeography,* 16(3), 265-280 (2007). 53. Altieri, M. A. Linking ecologists and traditional farmers in the search for sustainable agriculture. *Frontiers in Ecology and the Environment* 2(1), 35–42 (2004).
54. Bhagwat, S. A., Willis, K. J., Birks, H. J. B. & Whittaker, R. J. Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology and Evolution* 23(5), 261–267 (2008).
55. Donald, P. F. Biodiversity impacts of some agricultural commodity production systems. *Conservation Biology* 18(1), 17–38 (2004).
56. Bardhan, S., Jose, S., Biswas, S., Kabir, K. & Rogers, W. Homegarden agroforestry systems: An intermediary for biodiversity conservation in Bangladesh. *Agroforestry Systems* 85(1), 29–34 (2012).
57. Galluzzi, G., Eyzaguirre, P. & Negri, V. Home gardens: neglected hotspots of agro-biodiversity and cultural diversity. *Biodiversity and Conservation* 19(3), 3635–3654 (2010).
58. Chandler, R.B., King, D.I., Raudales, R., Trubey, R., Chandler, C. and Arce Chávez, V.J.. A small-scale land-sparing approach to conserving biological diversity in tropical agricultural landscapes. *Conservation Biology* 27(4),785-795 (2013) 59. Perfecto, I. & Snelling, R. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecological Applications* 5(4), 1084–1097 (1995).
60. Norgrove, L. & Beck, J. Biodiversity function and resilience in tropical agroforestry systems including shifting cultivation. *Current Forestry Reports* 2(1), 62-80.
61. Bos, M. M., Hohn, P., Saleh, S., Buche, B., Buchori, D., Steffan-Dewenter, I., & Tscharntke, T. Insect diversity responses to forest conversion and agroforestry management

in *Stability of Tropical Rainforest Margins* 277–294 (Springer Berlin Heidelberg, 2007).

62. Phalan, B., Onial, M., Balmford, A. & Green, R. E. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333(6047) 1289-1291 (2011).
63. Perfecto, I. & Vandermeer, J. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences* 107(13), 5786-5791. (2010).
64. Fitzherbert, E. B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F. & Phalan, B. How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution* 23(10), 538–545 (2008).
65. Koh, L. P. & Wilcove, D. S. Is oil palm agriculture really destroying tropical

biodiversity? *Conservation Letters* 1(2), 60–64 (2008).
66. Warren-Thomas, E., Dolman, P. & Edwards, D.P. Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conservation Letters* 8(4), 230-241 (2015).
67. Syafiq, M., Atiqah, A.R.N., Ghazali, A., Asmah, S., Yahya, M.S., Aziz, N., Puan, C.L. & Azhar, B. Responses of tropical fruit bats to monoculture and polyculture farming in oil palm smallholdings. *Acta Oecologica* 74, 11–18 (2016).
68. Ghazali, A., Asmah, S., Syafiq, M., Yahya, M.S., Aziz, N., Tan, L.P., Norhisham, A.R., Puan, C.L., Turner, E.C. & Azhar, B. Effects of monoculture and polyculture farming in oil palm smallholdings on terrestrial arthropod diversity. *Journal of Asia-Pacific Entomology* 19(2), 415-42 (2016).
69. Asmah, S., Ghazali, A., Syafiq, M., Yahya, M.S., Peng, T.L., Norhisham, A.R., Puan, C.L., Azhar, B. & Lindenmayer, D.B. Effects of polyculture and monoculture farming in oil palm smallholdings on tropical fruit-feeding butterfly diversity. *Agricultural and Forest Entomology* 19(1), 70-80. (2017).
70. Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P. & Sayer, J. Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* 17(5), 925–951 (2008).
71. Perry, J., Lojka, B., Quinones Ruiz, L.G., Van Damme, P., Houška, J.& Fernandez Cusimamani, E. How natural forest conversion affects insect biodiversity in the Peruvian Amazon: can agroforestry help?. *Forests* 7(4), 82 (2016).72. Bai, Y., Zhuang, C., Ouyang, Z., Zheng, H. & Jiang, B. Spatial characteristics between biodiversity and ecosystem services in a human-dominated watershed. *Ecological Complexity* 8(2), 177–183 (2011).
73. Jha, S. Bacon, C.M., Philpott, S.M., Ernesto Méndez, V., Läderach, P. & Rice, R.A. . Shade coffee: update on a disappearing refuge for biodiversity. *BioScience* 64(5), 416–428 (2014).
74. Gray, C. L. & Lewis, O. T. Do riparian forest fragments provide ecosystem services or disservices in surrounding oil palm plantations? *Basic and Applied Ecol.* 15(8), 693–700 (2014).
75. Gray, C. L., Slade, E. M., Mann, D. J. & Lewis, O. T. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? *Ecology and Evolution* 4(7), 1049–1060 (2014).
76. Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G. & Tscharntke, T. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282(1801), 20142620 (2015).
77. Mitchell, M.,Suarez-Castro, A.F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K.J., Johansen, K. & Rhodes, J.R. Reframing landscape fragmentation's effects on ecosystem services. *Trends in Ecology & Evolution* 30(4), 190-198 (2015). 78. Adams, M. O. & Fiedler, K. The value of targeted reforestations for local insect diversity: a case study from the Ecuadorian Andes. *Biodiversity and Conservation* 24(11), 2709–2734 (2015).
79. Rosenzweig, M. Reconciliation ecology and the future of species

diversity. *Oryx* 37(2), 194-205 (2003).

80. Porter-Bolland, L., Ellis, E.A., Guariguata, M.R., Ruiz-Mallén, I., Negrete-Yankelevich, S. & Reyes-García, V. Community managed forests and forest protected areas: An assessment of their conservation effectiveness across the tropics. *Forest ecology and management* 268, 6-17. (2012).
81. Rojas-Nossa, S. V., Sánchez, J. M. & Navarro, L. Effects of nectar robbing on male and female reproductive success of a pollinator-dependent plant. *Annals of Botany* 117(2), 291–297 (2016).
82. Ollerton, J. & Cranmer, L. Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos* 98(2), 340–350 (2002).
83. Rosas-Guerrero, V., Aguilar, R., Martén-Rodríguez, S., Ashworth, L., Lopezaraiza-Mikel, M., Bastida, J.M. & Quesada, M. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? *Ecology Letters* 17(3), 388–400 (2014).
84. Johnson, S. D. & Steiner, K. E. Generalization versus specialization in plant pollination systems. *Trends in Ecology and Evolution* 15 (4), 140–143 (2000).
85. Olesen, J. M. & Jordano, P. Geographic patterns in plant-pollinator mutualistic networks. *Ecology* 83(9), 2416–2424 (2002).
86. Bawa, K. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21(1), 399–422 (1990).
87. Gill, R.J., Baldock, K.C., Brown, M.J., Cresswell, J.E., Dicks, L.V., Fountain, M.T., Garratt, M.P., Gough, L.A., Heard, M.S., Holland, J.M. & Ollerton, J. Protecting an ecosystem service: approaches to understanding and mitigating threats to wild insect pollinators. In *Advances in Ecological Research* (Vol. 54, 135-206, Academic Press, 2016). .
88. Potts, S. G, Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E.. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution* 25(6), 345–353 (2010).
89. Stout, J. C. & Morales, C. L. Ecological impacts of invasive alien species on bees. *Apidologie* 40(3), 388–409 (2009).
90. Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M. & Blüthgen, N. Ecosystem restoration strengthens pollination network resilience and function. *Nature* 542(7640), 223–227 (2017).
91. Dáttilo, W., Aguirre, A., Quesada, M. & Dirzo, R. Tropical forest fragmentation affects floral visitors but not the structure of individual-based palm-pollinator networks. *PLoS ONE* 10(3), e0121275 (2015).
92. Calvillo, L. M., Ramírez, V. M., Parra-Tabla, V. & Navarro, J. Bee diversity in a fragmented landscape of the Mexican neotropic. *Journal of Insect Conservation* 14(4), 323–334 (2010).
93. Sargent, R. D. & Vamosi, J. C. The influence of canopy position, pollinator syndrome, and region on evolutionary transitions in pollinator guild size. *International Journal of Plant Sciences* 169(1), 39-47. (2008).
94. Sakai, S. Phenological diversity in tropical forests. *Population Ecology* 43(1), 77–86 (2001).
95. Kato, M., Kosaka, Y., Kawakita, A., Okuyama, Y., Kobayashi, C., Phimminith, T. and Thongphan, D. Plant-pollinator interactions in tropical monsoon forests in Southeast Asia. *American Journal of Botany* 95(11), 1375–1394 (2008).

96. Moles, A. T. & Ollerton, J. Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica* 48(2), 141–145 (2016).
97. Armbruster, W. S. The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation. *Functional Ecology* 31(1), 88–100 (2017).
98. Olschewski, R., Klein, A. M. & Tscharntke, T. Economic trade-offs between carbon sequestration, timber production, and crop pollination in tropical forested landscapes. *Ecological Complexity* 7(3), 314–319 (2010).
99. Moritz, R. F. A., Härtel, S. & Neumann, P. Global invasions of the western honeybee (Apis mellifera) and the consequences for biodiversity. *Ecoscience* 12(3), 289–301 (2005).
100. Landaverde-González, P., Enríquez, E., Ariza, M.A., Murray, T., Paxton, R.J.& Husemann, M. Fragmentation in the clouds? The population genetics of the native bee Partamona bilineata (Hymenoptera: Apidae: Meliponini) in the cloud forests of Guatemala. *Conservation Genetics* 18(3), 631–643 (2017).
101. Heard, T. A. The role of stingless bees in crop pollination. *Annual Review of Entomology* 44(1), 183–206 (1999).
102. Schmickl, T. & Karsai, I. How regulation based on a common stomach leads to economic optimization of honeybee foraging. *Journal of Theoretical Biology* 389, 274–286 (2016).
103. Slaa, E. J., Cevaal, A. & Sommeijer, M. J. Floral constancy in Trigona stingless bees foraging on artificial flower patches: a comparative study. *Journal of Apicultural Resear*ch 37(3), 191–198 (1998).
104. Ollerton, J., Winfree, R. & Tarrant, S. How many flowering plants are pollinated by animals? *Oikos* 120(3), 321–326 (2011).
105. Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. . Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences* 274(1608), 303-313(2007).
106. Cunningham, S. A. Human welfare and its connection to nature: What have we learned from crop pollination studies? *Austral Ecology* 42(1), 2–8 (2017).
107. Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T.A., Steffan-Dewenter, I. & Vázquez, D.P. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10(4), 299–314 (2007).
108. Blitzer, E. J., Gibbs, J., Park, M. G. & Danforth, B. N. Pollination services for apple are dependent on diverse wild bee communities. *Agriculture, Ecosystems and Environment* 221, 1–7 (2016).
109. Aizen, M. A. & Harder, L. D. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. . *Current Biology* 19(11), 915–918 (2009).
110. Burkle, L. A., Marlin, J. C. & Knight, T. M. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. 339(6127), 1611–1615 (2013).
111. Winfree, R. The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences* 1195(1), 169–197 (2010).
112. Nieto, A., Roberts, S.P., Kemp, J., Rasmont, P., Kuhlmann, M., García

Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P. & De Meulemeester, T. European red list of bees. *Luxembourg: Publication Office of the European Union*, 98 (2014).113. Oldroyd, B. & Wongsiri, S. *Asian honey bees: biology, conservation, and human interactions*. (Harvard University Press, 2009).

114. Oldroyd, B. P. & Nanork, P. Conservation of Asian honey bees. *Apidologie* 40(3), 296–312 (2009).
115. Pirk, C. W. W., Crewe, R. M. & Moritz, R. F. A. Risks and benefits of the biological interface between managed and wild bee pollinators. *Functional Ecology* 31(1), 47–55 (2017).
116. Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S. & Holzschuh, A. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters* 14(10), 1062–1072 (2011).
117. Cusser, S., Neff, J. L. & Jha, S. Natural land cover drives pollinator abundance and richness, leading to reductions in pollen limitation in cotton agroecosystems. *Agriculture Ecosystems & Environment* 226, 33–42 (2016).
118. Holzschuh, A., Dudenhöffer, J. H. & Tscharntke, T. Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation* 153, 101–107 (2012).
119. Garantonakis, N., Varikou, K., Birouraki, A., Edwards, M., Kalliakaki, V. & Andrinopoulos, F. Comparing the pollination services of honey bees and wild bees in a watermelon field. *Scientia horticulturae* 204, 138–144 (2016).
120. Jha, S. & Dick, C. W. Native bees mediate long-distance pollen dispersal in a shade coffee landscape mosaic. *Proceedings of the National Academy of Sciences* 107(31), 13760-13764 (2010).
121. Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London B: Biological Sciences* 270(1518), 955–61 (2003).
122. Ricketts, T. H., Daily, G. C., Ehrlich, P. R. & Michener, C. D. Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences of the United States of America* 101(34), 12579–12582 (2004).
123. Classen, A., Peters, M.K., Ferger, S.W., Helbig-Bonitz, M., Schmack, J.M., Maassen, G., Schleuning, M., Kalko, E.K., Böhning-Gaese, K. & Steffan-Dewenter, I. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proceedings of the Royal Society of London B: Biological Sciences* 281(1719), 20133148 (2014).
124. Garibaldi, L. A. Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O. & Bartomeus, I. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339(6127) 1608–1611 (2013).
125. Bretagnolle, V. & Gaba, S. Weeds for bees? A review. *Agronomy for Sustainable Development* 35(3), 891–909 (2015).
126. Greenleaf, S. S. & Kremen, C. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences* 103(37), 13890–13895 (2006).

127. Geslin, B., Oddie, M., Folschweiller, M., Legras, G., Seymour, C.L., Van Veen, F.F. & Thébault, E. Spatiotemporal changes in flying insect abundance and their functional diversity as a function of distance to natural habitats in a mass flowering crop. *Agriculture, Ecosystems & Environment* 229, 21–29 (2016).
128. Hoehn, P., Tscharntke, T., Tylianakis, J. M. & Steffan-Dewenter, I. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society of London B: Biological Sciences* 275(1648), 2283–2291 (2008).
129. Frund, J., Dormann, C. F., Holzschuh, A. & Tscharntke, T. Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology* 94(9), 2042–2054 (2013).
130. Sapir, G., Baras, Z., Azmon, G., Goldway, M., Shafir, S., Allouche, A., Stern, E. and Stern, R.A. Synergistic effects between bumblebees and honey bees in apple orchards increase cross pollination, seed number and fruit size. *Scientia Horticulturae* 219, 107–117 (2017).
131. Brittain, C., Kremen, C. & Klein, A. M. Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology* 19(2), 540–547 (2013).
132. Samnegard, U., Hambäck, P.A., Lemessa, D., Nemomissa, S. & Hylander, K. A heterogeneous landscape does not guarantee high crop pollination. *Proceedings of the Royal Society of London B: Biological Sciences* 283(1838), 20161472 (2016).
133. Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* 4(1), e1 (2005).
134. Dick, C. W., Etchelecu, G. & Austerlitz, F. Pollen dispersal of tropical trees (Dinizia excelsa: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest. *Molecular Ecology* 12(3), 753–764 (2003).
135. Delmas, C. E. L., Fort, T. L. C., Escaravage, N. & Pornon, A. Pollen transfer in fragmented plant populations: insight from the pollen loads of pollinators and stigmas in a mass-flowering species. *Ecology and Evolution* 6(16), 5663–5673 (2016).
136. Vamosi, J. C., Knight, T.M., Steets, J.A., Mazer, S.J., Burd, M. & Ashman, T.L. Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences of the United States of America* 103(4) 956–961 (2006).
137. Keitt, T. H. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecological Applications* 19(6), 1561–1573 (2009).
138. Lee, K. V. Steinhauer, N., Rennich, K., Wilson, M.E., Tarpy, D.R., Caron, D.M., Rose, R., Delaplane, K.S., Baylis, K., Lengerich, E.J. & Pettis, J.A national survey of managed honey bee 2013–2014 annual colony losses in the USA. *Apidologie* 46(3) 292–305 (2015).
139. Moritz, R. F. A. & Erler, S. Lost colonies found in a data mine: Global honey trade but not pests or pesticides as a major cause of regional honeybee colony declines. *Agriculture, Ecosystems and Environment* 216, 44–50 (2016).
140. Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J. & Ricketts, T.H. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of*

Sciences 113(1), 140–145 (2016).

141. Lima, M. A. P., Martins, G. F., Oliveira, E. E. & Guedes, R. N. C. Agrochemical-induced stress in stingless bees: peculiarities, underlying basis, and challenges. *Journal of Comparative Physiology* 202(9-10), 733–747 (2016).
142. Senapathi, D., Goddard, M. A., Kunin, W. E. & Baldock, K. C. R. Landscape impacts on pollinator communities in temperate systems: evidence and knowledge gaps. *Functional Ecology* 31(1), 26–37 (2017).
143. Ferreira, P. A., Boscolo, D. & Viana, B. F. What do we know about the effects of landscape changes on plant-pollinator interaction networks? *Ecological Indicators* 31, 35–40 (2013).
144. Xiao, Y., Li, X., Cao, Y. & Dong, M. The diverse effects of habitat fragmentation on plant–pollinator interactions. *Plant Ecology* 217(7), 857–868 (2016).
145. Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F. & Burel, F.. Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agriculture Ecosystems & Environment* 137(1-2), 143–150 (2010).
146. Lennartsson, T. Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. *Ecology* 83(11), 3060–3072 (2002).
147. Ferreira, P. A., Boscolo, D., Carvalheiro, L.G., Biesmeijer, J.C., Rocha, P.L. & Viana, B.F.Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest. *Landscape Ecology* 30(10), 2067–2078 (2015).
148. Weiner, C. N., Werner, M., Linsenmair, K. E. & Blüthgen, N. Land-use impacts on plant-pollinator networks: Interaction strength and specialization predict pollinator declines. *Ecology* 95(2), 466–474 (2014).
149. Sodhi, N. S., Koh, L.P., Clements, R., Wanger, T.C., Hill, J.K., Hamer, K.C., Clough, Y., Tscharntke, T., Posa, M.R.C. & Lee, T.M. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation* 143(10), 2375–2384 (2010).
150. Spiesman, B. J. & Inouye, B. D. Habitat loss alters the architecture of plant – pollinator interaction networks. *Ecology* 94(12), 2688–2696 (2013).
151. Biesmeijer, J.C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. P. & A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313(5785), 351–354 (2006).
152. Brosi, B. J. The complex responses of social stingless bees (Apidae: Meliponini) to tropical deforestation. *Forest Ecology and Management* 258(9), 1830–1837 (2009).
153. Brown, J.C. & Albrecht, C. The effect of tropical deforestation on stingless bees of the genus Melipona (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. *Journal of Biogeography* 28(5), 623–634 (2001).
154. Chacoff, N. P. & Aizen, M. A. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *Journal of Applied Ecology* 43(1), 18–27 (2006).
155. Jaffé, R. Castilla, A., Pope, N., Imperatriz-Fonseca, V.L., Metzger, J.P., Arias, M.C. & Jha, S. Landscape genetics of a tropical rescue pollinator.

Conservation Genetics 17(2), 267–278 (2016).

156. Meng, L. Z., Martin, K., Liu, J. X., Burger, F. & Chen, J. Contrasting responses of hoverflies and wild bees to habitat structure and land use change in a tropical landscape (southern Yunnan, SW China). *Insect Science* 19(6), 666–676 (2012)
157. Jauker, F., Diekötter, T., Schwarzbach, F. & Wolters, V. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology* 24(4), 547–555 (2009).
158. Tscharntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P. & Tylianakis, J.M. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89(4), 944-951 (2008).
159. Klein, A. M., Steffan-Dewenter, I. & Tscharntke, T. Pollination of Coffea canephora in relation to local and regional agroforestry management. *Journal of Applied Ecology* 40(5), 837–845 (2003).
160. Klein, A. M., Steffan-Dewenter, I. & Tscharntke, T. Bee pollination and fruit set of Coffea arabica and C. canephora (Rubiaceae). *American Journal of Botany* 90(1), 153–157 (2003).
161. Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M. & Morandin, L.A. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11(5), 499–515 (2008).
162. Ghazoul, J., Liston, K. A. & Boyle, T. J. B. Disturbance-induced density-dependent seed set in Shorea siamensis (Dipterocarpaceae), a tropical forest tree. *Journal of Ecology* 86(3), 462–473 (1998).
163. Ghazoul, J. Buzziness as usual? questioning the global pollination crisis. *Trends in Ecology and Evolution* 20(7), 367–373 (2005).
164. Lee, H. L., Sodhi, N. S. & Elmqvist, T. Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology* 38(1), 180–192 (2001).
165. Briggs, H. M., Perfecto, I. & Brosi, B. J. The role of the agricultural matrix: coffee management and euglossine bee (Hymenoptera: Apidae: Euglossini) communities in southern Mexico. *Environmental Entomology* 42(6), 1210–1217 (2013).
166. Jha, S. & Vandermeer, J. H. Impacts of coffee agroforestry management on tropical bee communities. *Biological Conservation* 143(6), 1423–1431 (2010).
167. Klein, A., Steffan-Dewenter, I., Buchori, D., & Tscharntke, T. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology* 16(4), 1003-1014 (2002).
168. Motzke, I., Klein, A. M., Saleh, S., Wanger, T. C. & Tscharntke, T. Habitat management on multiple spatial scales can enhance bee pollination and crop yield in tropical homegardens. *Agriculture, Ecosystems & Environment* 223, 144–151 (2016).
169. Matos, M. B., Sousa-Souto, L. & Almeida, R. Contrasting patterns of species richness and composition of solitary wasps and bees (Insecta: Hymenoptera) according to land-use. *Biotropica* 45(1), 73-79 (2013).
170. Zhang, W., Ricketts, T. H., Kremen, C., Carney, K. & Swinton, S. M. Ecosystem services and dis-services to agriculture. *Ecological Economics* 64(2), 253–260 (2007).

171. Basu, P., Parui, A.K., Chatterjee, S., Dutta, A., Chakraborty, P., Roberts, S. & Smith, B.. Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural landscapes. *Ecology and Evolution* 6(19), 6983–6992 (2016).
172. Gabriel, D. & Tscharntke, T. Insect pollinated plants benefit from organic farming. *Agriculture, Ecosystems & Environment* 118(1-4), 43–48 (2007).
173. Vinod, M., Naik, A. K., Biradar, R., Natikar, P. K. & Balikai, R. A. Bee pollination under organic and conventional farming systems: a review. *Journal of Experimental Zoology, India* 19(2), 643-652 (2016).
174. Brittain, C., Bommarco, R., Vighi, M., Settele, J. & Potts, S. G. Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation* 143(8), 1860–1867 (2010).
175. Winfree, R., Bartomeus, I. & Cariveau, D. P. Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics* 42, 1–22 (2011).
176. Redhead, J. W., Dreier, S., Bourke, A.F., Heard, M.S., Jordan, W.C., Sumner, S., Wang, J. & Carvell, C.. Effects of habitat composition and landscape structure on worker foraging distances of five bumblebee species. *Ecological Applications* 26(3), 726-739 (2016).
177. Jha, S. & Kremen, C. Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences* 110(2), 555–558 (2013).
178. Harris, L.F & Johnson, S. D. The consequences of habitat fragmentation for plant–pollinator mutualisms. *International Journal of Tropical Insect Science* 24(1), 29–43 (2004).
179. Breed, M. F., Ottewell, K.M., Gardner, M.G., Marklund, M.H., Dormontt, E.E. & Lowe, A.J.Mating patterns and pollinator mobility are critical traits in forest fragmentation genetics. *Heredity* 115(2), 108-114 (2013).
180. Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P., Steffan-Dewenter, I. & Öckinger, E.Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20092221 (2010).
181. Jauker, B., Krauss, J., Jauker, F. & Steffan-Dewenter, I. Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology* 28(1), 107–120 (2013).
182. Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landscape Ecology* 1449–1455 (2016).
183. Jaffé, R. Pope, N., Acosta, A.L., Alves, D.A., Arias, M.C., De la Rúa, P., Francisco, F.O., Giannini, T.C., González-Chaves, A., Imperatriz-Fonseca, V.L. & Tavares, M.G.Beekeeping practices and geographic distance, not land use, drive gene flow across tropical bees. *Molecular Ecology* 25(21), 5345–5358 (2016).
184. Benjamin, F. E., Reilly, J. R. & Winfree, R. Pollinator body size mediates the scale at which land use drives crop pollination services. *Journal of Applied Ecology* 51(2), 440–449 (2014).
185. Hoehn, P., Steffan-Dewenter, I. & Tscharntke, T. Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. *Biodiversity and Conservation* 19(8), 2189–2200 (2010).
186. Lander, T. A., Bebber, D. P., Choy, C. T. L., Harris, S. A. & Boshier, D. H. The Circe Principle explains how resource-rich land can waylay

pollinators in fragmented landscapes. *Current Biology* 21(15), 1302–1307 (2011).

187. Lundin, O., Rundlöf, M., Smith, H. G., Fries, I. & Bommarco, R. Neonicotinoid insecticides and their impacts on bees: A systematic review of research approaches and identification of knowledge gaps. *PLoS ONE* 10(8), e0136928 (2015).
188. Brittain, C. & Potts, S. G. The potential impacts of insecticides on the life-history traits of bees and the consequences for pollination. *Basic and Applied Ecology* 12(4), 321–331 (2011).
189. Wilfert, L., Long, G., Leggett, H.C., Schmid-Hempel, P., Butlin, R., Martin, S.J.M. & Boots, M.Deformed wing virus is a recent global epidemic in honeybees driven by Varroa mites. *Science* 351(6273), 594–597 (2016).
190. Anguiano-Baez, R., Guzman-Novoa, E., Hamiduzzaman, M. M., Espinosa-Montaño, L. G. & Correa-Benítez, A. Varroa destructor (Mesostigmata: Varroidae) parasitism and climate differentially influence the prevalence, levels, and overt infections of Deformed Wing Virus in honey bees (Hymenoptera: Apidae). *Journal of Insect Science* 16(1), (2016).
191. Fürst, M. A., McMahon, D. P., Osborne, J. L., Paxton, R. J. & Brown, M. J. F. Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature* 506(7488), 364–366 (2014).
192. Guzman-Novoa, E., Hamiduzzaman, M.M., Anguiano-Baez, R., Correa-Benítez, A., Castañeda-Cervantes, E. & Arnold, N.I.First detection of honey bee viruses in stingless bees in North America. *Journal of Apicultural Research* 54(2), 93–95 (2016).
193. Shanks, J. L., Haigh, A. M., Riegler, M. & Spooner-Hart, R. N. First confirmed report of a bacterial brood disease in stingless bees. *Journal of Invertebrate Pathology* 144, 7–10 (2017).
194. Tiedeken, E. J., Egan, P.A., Stevenson, P.C., Wright, G.A., Brown, M.J., Power, E.F., Farrell, I., Matthews, S.M. & Stout, J.C.Nectar chemistry modulates the impact of an invasive plant on native pollinators. *Functional Ecology* 30(6), 885–893 (2016).
195. Stevenson, P. C., Nicolson, S. W. & Wright, G. A. Plant secondary metabolites in nectar: impacts on pollinators and ecological functions. *Functional Ecology* 31(1), 65–75 (2017).
196. Marrero, H. J., Torretta, J. P., Vázquez, D. P., Hodara, K. & Medan, D. Exotic plants promote pollination niche overlap in an agroecosystem. *Agriculture, Ecosystems & Environment* 239, 304–309 (2017).
197. Ghazoul, J. Alien abduction: disruption of native plant-pollinator interactions by invasive species. *Biotropica* 36(2), 156–164 (2004).
198. Stout, J. C. & Tiedeken, E. J. Direct interactions between invasive plants and native pollinators: evidence, impacts and approaches. *Functional Ecology* 31(1), 38–46 (2017).
199. Memmott, J., Craze, P. G., Waser, N. M. & Price, M. V. Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* 10(8), 710–717 (2007).
200. Memmott, J., Waser, N. M. & Price, M. V. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B: Biological Sciences* 271(1557), 2605–2611 (2004).
201. Archer, C. R., Pirk, C. W. W., Carvalheiro, L. G. & Nicolson, S. W. Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. *Oikos* 123(4), 401–407 (2014).

202. Hadley, A. S. & Betts, M. G. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews* 87(3), 526-544.
203. Debinski, D. M. & Holt, R. D. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14(2), 342-355 (2000).
204. Brosi, B. J., Daily, G. C., Chamberlain, C. P. & Mills, M. Detecting changes in habitat-scale bee foraging in a tropical fragmented landscape using stable isotopes. *Forest Ecology and Management* 258(9), 1846–1855 (2009).
205. Loyola, R. D. & Martins, R. P. Habitat structure components are effective predictors of trap-nesting Hymenoptera diversity. *Basic and Applied Ecology* 9(6), 735–742 (2008).
206. Schuepp, C., Herzog, F. & Entling, M. H. Disentangling multiple drivers of pollination in a landscape-scale experiment. *Proceedings of the Royal Society of London B: Biological Sciences* 281(1774), 20132667 (2013).
207. King, C., Ballantyne, G. & Willmer, P. G. Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution* 4(9), 811–818 (2013).
208. Valverde, J., Gómez, J. M. & Perfectti, F. The temporal dimension in individual-based plant pollination networks. *Oikos* 125(4), 468–479 (2016).
209. Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L. & Totland, Ø. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12(2), 184–195 (2009).
210. Tylianakis, J., Klein, A. & Tscharntke, T. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology* 86(12), 3296-3302 (2005).
211. Martins, R. & Antonini, Y. Can pollination syndromes indicate ecological restoration success in tropical forests? *Restoration Ecology* 24(3), 373–380 (2016).
212. Dicks, L. V., Abrahams, A., Atkinson, J., Biesmeijer, J., Bourn, N., Brown, C., Brown, M.J., Carvell, C., Connolly, C., Cresswell, J.E. & Croft, P. Identifying key knowledge needs for evidence-based conservation of wild insect pollinators: A collaborative cross-sectoral exercise. *Insect Conservation and Diversity* 6(3), 435–446 (2013).
213. Garibaldi, L. A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Kremen, C. & Morandin, L. From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment* 12(8), 439–447 (2014).
214. Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C.& Dicks, L.V. Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters* 20(5), 673–689 (2017).
215. Batary, P., Baldi, A., Kleijn, D. & Tscharntke, T. Landscape-moderated biodiversity effects of agri-environmental management : a meta-analysis. *Proceedings of the Royal Society of London B: Biological Sciences* 278, 1894–1902 (2011).
216. Sardiñas, H. S., Tom, K., Ponisio, L. C., Rominger, A. & Kremen, C. Sunflower (Helianthus annuus) pollination in California's Central Valley is limited by native bee nest site location. *Ecological Applications* 26(2),

438–447 (2016).
217. Jha, S. Contemporary human-altered landscapes and oceanic barriers reduce bumble bee gene flow. *Molecular Ecology* 24(5), 993–1006 (2015).
218. Blaauw, B. R. & Isaacs, R. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology* 51(4), 890–898 (2014).
219. Nicholls, C. I. & Altieri, M. A. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development* 33(2), 257–274 (2013).
220. Peters, V. E., Carroll, C. R., Cooper, R. J., Greenberg, R. & Solis, M. The contribution of plant species with a steady-state flowering phenology to native bee conservation and bee pollination services. *Insect Conservation and Diversity* 6(1), 45–56 (2013).
221. Brosi, B. J., Armsworth, P. R. & Daily, G. C. Optimal design of agricultural landscapes for pollination services. *Conservation Letters* 1(1), 27–36 (2008).
222. MacIvor, J. S. Cavity-nest boxes for solitary bees: a century of design and research. *Apidologie* 48(3), 311–327 (2017).
223. Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., M'gonigle, L.K., Rader, R. & Ricketts, T.H.. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications* 6, 7414 (2015).
224. Priess, J. A., Mimler, M., Klein, A.M., Schwarze, S., Tscharntke, T. & Steffan-Dewenter, I.. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. *Ecological Applications* 17(2), 407–417 (2007).
225. Amarnath, G., Murthy, M. S. R., Britto, S. J., Rajashekar, G. & Dutt, C. B. S. Diagnostic analysis of conservation zones using remote sensing and GIS techniques in wet evergreen forests of the Western Ghats – An ecological hotspot, Tamil Nadu, India. *Biodiversity & Conservation* 12(12), 2331–2359 (2003).
226. Davidar, P., Rajagopal, B., Mohandass, D., Puyravaud, J.P., Condit, R., Wright, S.J. & Leigh, E.G.The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography* 16(4), 510–518 (2007).
227. Mittermeier, R., Myers, N., Thomsen, J.B., Da Fonseca, G.A. & Olivieri, S. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12(3), 516-520 (1998).
228. Myers, N., Mittermeier, R.,Mittermeier, C., Da Fonseca, G.A. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* 403(6772), p.853 (2000).
229. Saout, S. Le, Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H., Stuart, S.N., Badman, T. & Rodrigues, A.S. Protected areas and effective biodiversity conservation. (2013).
230. Gunawardene, N. R., Daniels, D.A., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., Karunakaran, P.V., Nayak, G.K., Prasad, S., Puyravaud, P., Ramesh, B.R., Subramanian, K.A. & Vasanthy, G. . A brief overview of the Western Ghats - Sri Lanka biodiversity hotspot. *Current Science* 93(11), 1567–1572 (2007).
231. Chitale, V. S., Behera, M. D. & Roy, P. S. Global biodiversity hotspots in

India: significant yet under studied. *Current Science* 108(2), 149–150 (2015).

232. Satish, K. V., Saranya, K.R.L., Reddy, C.S., Krishna, P.H., Jha, C.S. & Rao, P.P. Geospatial assessment and monitoring of historical forest cover changes (1920–2012) in Nilgiri Biosphere Reserve, Western Ghats, India. *Environmental Monitoring and Assessment* 186(12), 8125–8140 (2014).
233. Karanth, K. K., Curran, L. M. & Reuning-Scherer, J. D. Village size and forest disturbance in Bhadra Wildlife Sanctuary, Western Ghats, India. *Biological Conservation* 128(2), 147–157 (2006).
234. Daniels, R. J. R. Landscape ecology and conservation of birds in the Western Ghats, South India. *Ibis* 138(1), 64–69 (1996).
235. Cincotta, R. P., Wisnewski, J. & Engelman, R. Human population in the biodiversity hotspots. *Nature* 404(6781), 990–992 (2000).
236. Subash-Chandran, M. D. On the ecological history of the Western Ghats. *Current Science* 73(2), 146–155 (1997).
237. Nogué, S., Tovar, C., Bhagwat, S. A., Finsinger, W. & Willis, K. J. Exploring the ecological history of a tropical agroforestry landscape using fossil pollen and charcoal analysis from four sites in Western Ghats, India. *Ecosystems* 21(45) (2017). doi:10.1007/s10021-017-0132-1
238. Gardner, T. A., Barlow, J., Sodhi, N. S. & Peres, C. A. A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation* 143(10), 2293–2300 (2010).
239. Ranganathan, J., Daniels, R. J. R., Chandran, M. D. S., Ehrlich, P. R. & Daily, G. C. Sustaining biodiversity in ancient tropical countryside. *Proceedings of the National Academy of Sciences* 105(46), 17852–17854 (2008).
240. Chandran, M. On the ecological history of the Western Ghats. *Current Science* 73(2), 146-155 (1997).
241. Menon, S. & Bawa, K. S. Applications of geographical information systems, remote sensing and a landscape ecology approach to biodiversity conservation in the Western Ghats. *Current Science* 73(2), 134–145 (1997).
242. Anand, M. O., Krishnaswamy, J., Kumar, A. & Bali, A. Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: Remnant forests matter. *Biological Conservation* 143(10), 2363–2374 (2010).
243. Reddy, C. S., Sreelekshmi, S., Jha, C. S. & Dadhwal, V. K. National assessment of forest fragmentation in India: Landscape indices as measures of the effects of fragmentation and forest cover change. *Ecological Engineering* 60, 453–464 (2013).
244. Drigo, R., Lasserre, B. & Marchetti, M. Patterns and trends in tropical forest cover. *Plant Biosystems* 143(2), 311–327 (2009).
245. Athira, K., Reddy, C. S., Saranya, K. R. L., Joseph, S. & Jaishanker, R. Habitat monitoring and conservation prioritisation of protected areas in Western Ghats, Kerala, India. *Environmental Monitoring and Assessment* 189(6), 295 (2017).
246. Kale, M. P., Chavan, M., Pardeshi, S., Joshi, C., Verma, P.A., Roy, P.S., Srivastav, S.K., Srivastava, V.K., Jha, A.K., Chaudhari, S.& Giri, Y.Land-use and land-cover change in Western Ghats of India. *Environmental Monitoring and Assessment* 188(7), 387 (2016).
247. Kodandapani, N., Cochrane, M. A. & Sukumar, R. Conservation threat of

increasing fire frequencies in the Western Ghats, India. *Conservation Biology* 18(6), 1553–1561 (2004).

248. Anitha, K., Joseph, S., Chandran, R. J., Ramasamy, E. V. & Prasad, S. N. Tree species diversity and community composition in a human-dominated tropical forest of Western Ghats biodiversity hotspot, India. *Ecological Complexity* 7(2), 217–224 (2010).
249. Niyas, P., Kunhamu, T., Ali, S., Jothsna, C., Aneesh, C.R., Kumar, N. & Sukanya, R. Functional diversity in the selected urban and peri-urban homegardens of Kerala, India. *Indian Journal of Agroforestry* 18(1), 39–46 (2016).
250. Nayar, N. M. Agrobiodiversity in a biodiversity hotspot: Kerala State, India. Its origin and status. *Genetic Resources and Crop Evolution*, 58(1), 55-82 (2011).
251. Garcia, C. A., Bhagwat, S.A., Ghazoul, J., Nath, C.D., Nanaya, K.M., Kushalappa, C.G., Raghuramulu, Y., Nasi, R. & Vaast, P. Biodiversity conservation in agricultural landscapes: challenges and opportunities of coffee agroforests in the Western Ghats, India. *Conservation Biology* 24(2), 479–488 (2010).
252. Mohan, S., Nair, P. K. R. & Long, A. J. An assessment of ecological diversity in homegardens: A case study from Kerala State, India. *Journal of Sustainable Agriculture* 29(4), 135–153 (2007).
253. Gaucherel, C., Alet, J.& Garcia, C.. Coffee monoculture trends in tropical agroforested landscapes of Western Ghats (India). *Environmental Conservation* 44(2),183-190 (2017)
254. Ghazoul, J. Challenges to the uptake of the ecosystem service rationale for conservation. *Conservation Biology* 21(6), 1651–1652 (2007).
255. Kumar, B. M. Land use in Kerala : changing scenarios and shifting paradigms. *Journal of Tropical Agriculture* 43, 1–12 (2006).
256. Jose, M. & Padmanabhan, M. Dynamics of agricultural land use change in Kerala: a policy and social-ecological perspective. *International Journal of Agricultural Sustainability* 14(3), 307–324 (2016).
257. Warren-Thomas, E., Dolman, P. M. & Edwards, D. P. Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conservation Letters* 8(4), 230–241 (2015).
258. Raman, T. R. S. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. pp. 517-547 in *Forest Diversity and Management* (Springer, Dordrecht, 2006).
259. Karanth, K. K., Sankararaman, V., Dalvi, S., Srivathsa, A., Parameshwaran, R., Sharma, S., Robbins, P. & Chhatre, A., Producing diversity: agroforests sustain avian richness and abundance in India's Western Ghats. *Frontiers in Ecology and Evolution* 4, 111 (2016).
260. Mandle, L. & Ticktin, T. Moderate land use changes plant functional composition without loss of functional diversity in India's Western Ghats. *Ecological Applications* 25(6), 1711–1724 (2015).
261. Rahman, P. M., Varma, R. V. & Sileshi, G. W. Abundance and diversity of soil invertebrates in annual crops, agroforestry and forest ecosystems in the Nilgiri biosphere reserve of Western Ghats, India. *Agroforestry Systems* 85(1), 165–177 (2012).
262. Corlett, R. T. Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biological Reviews* 79(3), 497–532 (2004).

263. Thomas, S. G., Rehel, S. M., Varghese, A., Davidar, P. & Potts, S. G. Social bees and food plant associations in the Nilgiri Biosphere Reserve, India. *Tropical Ecology* 50(1), 79–88 (2009).
264. Hepburn, H. R. & Radloff, S. E. *Honeybees of Asia*. (Springer Science & Business Media, 2011). doi:10.1007/978-3-642-16422-4
265. Mayfield, M. & Belavadi, V. Cardamom in the Western Ghats: Bloom sequences keep pollinators in fields. pp. 69-83 in *Initial survey of good pollination practices* (FAO, 2008).
266. Muttoo, R. Facts about beekeeping in India. *Bee World* 37(7), 125-133 (1956).
267. Koetz, A. & H., A. Ecology, behaviour and control of Apis cerana with a focus on relevance to the Australian incursion. *Insects* 4(4), 558–592 (2013).
268. Abrol, D. P. Current scenario of beekeeping in India - challenges and opportunities. p. 11 in *Beneficial Insect Farming-Benefits and Livelihood Generation* (ICAR-Indian Institute of Natural Resins and Gums, Ranchi, India, 2016).
269. Baskaran, M. Variation in the morphological characters of the Indian honey bee *Apis cerana indica* (Fabr.) from northern to southern India. *Journal of Apicultural Research* 55(3), 221–227 (2016).
270. Ken, T., Hepburn, H.R., Radloff, S.E., Yusheng, Y., Yiqiu, L., Danyin, Z. & Neumann, P.. Heat-balling wasps by honeybees. *Naturwissenschaften* 92(10), 492–495 (2005).
271. Abrol, D. P. Defensive behavior of Apis cerana F. against predatory wasp. *Journal of Apicultural Science* 50(2), 39–46 (2006).
272. Pradeepa, S. & Bhat, N. Survey on absconding of Apis cerana indica F. colonies at different traditional beekeeping areas of Karnataka. *Current Biotica* 8(2), 174–178 (2014).
273. Dong, S., Wen, P., Zhang, Q., Li, X., Tan, K. & Nieh, J.. Resisting majesty: Apis cerana, has lower antennal sensitivity and decreased attraction to queen mandibular pheromone than Apis mellifera. *Scientific Reports* 7, 44640 (2017).
274. Oldroyd, B., Halling, L.A., Good, G., Wattanachaiyingcharoen, W., Barron, A.B., Nanork, P., Wongsiri, S. & Ratnieks, F.L. Worker policing and worker reproduction in Apis cerana. *Behavioural Ecology and Sociobiology* 50(4), 371–377 (2001).
275. Holmes, M. J., Tan, K., Wang, Z., Oldroyd, B. P. & Beekman, M. Honeybee (Apis cerana) guards do not discriminate between robbers and reproductive parasites. *Insectes Sociaux* 60(2), 265–271 (2013).
276. Nanork, P., Chapman, N.C., Wongsiri, S., Lim, J., Gloag, R.S. & Oldroyd, B.P., Social parasitism by workers in queenless and queenright Apis cerana colonies. *Molecular Ecology* 16(5), 1107–1114 (2007).
277. Oldroyd, B. & Nanork, P. Conservation of Asian honey bees. *Apidologie* 40(3), 296-312 (2009).
278. Dhaliwal, G. S. & Atwal, A. S. Interspecific Relations Between Apis cerana indica and Apis mellifera. *Journal of Apicultural Research* 9(2), 53–59 (1970).
279. Fries, I., Huazhen, W., Wei, S. & Jin, C. S. Grooming behavior and damaged mites (Varroa jacobsoni) in Apis cerana cerana and Apis mellifera ligustica. *Apidologie* 27(1), 3–11 (1996).
280. Byatt, M. A., Chapman, N. C., Latty, T. & Oldroyd, B. P. The genetic consequences of the anthropogenic movement of social bees. *Insectes*

Sociaux 63(1), 15–24 (2016).

281. Gloag, R., Tan, K., Wang, Y., Song, W., Luo, W., Buchman, G., Beekman, M. & Oldroyd, B.P. No evidence of queen thelytoky following interspecific crosses of the honey bees Apis cerana and Apis mellifera. *Insectes Sociaux* 64(2), 241–246 (2017).
282. Francoy, T. M., Bonatti, V., Viraktamath, S. & Rajankar, B. R. Wing morphometrics indicates the existence of two distinct phenotypic clusters within population of Tetragonula iridipennis (Apidae: Meliponini) from India. *Insectes Sociaux* 63(1), 109–115 (2016).
283. Danaraddi, C. S., Viraktamath, S., Basavanagoud, K. & Bhat, A. R. S. Nesting habits and nest structure of stingless bee, Trigona iridipennis Smith at Dharwad, Karnataka. *Karnataka Journal of Agricultural Sciences* 22(2), 310–313 (1996).
284. Raju, A. J. S., Rao, K. S, &Rao, N. G. Association of Indian stingless bee, Trigona iridipennis Smith (Apidae: Meliponinae) with red-listed Cycas sphaerica. *Current Science* 96(11), 1435–1436 (2009).
285. Duangphakdee, O., Koeniger, N., Deowanish, S., Hepburn, H. R. & Wongsiri, S. Ant repellent resins of honeybees and stingless bees. *Insectes Sociaux* 56(4), 333–339 (2009).
286. Divya, K., Amritha, V. & Devanesan, S. Nest architecture of stingless bees. *Advances in Life Sciences* 5(6), 2035–2038 (2016).
287. Vazhacharickal, P. Swarming, drone movements, foraging behavior and associated plants of stingless bees (Trigona iridipennis Smith) in Kerala. (Grin Verlag, Munich, 2014).
288. Rasmussen, C. Stingless bees (Hymenoptera: Apidae: Meliponini) of the Indian subcontinent: diversity, taxonomy and current status of knowledge. *Zootaxa* 3647(3), 401–428 (2013).
289. Vijayakumar, K. & Jeyaraaj, R. Taxonomic notes on stingless bee Trigona (Tetragonula) iridipennis Smith (Hymenoptera: Apidae) from India. *Journal of Threatened Taxa* 6(11), 6480–6484 (2014).
290. Singh, A., Jaiswal, D., Singh, H., & Thakur, R.K. Diversity of bees' flora and floral calendar of native honeybees in Nagaland, India. *Advances in Life Sciences* 5(6), 2285–2292 (2016).
291. Kothai, S. & Jayanthi, B. Environmental impact on stingless bee propolis (Tetragonula iridipennis) reared from two different regions of Tamilnadu–a comparative study. *International Journal of ChemTech Research* 7(7), 3081–3088 (2015).
292. Choudhari, M. K., Punekar, S. A., Ranade, R. V. & Paknikar, K. M. Antimicrobial activity of stingless bee (Trigona sp.) propolis used in the folk medicine of Western Maharashtra, India. *Journal ofEthnopharmacology* 141(1), 363–367 (2012).
293. Leonhardt, S. D. Chemical ecology of stingless bees. *Journal of Chemical Ecology* 43(4), 385–402 (2017).
294. Raju, A. & Rao, S. Nesting habits, floral resources and foraging ecology of large carpenter bees (Xylocopa latipes and Xylocopa pubescens) in India. *Current Science* 90(9), 1210–1217 (2006).
295. Somanathan, H. & Borges, R. M. Nocturnal pollination by the carpenter bee Xylocopa tenuiscapa (Apidae) and the effect of floral display on fruit set of Heterophragma quadriloculare (Bignoniaceae) in India. *Biotropica* 33(1), 78-89(2001).
296. Somanathan, H., Borges, R. M., Warrant, E. J. & Kelber, A. Nocturnal bees learn landmark colours in starlight. *Current Biology* 18(21), R996–

R997 (2008).

297. Carr, S. A. & Davidar, P. Pollinator dependency, pollen limitation and pollinator visitation rates to six vegetable crops in southern India. *Journal of Pollination Ecology* 16(8), 51–57 (2015).
298. Aswini, S., Amritha, V. & Devanesan, S. Melissopalynology studies on the Indian honey bee (Apis cerana indica Fab.) in southern Kerala. *Entomon* 40(1), 1–10 (2015).
299. Karunaratne, W. A. I. P., Edirisinghe, J. P. & Gunatilleke, C. S. Floral relationships of bees in selected areas of Sri Lanka. *Ceylon Journal of Science* 34, 27–45 (2005).
300. Roubik, D. W. Tropical pollinators in the canopy and understory: Field data and theory for stratum ‘preferences’. *Journal of Insect Behaviour* 6(6), 659–673 (1993).
301. Bhat, D. M. & Murali, K. S. Phenology of understorey species of tropical moist forest of Western Ghats region of Uttara Kannada district in South India. *Current Science* 81(7), 799–805 (2001).
302. Murali, K. S. & Sukumar, R. Reproductive phenology of a tropical dry forest in Mudumalai, southern India. *Journal of Ecology* 82(4), 759–767 (1994).
303. Devy, M. S. & Davidar, P. Pollination systems of trees in Kakachi, a mid-elevation wet evergreen forest in Western Ghats, India. *American Journal of Botany* 90(4), 650–7 (2003).
304. Krishnan, R. *PhD thesis*. Ecology of understorey shrubs in a wet forest of south India. (1994).
305. Devy, M. S. & Davidar, P. Breeding systems and pollination modes of understorey shrubs in a medium elevation wet evergreen forest, southern Western Ghats, India. *Current Science* 90(6), 838–842 (2006).
306. Sharma, M.V., Kuriakose, G. & Shivanna, K.R.Reproductive strategies of Strobilanthes kunthianus, an endemic, semelparous species in southern Western Ghats, India. *Botanical Journal of the Linnean Society* 157(1), 155–163 (2008).
307. Anitha, K. & Prasad, S. Mass flowering and pollinators of Strobilanthes consanguinea in the Western Ghats, South India. *Current Science* 92(12), 1680–1681 (2007).
308. Kulloli, S. K. & Sreekala, A. K. Pollination ecology of Rauvolfia micrantha Hook. F. (apocynaceae): a critically endangered medicinal plant from the southern Western Ghats. *Phytomorphology* 59(3&4), 96–101 (2009).
309. Ramasubbu, R., Sreekala, A. & Pandurangan, A. Reproductive ecology of Impatiens platyadena Fischer, a critically endangered balsam of Western Ghats. *Current Science* 100(10) 1550–1554 (2011).
310. Kumar, C. & Somashekar, R. Pollination ecology and reproductive biology of Canarium strictum Roxb. from evergreen forests of Central Western Ghats, India. *Journal of Environmental Biology* 36(5), 1131 (2015).
311. Sinu, P. A. & Shivanna, K. R. Pollination ecology of cardamom (Elettaria cardamomum) in the Western Ghats, India. *Journal of Tropical Ecology* 23(4), 493-496 (2007).
312. Chaudhary, O. P. & Kumar, R. Studies on honeybee foraging and pollination in cardamom (Elettaria cardamomum Maton). *Journal of Spices and Aromatic Crops* 9(1), 37–42 (2000).
313. Kuriakose, G., Sinu, P. A. & Shivanna, K. R. Domestication of cardamom (Elettaria cardamomum) in Western Ghats, India: Divergence in productive traits and a shift in major pollinators. *Annals of Botany* 103(5),

727–733 (2009).

314. Krishnan, S., Kushalappa, C. G., Shaanker, R. U. & Ghazoul, J. Status of pollinators and their efficiency in coffee fruit set in a fragmented landscape mosaic in South India. *Basic and Applied Ecology* 13(3), 277–285 (2012).
315. Boreux, V., Krishnan, S., Cheppudira, K. G. & Ghazoul, J. Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agro-forests. *Agriculture, Ecosystems and Environment* 172(1), 42-48 (2012).
316. Boreux, V., Kushalappa, C. G., Vaast, P. & Ghazoul, J. Interactive effects among ecosystem services and management practices on crop production: pollination in coffee agroforestry systems. *Proceedings of the National Academy of Sciences U.S.A.* 110(21), 8387–92 (2013).
317. Munj, A., Zote, V., Raut, R. & Salvi, B. Survey and surveillance of pollinators of mango in South Konkan coastal region of Maharashtra. *Journal of Entomology and Zoology Studies* 5(3), 190–192 (2017).
318. Koshy, K. C., Harikumar, D. & Narendran, T. C. Insect visits to some bamboos of the Western Ghats, India. *Current Science* 81(7), 833–838 (2001).
319. Theisen-Jones, H. & Bienefeld, K. The Asian honey bee (Apis cerana) is significantly in decline. *Bee World* 93(4), 90–97 (2016).
320. Basu, P., Bhattacharya, R. & Iannetta, P. P. M. A decline in pollinator dependent vegetable crop productivity in India indicates pollination limitation and consequent agro-economic crises. *Nature Precedings* 1–9 (2011).
321. Sharma, M., Shaanker, R. U., Leather, S., Vasudeva, R. & Shivanna, K. R. Floral resources, pollinators and fruiting in a threatened tropical deciduous tree. *Journal of Plant Ecology* 4(4), 259–267 (2010).
322. Vazhacharickal, P. Nesting behavior and habitats of the stingless bee Trigona iridipennis Smith in Kerala. (Grin Verlag, Munich 2016).
323. Devanesan, S. & Jacob, A. Thai sacbrood virus disease of Asian honeybee Apis cerana indica Fab. *Kerala, India. Proceedings 37th International Apiculture Congress.* (2001).
324. Tan, K., Chen, W., Dong, S., Liu, X., Wang, Y. & Nieh, J.C. A neonicotinoid impairs olfactory learning in Asian honey bees (Apis cerana) exposed as larvae or as adults. *Scientific Reports* 5, 10989 (2015).
325. Tan, K.,Chen, W., Dong, S., Liu, X., Wang, Y. & Nieh, J.C. Imidacloprid alters foraging and decreases bee avoidance of predators. *PLoS ONE*9(7), e102725 (2014).
326. Li, Z., Li, M., He, J., Zhao, X., Chaimanee, V., Huang, W.F., Nie, H., Zhao, Y. & Su, S.. Differential physiological effects of neonicotinoid insecticides on honey bees: a comparison between Apis mellifera and Apis cerana. *Pesticide Biochemistry and Physiology* 140, 1-8 (2017).
327. Yasuda, M., Sakamoto, Y., Goka, K., Nagamitsu, T. & Taki, H. Insecticide susceptibility in Asian Hhney bees (Apis cerana (Hymenoptera: Apidae)) and implications for wild honey bees in Asia. *Journal of Economic Entomology* 110(2), 447–452 (2017).
328. Stanley, J., Chandrasekaran, S., Preetha, G. & Kuttalam, S. Toxicity of diafenthiuron to honey bees in laboratory, semi-field and field conditions. *Pest Management Science* 66(5), 505–510 (2010).
329. Stanley, J., Preetha, G., Chandrasekaran, S. & Kuttalam, S. Honey bees of the cardamom ecosystem and the selective toxicity of diafenthiuron to

four different bee species in the laboratory. *Journal of Apicultural Research* 48(2), 91–98 (2009).

330. Devi, I. Pesticides in agriculture–a boon or a curse? a case study of Kerala. *Economic and Political Weekly* 45(26/27), 199–207 (2010).
331. Khan, M. S., Kumari, B., Rohilla, H. R., Kaushik, H. D. & Arora, R. K. Analysis of insecticide residues in honeys from apiary (Apis mellifera) and wild honey bee (Apis dorsata and Apis florea) colonies in India. *Journal of Apicultural Research* 43(3), 79–82 (2004).
332. Raman, T. R. S., Mudappa, D. & Kapoor, V. Restoring rainforest fragments: survival of mixed-native species seedlings under contrasting site conditions in the Western Ghats, India. *Restoration Ecology* 17(1), 137–147 (2009).
333. Waser, N. M., Chittka, L., Price, M. V., Williams, N. M. & Ollerton, J. Generalization in pollination systems, and why it matters. *Ecology* 77(4), 1043–1060 (1996).
334. Maia-Silva, C., Hrncir, M., Imperatriz-Fonseca, V. L. & Schorkopf, D. L. P. Stingless bees (Melipona subnitida) adjust brood production rather than foraging activity in response to changes in pollen stores. *Journal of Comparative Physiology A* 202(9-10), 723–732 (2016).
335. Eltz, T., Brühl, C. A., Van der Kaars, S., Chey, V. K. & Linsenmair, K. E. Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. *Insectes Sociaux* 48(3), 273–279 (2001).
336. Suryanarayana, M., Rao, G. M. & Singh, T. Studies on pollen sources for Apis cerana Fabr and Apis mellifera L bees at Muzaffarpur, Bihar, India. *Apidologie* 23(1), 33–46 (1992).
337. Nagamitsu, T. & Inoue, T. Differences in pollen sources of Apis cerana and Apis mellifera at a primary beech forest in central Japan. *Journal of Apicultural Research* 38(1-2), 71–78 (1999).
338. Nagamitsu, T. & Inoue, T. Foraging activity and pollen diets of subterranean stingless bee colonies in response to general flowering in Sarawak, Malaysia. *Apidologie* 33(3), 303–314 (2002).
339. Abrol, D. P. Foraging in honeybees Apis cerana indica F. and Apis dorsata F. (Hymenoptera: Apidae): activity and weather conditions. *Journal of the Indian Institute of Science* 72(5), 395–401 (1992).
340. Abrol, D. P. Diversity of pollinating insects visiting litchi flowers (Litchi chinensis Sonn.) and path analysis of environmental factors influencing foraging behaviour of four honeybee species. *Journal of Apicultural Research* 45(4), 180–187 (2006).
341. Reddy, C. Observations on the annual cycle of foraging and brood rearing by Apis cerana indica colonies. *Journal of Apicultural Research* 19(1), 17–20 (1980).
342. Rami Reddy, P. V., Rashmi, T. & Verghese, A. Foraging activity of Indian honey bee, Apis cerana in relation to ambient climate variables under tropical conditions. *Journal of Environmental Biology* 36(3), 577–581 (2015).
343. Mattu, V. K. & Verma, L. R. Studies on the annual foraging cycle of Apis cerana indica F. in Simla hills of Northwest Himalayas. *Apidologie* 16(1), 1–18 (1985).
344. Devanesan, S., Nisha, M. M., Bennet, R. & Shailaja, K. K. Foraging behaviour of stingless bee, Trigona iridipennis Smith. *Insect Environment* 8, 131–133 (2002).

345. Danaraddi, C. & Hakkalappanavar, S. Studies on foraging behaviour of stingless bee, Trigona iridipennis Smith at Dharwad, Karnataka. *International Journal of Forestry and Crop Improvement* 2(2), 163–169 (2011).
346. Saravanan, P. & Alagar, M. Foraging activity of stingless bee, Trigona iridipennis Smith. *Journal of Plant Protection and Environment* 4(2), 65–69 (2007).
347. Managanvi, K., Khan, M. S. & Srivastava, P. Foraging activity of stingless bee (Trigona laeviceps). *Research Journal of Agricultural Sciences* 3(1), 169–172 (2012).
348. Inoue, T., Salmah, S., Abbas, I. & Yusuf, E. Foraging behavior of individual workers and foraging dynamics of colonies of three Sumatran stingless bees. *Researches on Population Ecolgy* 27(2), 373–392 (1985).
349. Mohapatra, L. & Satapathy, C. Foraging activity of stingless bee, Trigona iridipennis Smith, at Bhubaneswar. *Journal of Plant Protection and Environment* 11(1), 57–59 (2014).
350. Singh, P. & Khan, M. Assessment of comparative foraging activity in queen right and queen less colony of stingless bee, Tetragonula iridipennis Smith (Hymenoptera: Apidae). *International Journal of Advanced Research* 3(7), 498-502 (2015).
351. Shivaramu, K. & Sakthivel, T. Preliminary observations on insect pollinator activity on Macadamia nut (Macadamia integrifolia Maiden & Betche) in Kodagu, Karnataka. *Pest Management in Horticultural Ecosystems* 18(2), 233 (2013).
352. Heard, T. A. Behaviour and pollinator efficiency of stingless bees and honey bees on macadamia flowers. *Journal of Apicultural Research* 33(4), 191–198 (1994).
353. Shivaramu, K., Sakthivel, T. & Reddy, P. Diversity and foraging dynamics of insect pollinators on rambutan (Nephelium lappacum L.). *Pest Management in Horticultural Ecosystems* 18(2), 158–160 (2013).
354. Shilpa, P., Sowmya, K. & Srikanth, C. Pollinator diversity and foraging activity on fennel, Foeniculum vulgare Mill. and African marigold, Tagetus minuta L. *Pest Management in Horticultural Ecosystems* 20(2), 236–239 (2014).
355. Balachandran, C., Chandran, M.S., Vinay, S., Shrikant, N. & Ranachandra, T.V. Pollinator diversity and foraging dynamics on monsoon crop of cucurbits in a traditional landscape of South Indian west coast. *Biotropia - The Southeast Asian Journal of Tropical Biology* 24(1), 16–27 (2017).
356. Jayasinghe, U. & Silva, T. Buzzing wild bee visits enhance seed set in eggplant, Solanum melongena. *Psyche: A Journal of Entomology* 2017, 4624062 (2017).
357. Putra, R. E., Permana, A. D. & Kinasih, I. Application of Asiatic honey bees (Apis cerana) and stingless bees (Trigona laeviceps) as pollinator agents of hot pepper (Capsicum annuum L.) at local Indonesia farm system. *Psyche: A Journal of Entomology* 2014, 687979 (2014).
358. Ahmad, S., Dar, S. & Pandith, B. Comparative foraging behaviour of honey bees, Apis cerana f. and Apis mellifera l.(Hym: Apidae) on apple bloom. *Journal of Entomology and Zoology Studies* 5(1), 474–482 (2017).
359. Aryal, L. N., Thapa, R. B., Tiwari, S. & Chaudhary, N. K. Foraging behavior of native honeybee (Apis cerana F.) and European honeybee (Apis mellifera L.) on flowers of common buckwheat (Fagopyrum

esculentum M.) in Chitwan, Nepal. *International Journal of Applied Sciences and Biotechnology* 4(2), 236-239 (2016).

360. Cui, Q. & Corlett, R. T. Seasonal and diurnal patterns of activity in honeybees (Apis spp.) on the northern edge of the Asian tropics; their implications for the climate-change resilience of pollination. *Tropical Conservation Science* 9(3), 1940082916667142 (2016).
361. Dyer, A. G., Streinzer, M. & Garcia, J. Flower detection and acuity of the Australian native stingless bee *Tetragonula carbonaria* Sm. *Journal of Comparative Physiology A* 202(9-10), 629–639 (2016).
362. Sánchez, D. & Vandame, R. Color and shape discrimination in the stingless bee Scaptotrigona mexicana Guérin (Hymenoptera, Apidae). *Neotropical Entomology* 41(3), 171–177 (2012).
363. Tatsuno, M. & Osawa, N. Flower visitation patterns of the coexisting honey bees Apis cerana japonica and Apis mellifera (Hymenoptera: Apidae). *Entomological Science* 19(3), 255–267 (2016).
364. Koethe, S., Bossems, J., Dyer, A. G. & Lunau, K. Colour is more than hue: preferences for compiled colour traits in the stingless bees Melipona mondury and M. quadrifasciata. *Journal of Comparative Physiology A* 202(9-10), 615–627 (2016).
365. Streinzer, M., Huber, W. & Spaethe, J. Body size limits dim-light foraging activity in stingless bees (Apidae: Meliponini). *Journal of Comparative Physiology A* 202(10), (2016).
366. Menzel, R., Ventura, D., Werner, A., Joaquim, L. & Backhaus, W. Spectral sensitivity of single photoreceptors and color vision in the stingless bee, Melipona quadrifasciata. *Journal of Comparative Physiology A* 166(2), 151–164 (1989).
367. Tan, K., Hu, Z., Chen, W., Wang, Z., Wang, Y. & Nieh, J.C., 2013. Fearful foragers: honey bees tune colony and individual foraging to multi-predator presence and food quality. *PLoS ONE* 8(9), e75841 (2013).
368. Roubik, D. W. & Buchmann, S. L. Nectar selection by Melipona and Apis mellifera (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. *Oecologia* 61(1), 1–10 (1984).
369. Kim, Y. S. & Smith, B. H. Effect of an amino acid on feeding preferences and learning behavior in the honey bee, Apis mellifera. *Journal of Insect Physiology* 46(5), 793–801 (2000).
370. Roubik, D. Foraging behavior of competing Africanized honeybees and stingless bees. *Ecology* 61(4), 836–845 (1980).
371. Gardener, M. C., Rowe, R. J. & Gillman, M. P. Tropical bees (Trigona hockingsi) show no preference for nectar with amino acids. *Biotropica* 35(1), 119–125 (2003).
372. Cook, S. M., Awmack, C. S., Murray, D. A. & Williams, I. H. Are honey bees’ foraging preferences affected by pollen amino acid composition? *Ecological Entomology* 28(5), 622–627 (2003).
373. Greenleaf, S. S., Williams, N. M., Winfree, R. & Kremen, C. Bee foraging ranges and their relationship to body size. *Oecologia* 153(3), 589–596 (2007).
374. Van Nieuwstadt, M. G. L. & Ruano Iraheta, C. E. Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie* 27(4), 219–228 (1996).
375. Dhaliwal, H. S. & Sharma, P. L. Foraging range of the Indian honeybee. *Journal of Apicultural Research* 13(2), 137–141 (1974).
376. Shah, F. & Shah, T. Flight range of Apis cerana from Kashmir. *Indian Bee*

Journal 42(2), 48 (1980).

377. Beekman, M. & Ratnieks, F. L. W. Long-range foraging by the honey-bee, Apis mellifera L. *Functional Ecology* 14(4), 490–496 (2000).
378. He, X., Wang, W., Qin, Q., Zeng, Z., Zhang, S. & Barron, A.B.Assessment of flight activity and homing ability in Asian and European honey bee species, Apis cerana and Apis mellifera, measured with radio frequency tags. *Apidologie* 44(1), 38–51 (2013).
379. Kuhn-Neto, B., Contrera, F. A. L., Castro, M. S. & Nieh, J. C. Long distance foraging and recruitment by a stingless bee, Melipona mandacaia. *Apidologie* 40(4), 472–480 (2009).
380. Smith, J. P., Heard, T. A., Beekman, M. & Gloag, R. Flight range of the Australian stingless bee Tetragonula carbonaria (Hymenoptera: Apidae). *Austral Entomology* 56(1), 50–53 (2017).
381. Koeniger, N. & Vorwohl, G. Competition for food among four sympatric species of Apini in Sri Lanka (Apis dorsata, Apis cerana, Apis florea and Trigona iridipennis). *Journal of Apicultural Research* 18(2), 95–109 (1979).
382. Erancheri, P. & Sunojkumar, P. Nectar robbery in some South Indian Lamiaceae. *Annals of Plant Sciences* 2(10), 386–387 (2013).
383. Nagamitsu, T. & Inoue, T. Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest. *Oecologia* 110(3), 432–439 (1997).
384. Rinderer, T., Marx, B., Gries, M. & Tingek, S. A scientific note on stratified foraging by Sabahan bees on the yellow flame tree (Peltophorum pferocarpum). *Apidologie* 27(5), 423–425 (1996).
385. Leonhardt, S. D., Kaluza, B. F., Wallace, H. & Heard, T. A. Resources or landmarks: which factors drive homing success in Tetragonula carbonaria foraging in natural and disturbed landscapes? *Journal Comparative Physiology A* 202(9-10), 701–708 (2016).
386. Srinivasan, M., Zhang, S., Lehrer, M. & Corlett, T. Honeybee navigation en route to the goal: visual flight control and odometry. *Journal of Experimental Biology* 199(1), 237–244 (1996).
387. Esch, H. E., Zhang, S., Srinivasan, M. V & Tautz, J. Honeybee dances communicate distances measured by optic flow. *Nature* 411(6837), 581–583 (2001).
388. Hrncir, M., Jarau, S., Zucchi, R. & Barth, F. G. A stingless bee [Melipona seminigra] uses optic flow to estimate flight distances. *Journal of Comparative Physiology* 189(10), 761–768 (2003).
389. Sen Sarma, M., Rodriguez-Zas, S.L., Gernat, T., Nguyen, T., Newman, T. & Robinson, G.E. Distance-responsive genes found in dancing honey bees. *Genes, Brain and Behaviour* 9(7), 825–830 (2010).
390. Esch, H. & Burns, J. Distance estimation by foraging honeybees. *Journal of Experimental Biology* 199(1), 155–62 (1996).
391. Eckles, M. A., Roubik, D. W. & Nieh, J. C. A stingless bee can use visual odometry to estimate both height and distance. *Journal of Experimental Biology* 215(18), 3155–3160 (2012).
392. Leonhardt, S. D., Zeilhofer, S., Blüthgen, N. & Schmitt, T. Stingless bees use terpenes as olfactory cues to find resin sources. *Chemical Senses* 35(7), 603–611 (2010).
393. Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83(5), 1421–1432 (2002).

394. Hrncir, M., Maia-Silva, C., Mc Cabe, S. I. & Farina, W. M. The recruiter's excitement – features of thoracic vibrations during the honey bee's waggle dance related to food source profitability. *Journal of Experimental Biology* 214(23), 4055-4064 (2011).
395. Tan, K., Wang, Z., Yang, M., Fuchs, S., Luo, L., Zhang, Z., Li, H., Zhuang, D., Yang, S., Tautz, J. & Beekman, M. Asian hive bees, Apis cerana, modulate dance communication in response to nectar toxicity and demand. *Animal Behaviour* 84(6), 1589–1594 (2012).
396. Dyer, F. C. & Seeley, T. D. Dance dialects and foraging range in three Asian honey bee species. *Behavioral Ecology and Sociobiology* 28(4), 227–233 (1991).
397. Punchihewa, R. W. K., Koeniger, N., Kevan, P. G. & Gadawski, R. M. Observations on the dance communication and natural foraging ranges of Apis cerana, Apis dorsata and Apis florea in Sri Lanka. *Journal of Apicultural Research* 24(3), 168–175 (1985).
398. Su, S., *C*ai, F., Si, A., Zhang, S., Tautz, J. & Chen, S. East learns from west: Asiatic honeybees can understand dance language of European honeybees. *PLoS ONE* 3(6), e2365 (2008).
399. Nieh, J. C. Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie* 35(2), 159–182 (2004).
400. Flaig, I. C., Aguilar, I., Schmitt, T. & Jarau, S. An unusual recruitment strategy in a mass-recruiting stingless bee, Partamona orizabaensis. *Journal of Comparative Physiology A*202(9-10), 679–690 (2016).
401. Aguilar, I., Fonseca, A. & Biesmeijer, J. C. Recruitment and communication of food source location in three species of stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie* 36(3), 313–324 (2005).
402. Frisch, K. Von. The dance language and orientation of bees. (Harvard University Press, Cambridge, MA, USA, 1967).
403. Nieh, J., Tautz, J., Spaethe, J. & Bartareau, T. The communication of food location by a primitive stingless bee. *Zoology* 102(1999), 238–246 (2000).
404. Biesmeijer, J.C. & Slaa, E.J. Information flow and organization of stingless bee foraging. *Apidologie* 35(2), 143-157 (2004).
405. Tautz, J., Zhang, S., Spaethe, J., Brockmann, A., Si, A. & Srinivasan, M.Honeybee odometry: Performance in varying natural terrain. *PLoS Biology* 2(7), e211 (2004).
406. Lichtenberg, E. M., Imperatriz-Fonseca, V. L. & Nieh, J. C. Behavioral suites mediate group-level foraging dynamics in communities of tropical stingless bees. *Insectes Sociaux* 57(1), 105–113 (2010).
407. Ogilvie, J. E. & Thomson, J. D. Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. *Ecology* 97(6), 1442–1451 (2016).
408. Thomson, J. D., Slatirin, M. & Thomson, B. A. Trapline foraging by bumble bees: II. Definition and detection from sequence data. *Behavioral Ecology* 8(2), 199–210 (1997).
409. Ramesh, A., Somanathan, H. & Hempel de Ibarra, N. Foraging division of labour in the Asian honeybee, Apis cerana. in *16th congress of the International Society for Behavioural Ecology* (2016).
410. Hall, K., Nevard, L., Somanathan, H. & Hempel de Ibarra, N. Foraging ranges of Eastern honeybees, Apis cerana, in South India. in *16th congress of the International Society for Behavioural Ecology* (2016).
411. Nicholls, E. & Hempel de Ibarra, N. Assessment of pollen rewards by

foraging bees. *Functional Ecology* 31(1), 76–87 (2017).

412. Kühnholz, S. & Seeley, T. D. The control of water collection in honey bee colonies. *Behavioral Ecology and Sociobiology* 41(6), 407–422
413. Thomas, R. & Josephrajkumar, A. Flowering and pollination biology in coconut. *Journal of Plantation Crops* 41(2), 109-117 (2013).
414. Jarau, S., Hrncir, M., Zucchi, R. & Barth, F. G. Recruitment behavior in stingless bees, Melipona scutellaris and M-quadrifasciata. I. Foraging at food sources differing in direction and distance. *Apidologie* 31(1), 81–91 (2000).