

# Effects of forest and cave proximity on fruit set of tree crops in tropical orchards in Southern Thailand

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**Abstract:** Deforestation and forest fragmentation are contributing to declines in crop pollinator populations worldwide. Several studies have examined the impact of forest proximity on plant pollination ecology, but concentrated on single crop species. However, it can be more informative to investigate multiple crop and pollinator species in a community, because different pollinator groups may respond differently to forest distance. We evaluated flower visitor diversity, visitation frequency, and fruit set for three crop species (rambutan, durian and mango) in 10 pairs of mixed fruit orchards. Each pair consisted of one orchard near (< 1 km) and one orchard far from (> 7 km) the forest edge. Rambutan fruit set was significantly influenced by distance to forest. The main visitors of rambutan flowers were stingless bees. In contrast, the dominant visitors to durian and mango flowers were nectarivorous bats and flies, respectively, and the fruit set of these crops were not significantly influenced by distance to forest. However, durian fruit set was negatively affected by distance to the nearest cave inhabited by nectarivorous bats. This study demonstrates that both caves and forests can be important pollinator sources for agricultural crops, and that the dispersal success of pollinators is related to isolation from source habitats. Maintaining forest patches and limestone karsts may provide stepping stones across fragmented landscapes, and attract greater numbers of pollinators to agricultural areas.

**Key Words:** bat, cave, durian, forest proximity, mango, rambutan, stingless bee, tropical rain forest

## INTRODUCTION

Deforestation is a major source of disturbance in the tropics, leading to smaller and more isolated tropical forest patches. Since forests are important pollinator sources for agricultural crops in tropical regions (Klein *et al.* 2003a, Ricketts 2004), forest loss and fragmentation may reduce the species richness and abundance of crop pollinators. Pollen transfer success (e.g. the number of pollen grains deposited on stigmas, or the number of pollen tubes found in styles) and reproductive success in some crops rely on the number of visitor species and visitor abundance, which is often negatively correlated with distance from natural habitats (Greenleaf & Kremen 2006a, b; Kremen *et al.* 2002, 2004; Morandin & Winston 2006, Morandin *et al.* 2007, Ricketts *et al.* 2008, Winfree *et al.* 2007). However, most studies examining

the effect of natural habitat proximity on crop pollination come from temperate regions, and there have been few studies in tropical forests (Blanche *et al.* 2006, Blanche & Cunningham 2005, Heard & Exley 1994, Klein *et al.* 2003b). Yet tropical studies are particularly needed given that most tropical tree species are self-incompatible (and consequently solely dependent on animal pollination) (Bawa 1990, Ollerton *et al.* 2010).

Further pollination studies in the tropics are also necessary given that many pollinator taxa, such as nectarivorous bats, are found only in these regions. While some economic crops common in South-East Asia (such as rambutan and mango) depend on insect pollination (Carvalho *et al.* 2010, Dag & Gazit 2000, Heard 1999, Shivaramu *et al.* 2012), others rely on bats (e.g. durian, *Durio zibethinus* L.) or both insects and bats (e.g. bitter bean, *Parkia speciosa* Hassk.). For these two plant species, the cave-dwelling nectar bat, *Eonycteris spelaea*, is clearly a principal pollinator (Bumrungsri *et al.* 2008, 2009). Moreover, other cave-dwelling frugivorous bats,

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*Rousettus* spp., also facultatively feed on nectar (Nathan 2005). Thus, proximity to caves might affect durian pollination. Few studies have evaluated the consequences of forest fragmentation on the relationship between bat pollinators and plant reproductive success (Quesada *et al.* 2003, 2004) and no studies have yet directly evaluated the effect of distance to caves on the reproductive success of chiropterophilous plants.

To date, the majority of studies examining how natural habitat proximity affects crop pollination and reproductive success have been conducted in farms dominated by a single plant species (Greenleaf & Kremen 2006a, b; Morandin & Winston 2006, Morandin *et al.* 2007, Ricketts *et al.* 2008). Tropical farms often grow multiple crop species together, creating mixed fruit orchards (Jha & Dick 2010, Kusumaningtyas *et al.* 2006, Michon & Mary 1994). Such mixed orchards can provide high-quality foraging habitat for pollinators, as diverse crops can offer nutritionally complementary rewards. Additionally, phenological complementarity of different crops can sustain pollinator populations across staggered flowering seasons (Blüthgen & Klein 2011, Moeller 2004). Therefore, the negative effects of isolation from forest on the pollinator community may be less prevalent in areas dominated by mixed crop orchards than in areas dominated by monocultures.

In this study, we aimed to investigate the effect of proximity to forest patches and caves on pollination success by examining three sympatric species of tropical economic crops that vary in their pollinator requirement. We hypothesized that the abundance and species richness of pollinators, as well as crop reproductive success, would be greater in farms close to the forest. In addition, we predicted that abundance and species richness of frugivorous/nectarivorous bats would be strongly related to cave proximity, leading to higher reproductive success for chiropterophilous plant species closer to caves.

## METHODS

### Study sites

Mixed fruit orchards are commonly found around traditional villages in South-East Asia, supplying products both for household use and local markets. The typical size of an orchard patch ranges from 300 m<sup>2</sup> to 1 km<sup>2</sup>. Each orchard consists of planted fruit crops and certain native tree species, as well as herb and shrub species. This multi-storied system thus resembles a forest in both structure and diversity. The best-known examples in Thailand are found in the Lan Saka District, Nakhon Si Thammarat Province, where fruit orchards or 'suan-somrom' have operated for over 100 y. The main fruit trees are durian

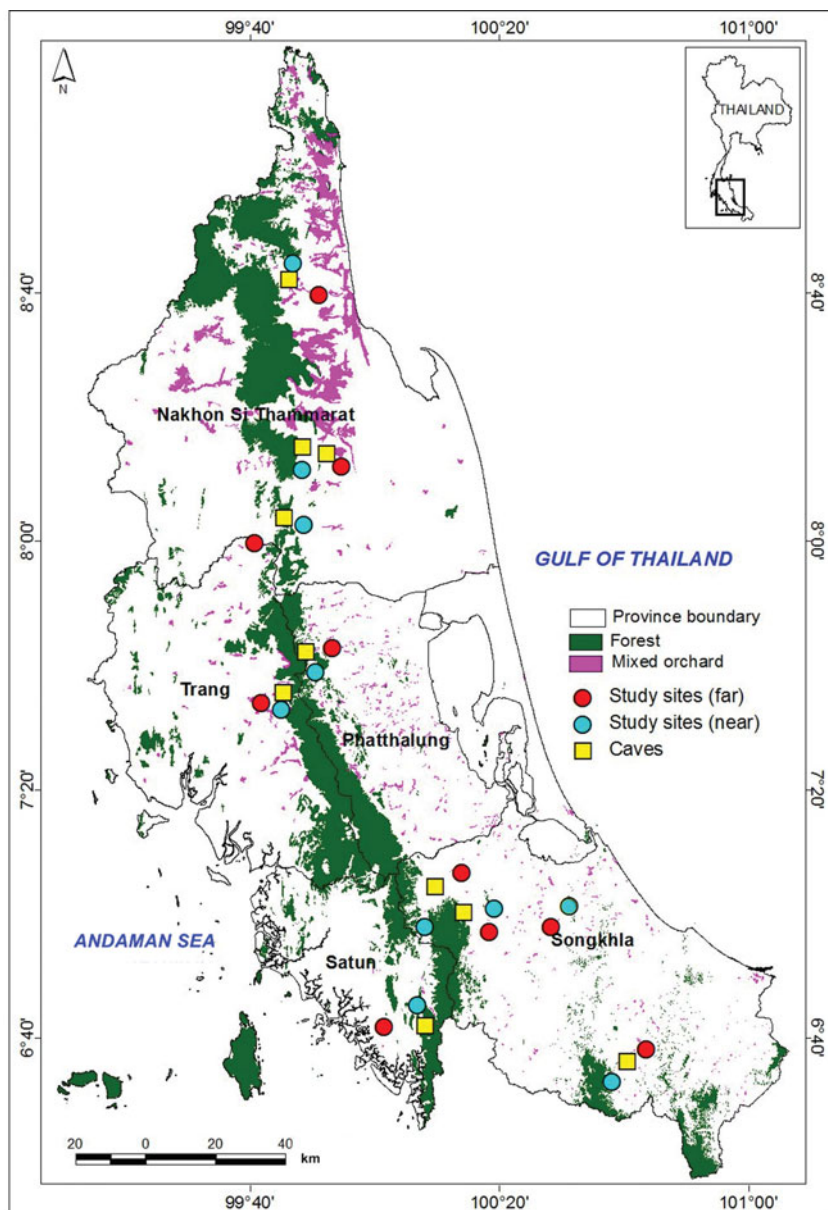
(*Durio zibethinus* L.), bitter bean (*Parkia speciosa* Hassk.), mangosteen (*Garcinia mangostana* L.), domestic jackfruit (*Artocarpus integer* (Thunb.) Merr.), langsung (*Lansium domesticum* Corrêa), rambutan (*Nephelium lappaceum* L.) and mango (*Mangifera indica* L.).

Mixed fruit orchards in southern Thailand are distributed among forest patches (Figure 1). The study took place from September 2012 to June 2013, using 20 mixed-fruit orchards situated at varying distances from 10 forest patches in southern Thailand (Nakhon Si Thammarat, Phattalung, Trang, Satun and Songkhla provinces; 6°20'–8°20'S and 99°40'–110°00'E). The actual size of the 10 patches of tropical rainforest, excluding rubber and oil palm plantations, ranged in area between 3.6 to 650 km<sup>2</sup> and occurred at altitudes between 230 to 1090 m asl. We used 1:133 400 scale photographic imagery from Landsat Thematic Mapper data with a geographic information system (ARC GIS 10.2) to create a map of land use. From this map, we could determine forest patch size and the distance from each orchard to the nearest forest edge, as well as to the nearest cave. We also calculated the proportion of forest fractions within a 20-km radius around each study orchard. All study species (durian, rambutan and mango), were found in each study orchard.

For each forest patch, we selected a pair of orchards (one near to and one far from the forest patch) that were managed without pesticide use. We used pollinator foraging distances to determine the cut-off distances for near and far orchards. Since previous work indicates that the mean foraging distance of local pollinator species ranges 2–7 km (1.97 km for a stingless bee (Wahala & Huang 2005); 1.7–6.9 km for *Rousettus* bats (Bonaccorso *et al.* 2014); 4.4 km for *Eonycteris spelaea* bats (Acharya *et al.* 2015)), we classified orchards as near if they were < 1 km away from the nearest rainforest patch and as far if they were >7 km away from rainforest. All pairs of orchards were at least 10 km apart. The distance from each study orchard to the nearest caves (potential roosts for nectarivorous bats) ranged from 0.7 to 29 km (mean distance to caves  $\pm$  SD: 9.42  $\pm$  7.24 km). Cave with roosting bats were listed by Bumrungsri (1997) and the Shepton Mallet Caving Club (<http://www.thailandcaves.shepton.org.uk>).

### Study species

*Nephelium lappaceum* L. (rambutan, Sapindaceae) typically flowers from March–May, with occasional flowering from August to October, depending on local weather conditions (Whitehead 1959). The flowers are white, and inflorescences are either male or hermaphroditic. Rambutan can be monoecious or dioecious, but male-only plants are rare. On male



**Figure 1.** Map of study area. Visitors and fruit set were sampled from 20 orchards at varying distances from 10 forest patches in southern Thailand.

panicles, there are *c.* 1000–5000 flowers per inflorescence (Lim 1984, Shivaramu *et al.* 2012). For panicles with hermaphroditic flowers, each panicle may contain around 200–800 flowers (Lim 1984, Shivaramu *et al.* 2012). Anthesis starts at about 07h00 and co-occurs with nectar secretion and stigma receptivity. Stigmas remain receptive for a single day (Lim 1984, Shivaramu *et al.* 2012). Rambutan is self-incompatible and therefore depends on pollinators such as *Trigona* and *Apis ceranna* bees (Heard 1999, Lim 1984, Shivaramu *et al.* 2012, Van Welzen *et al.* 1988).

*Durio zibethinus* L. (durian, Bombacaceae) is widely distributed and cultivated throughout South-East Asia.

In southern Thailand, flowering starts sometime during March–May and lasts for only 2–3 wk (Bumrungsri *et al.* 2009). Each inflorescence is composed of 3–100 greenish-white hermaphroditic flowers. Flowers open late in the afternoon (16h00) and nectar secretion begins soon after (Bumrungsri *et al.* 2009). Pollen dehiscence begins around 19h30–20h00 and the stigma is already receptive when anthers release pollen. Bumrungsri *et al.* (2009) found durian trees to be highly self-incompatible. Pollen limitation was found in previous studies, and the main visitors are nectarivorous bats (*Eonycteris spelaea*) and the giant honey bee (*Apis dorsata*) (Bumrungsri *et al.* 2009, Stewart *et al.* 2014).

*Mangifera indica* L. (mango, Anacardiaceae) plants in our study area were primarily of the Bao variety, which shows two flowering peaks (February and September). The flowering period of each tree lasts for 10 d after the first bud opens. Mango inflorescences are composed of hermaphroditic and male flowers (in which the pistil is abortive; Dag & Gazit 2000). The percentage of hermaphroditic flowers varies from 1.25–35.6% (Sharma & Singh 1970). Mango flowers open during the night and early morning (by 08h00). Nectar production and stigma receptivity begin soon after the flower opens (Sharma & Singh 1970) but anther dehiscence does not occur until 11h30, and continues until 15h45. Self-pollinated flowers produced fewer fruits (0.0–1.68%) than cross-pollinated flowers (6.4–23.4%), and overall fruit set in the wild is very low (only 0.1% of hermaphroditic flowers set fruits that reach maturity) (Carvalho *et al.* 2010, Sharma & Singh 1970). The main flower visitors are insects from the orders Diptera, Hymenoptera, Lepidoptera and Coleoptera (Carvalho *et al.* 2010, Dag & Gazit 2000, Sharma & Singh 1970).

### Sampling of flower visitors

We determined the flower visitors to our three study species using 10 trees per species per orchard. We selected three inflorescences of a similar size from the middle of the canopy, selecting trees with many flowers. We observed all insect visits for approximately 5 min per inflorescence (15 min total per tree). When insects were observed visiting flowers, we stopped the timer to identify and count the number of insects. In addition to recording visitation data, we also recorded the number of flowers observed. Surveys were conducted from 08h00 to 11h00 and from 15h00 to 19h00 on days with calm weather (i.e. sunny and without rain, temperature ranging from 31–38°C). Following observations, we collected samples of flower visitors with sweep nets. Common insects that could not be identified to species were grouped by morphotype (Memmott & Godfray 1993). For each forest patch, both the near and far orchards were sampled on the same day.

We placed camera traps (Moultrie game spy d55-IRXT infrared flash camera) *c.* 5–10 m from each study inflorescence (three inflorescences per tree) using the same 30 trees (10 trees per species) examined during flower visitor observations. Camera-trap data were used to determine the visitation rates of each bat species (number of visits per night) to each inflorescence. To confirm the species identity of bats observed via camera traps, we also mist-netted in each study orchard between 19h00 to 02h00. We used three mist nets (2.6 × 6 m) for two nights per orchard. Mist nets were placed as close as possible to the flowers of durian trees, and netted bats were identified to species following Francis & Barrett (2008).

### Reproductive success

To assess the effect of distance from forest on reproductive success, we compared fruit set resulting from open pollination in orchards near and far from forest patches. Three inflorescences were marked with twist ties for each of the 30 study trees (10 trees per species), choosing inflorescences with a similar number of flower buds. We counted the number of fruits per inflorescence for each study tree *c.* 2 wk after the tree finished flowering (so that our measure of pollination success was not influenced by any potential effects of resource limitation). However, for durian we examined the number of fruits set 4 wk after the tree finished flowering, because this species shows late-acting self-incompatibility (Bumrungsri *et al.* 2009, Honsho *et al.* 2007).

### Analysis of data

For each of the three crop species, the response variable (number of fruits set in each inflorescence) was examined using a generalized linear mixed model (GLMM), comprising a logit link function. Distance to forest, forest patch size, distance to nearest cave, proportion of forest surrounding study sites, visitor richness and visitor frequency were included as explanatory variables. Individual tree, study orchard and forest patch were treated as random factors. To find the best scale for forest proportion, we conducted a regression between the proportion of forest surrounding each study site at different radius scales (2, 4, 8 km) and the number of fruits set for the three crop species. The number of parameters minimized the goodness-of-fit given by the Akaike's information criterion (AIC, Burnham & Anderson 2004). To determine the best predictive model, the GLMM with the lowest AIC was selected.

For crops in which distance to forest was found to be a significant variable explaining fruit set, Generalized Linear Models (GLM) were conducted to examine the relationship between the stingless bee visitation frequency, number of visiting insect species and distance to forest. All statistical analyses were performed using R, version 2.13.0 (<http://www.R-project.org>).

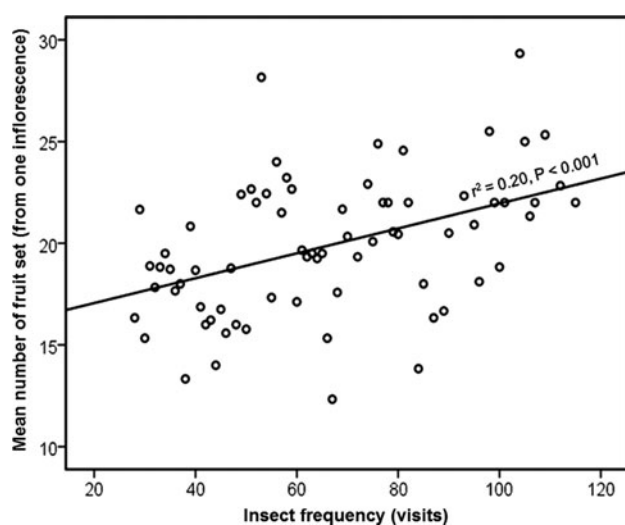
## RESULTS

### Rambutan

The number of fruits set per inflorescence in orchards near forest patches (mean ± SD: 22.5 ± 6.33) was significantly higher than in orchards far from forest patches (16.8 ± 4.72). There was also a positive linear relationship between insect visitation frequency and the number of

**Table 1.** Results of generalized linear mixed models for the number of fruit set for three different crops in southern Thailand. For rambutan, fixed effects are distance to the forest edge, insect richness and insect abundance. For durian, fixed effects include distance to the forest edge, distance to cave, bat visitation frequency, proportion of forest within a 20-km radius, and insect visitation frequency. For mango, fixed effects include distance to the forest edge, forest patch size, insect richness, and insect visitation frequency.

Plant species	Explanatory fixed variable	Estimate	SE	z-value	P value	
Rambutan (AIC = 946.5)	Intercept	2.815	0.020	142	<0.001	
	Distance to forest edge (Near)	0.268	0.024	11.3	<0.001	
	Insect richness	-0.003	0.023	-0.15	0.880	
	Insect visit frequency	0.049	0.023	2.18	0.030	
	Distance to forest edge × Insect richness	0.076	0.027	2.88	0.004	
	Distance to forest edge × Insect visit frequency	0.048	0.025	-1.89	0.059	
	Insect visit frequency × Insect richness	0.036	0.022	1.66	0.096	
	Distance to forest edge × Insect visit frequency × Insect richness	-0.035	0.025	-1.43	0.152	
	Durian (AIC = 627.5)	Intercept	1.919	0.082	23.3	<0.001
		Distance to forest edge (Near)	0.010	0.049	0.21	0.832
		Distance to cave	-0.119	0.053	-2.25	0.025
Proportion of forest area		-0.215	0.226	-0.95	0.342	
Insect visit frequency		-0.008	0.034	-0.25	0.805	
Bat visit frequency		0.199	0.042	4.66	<0.001	
Mango (AIC= 621.2)	Intercept	2.080	0.025	84.0	<0.001	
	Distance to forest edge (Near)	0.057	0.040	1.43	0.154	
	Forest patch size	0.033	0.047	0.70	0.482	
	Insect richness	-0.023	0.031	-0.75	0.454	
	Insect visit frequency	-0.020	0.046	-0.43	0.665	



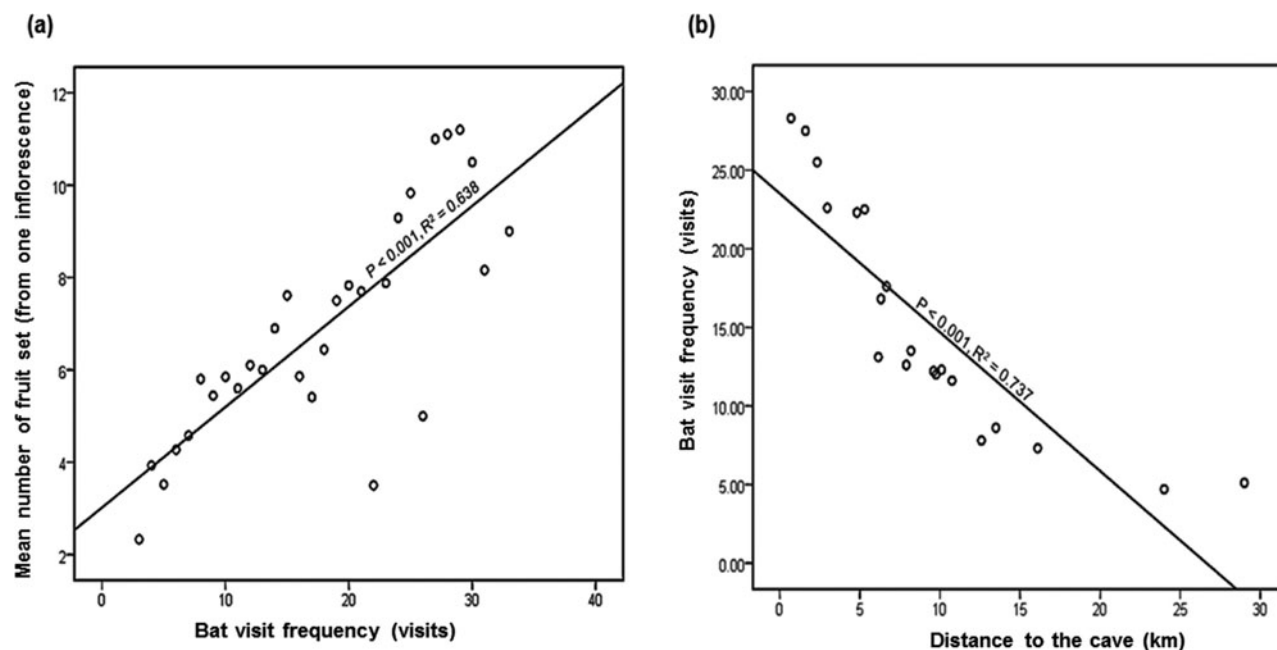
**Figure 2.** A linear regression plot for the number of rambutan fruits set and insect visitation frequency to rambutan flowers in mixed fruit orchard in southern Thailand. Each data point is based on the mean number of fruits set from one inflorescence.

fruits set (Figure 2, Table 1). However, forest patch size and insect richness had no effect on fruit set. There was a significant positive correlation between proximity to forest patch and insect richness (Table 1). The most

abundant flower visitors were stingless bees (70.9%) and honey bees (*Apis cerana*, 10.7%), followed by Diptera (9.34%) and other insects (9.11%) ( $n = 4756$ ). Stingless bees were significantly more frequent at rambutan flowers near forest patches ( $40.8 \pm 23.5$  visits per 15-min observation) than at flowers far from forest patches ( $25.4 \pm 17.4$  visits per 15-min observation;  $F_{1, 598} = 897$ ,  $P < 0.001$ ). We found that the proportion of forest within a 2-km radius around each orchard showed a significant positive effect on the number of fruits set in rambutan (GLM,  $F = 23.2$ ,  $df = 598$ ,  $P < 0.001$ ).

### Durian

The number of fruits set per inflorescence of durian was not significantly affected by distance to forest; however, there was a significant negative effect of distance to the nearest cave on the number of fruits set. Bat visitation frequency was significantly negatively correlated with distance to the nearest cave (Figure 3, Table 1). Nocturnal flower visitors included fruit bats (Pteropodidae) and giant honey bee (*Apis dorsata*), while diurnal visitors included stingless bees (Meliponini), giant honey bee (*Apis dorsata*) and honey bee (*Apis cerana*). Bat visitation frequency (as determined from camera traps) declined



**Figure 3.** A linear regression plot for the number of durian fruits set and bat visit frequency to durian flowers in mixed fruit orchard in southern Thailand (a). A linear regression plot for bat visitation frequency to durian flowers and distance to the nearest bat roosting cave. Each data point represents the number of fruits set from one inflorescence (b).

sharply with distance to caves (Figure 3). Camera-trap data revealed that the main bat species were *Eonycteris spelaea* (63.9%), *Cynopterus* spp. (19.6%), other species (16.5%) ( $n = 3039$  photos). We netted 271 individuals of six fruit bat species (94 *E. spelaea*, 52 *Macroglossus sobrinus*, 51 *Rousettus amplexicaudatus*, 30 *R. leschenaulti*, 20 *Cynopterus horsfieldi* and 25 *C. brachyotis*) across 480 h of mist-netting.

### Mango

When examining fruit set per inflorescence in mangos, we found no significant difference between sites near forest patches ( $8.37 \pm 2.98$ ) and far from forest patches ( $8.11 \pm 2.90$ ) or with forest patch size (Table 1). None of the visitor variables affected the number of fruits set per inflorescence (Table 1). The main flower visitors were flies (65.2%), stingless bees (9.45%), honey bees (12.2%), beetles (5.24%) and other insects (7.86%). The main fly visitors were from the families Muscidae (house fly), Calliphoridae (blow fly) and Syrphidae (hover fly). Fly visitation frequency alone also did not significantly affect the number of fruits set (GLM,  $F = 0.0003$ ,  $df = 598$ ,  $P = 0.986$ ).

### DISCUSSION

This study highlights the influence of distance to forest patches and caves on crop pollination. There are

two important results. First, proximity to forests and caves affects the number of fruits set in some crops. Second, proximity to forest patches and caves affects the species richness and abundance of flower visitors, leading to changes in crop reproductive success. We will discuss each of these aspects including implications for conservation.

### Proximity to forest on fruit set

Our results show that the effect of distance to forest on fruit set differed by plant species depending on the pollinating guild. Pollination success in rambutan was enhanced substantially by proximity to forest, while distance to forest was less influential for fruit set in durian and mango. This pattern was likely due to the different flower visitors, and the dependence of these visitors on forest habitat. Pollination success in rambutan was positively correlated with insect visitation frequency. Since stingless bees made up more than 50% of the visitors to rambutan, these results suggest that stingless bees are potentially the major pollinating insects for this species. A previous Neotropical study also found that rambutan is highly dependent on pollinators, as the fruit set of trees with pollinators was about 10 times greater than trees without pollinators (Rincón-Rabanales *et al.* 2015). For rambutan, we established for the first time that pollination success, represented by the number of fruits set per inflorescence, is dependent on insect

visitation frequency. Similar findings have been reported for other plant species such as coffee, in which fruit set was positively correlated with the richness of flower-visiting bee species (Klein *et al.* 2003a). Additionally, pollination success in both macadamia and longan were negatively correlated with the distance to tropical rainforest, and the major pollinating insects of longan are stingless bees (Blanche *et al.* 2006). Ricketts (2004) found that bee diversity, visitation rate, pollen deposition rate and fruit set were all affected by proximity to forest (Ricketts 2004). Such evidence implies that insects from the forest (e.g. stingless bees) mainly collect pollen and consistently contact stigmas during foraging, resulting in greater reproductive success; in contrast, non-forest insects (e.g. *Apis mellifera*, *A. cerana*) primarily collect nectar and contact stigmas less often. Moreover, we found a positive correlation between the proportion of forest within a 2-km radius around each orchard and the number of fruits set by rambutan plants, similar to studies by Kremen *et al.* (2004) and Winfree *et al.* (2007) which showed that the proportion of natural habitats strongly affected native bee communities. However, our GLMM analyses did not find that rambutan fruit set was significantly influenced by the proportion of forest around each orchard; this might be a consequence of autocorrelation between the proportion of forest around study sites and distance to forest.

The distance to forest patches did not affect fruit set quantity in durian, presumably because insects contribute little to the pollination success of this crop (Bumrungsri *et al.* 2009). Nectarivorous bats, especially *E. spelaea*, are the most important pollinators of durian (Bumrungsri *et al.* 2009), even though our results showed that the giant honey bee (*Apis dorsata*) was the most frequent nocturnal visitor to the flowers. Bumrungsri *et al.* (2009) found that insect-pollinated durian flowers set no fruit, compared with 10% fruit set in flowers that were exposed to bat visitors. Our results show a strong negative relationship between distance to cave and number of fruits set in durian. Results from a previous study support our finding that a cave-roosting nectarivorous bat, *E. spelaea*, was a more frequent pollinator than foliage-roosting bats (Stewart *et al.* 2014). There are only a few studies of bat pollinators in relation to forest fragmentation. Previous authors have found that pollination success of chiropterophilous plants was affected by forest fragmentation (Quesada *et al.* 2003, 2004; Stoner *et al.* 2002). This is the first study to document that bat visitation frequency decreases with distance from caves, and reduces pollination success of chiropterophilous species.

Distance to forest patches did not significantly influence fruit set of mango trees. Since flies were the most frequent visitors to mango flowers, it seems likely that their abundance is not sensitive to forest proximity, as has

previously been demonstrated in hover flies (Steffan-Dewenter & Tscharntke 1999). A study in Israel found that blow flies are as effective as honey bees in pollinating mango trees (Dag & Gazit 2000). However, the most abundant mango flower visitors in South Africa were ants and honey bees, and increasing distance from natural habitats led to strong declines in fruit production (Carvalho *et al.* 2010). Our results corroborate previous work indicating that dipterans are much less sensitive to forest proximity than hymenopterans (Steffan-Dewenter & Tscharntke 1999). In addition, apomixis also occurs in mango (Singh *et al.* 2011), presumably reducing the negative effects of pollen limitation on mango reproductive success.

### Proximity to forest patches and caves on species richness and abundance of flower visitors

The foraging distance of animal can strongly affect their population dynamic, life history, and community interaction including pollination (Holling 1994, Ritchie & Olf 1999) and foraging distance has been shown to increase with body size for various taxa (Greenleaf *et al.* 2007). The negative effects of isolation from forest may be even greater for small bee species (Araújo *et al.* 2004, Gathmann & Tscharntke 2002, Greenleaf *et al.* 2007, Steffan-Dewenter & Tscharntke 1999). Stingless bees were more frequent visitors to rambutan flowers in orchards near forest patches, suggesting that rainforests provide important habitats for these bees. Similarly, bee sampling in Indonesian agroforestry systems detected a decrease in both the richness and abundance of social bees (Meliponini stingless bees and Apini honey bees) with increasing distance from forest (Klein *et al.* 2003a). Since most stingless bees nest in tree cavities, they are sensitive to disturbance, especially deforestation (Brown & Albrecht 2001, Eltz *et al.* 2002). While visitor abundance decreased with distance from forest, we did not detect an effect of forest proximity on visitor species richness. This lack of correlation may be due to low taxonomic resolution, since we were not able to identify every insect to species level.

The higher visitation rate of bats to durian flowers near caves emphasizes the role of caves as sources of pollinators to surrounding durian trees. The cave nectar bat, *E. spelaea*, was the most abundant bat species (c. 60% of bats observed at flowers) and has previously been shown to be an important pollinator of durian (Bumrungsri *et al.* 2009). Furthermore, durian pollen was the most abundant species (42%) carried by *E. spelaea* in March and April (during durian's flowering season), showing that *E. spelaea* is a faithful visitor to durian flowers (Bumrungsri *et al.* 2013). In addition, our mist-net data showed that about 30% of captured bats were *Rousettus*, which is also

a cave-roosting bat. Based on these data, we suggest that this bat genus is probably also important for pollination of durian orchards near roosting caves (as corroborated by A. Stewart, pers. comm.), even though no individuals were observed at durian flowers with our camera traps.

### Implications for conservation

Forest fragmentation and deforestation can directly affect a complex set of plant and animal interactions (Fortuna & Bascompte 2006), promoting a higher rate of self-pollination and consequently reducing pollination success of animal-pollinated plant species (Lennartsson 2002). This can lead to changes in functional diversity in natural areas (Girão *et al.* 2007). Our results highlight the roles of different groups of pollinators visiting plant species with different pollination syndromes. Varying degrees of pollen limitation in these three native plant species indicate that the effect of pollinator abundance on plant reproductive success varies by plant taxa, and that the dispersal success of pollinators is related to isolation from source habitats. It is clear that rainforest patches can act as reservoirs for stingless bees, and probably other pollinator species as well. Preservation of forest, even forest patches, will ultimately protect the nesting and foraging habitat of many key pollinators, and thus maintain the richness and abundance of these vital pollinators (Ricketts 2004). However, most intensive agricultural farms do not incorporate nesting and foraging site options in their normal farming practice (Kremen *et al.* 2002, Tscharrntke *et al.* 2005). For bees, our most important pollinator, nest provisioning is an alternative way to maintain populations in areas far from forests. Over the last 10 y, stingless bee-keeping has grown rapidly in Australia, and 24% of bee keepers are using these bees for crop pollination such as macadamia, lychee, watermelon, avocado and mango (Halcroft *et al.* 2013, Heard & Dollin 2000). In eastern Thailand, stingless bee domestication has been applied in rambutan orchards, however, stingless bee-keeping in other regions of Thailand and tropical countries has not yet been widely applied to crop pollination. Thus, we recommend that fruit growers keep bee hives on their farms and preserve forest remnants. In addition, more environmentally friendly agricultural practices such as agroforestry should be implemented over larger scales to provide greater nesting options and floral resources for pollinators throughout the entire year.

In addition to forest and insect pollinators, caves and nectarivorous bat populations should also be protected. Due to durian's self-incompatibility and reliance on nectarivorous bats for pollination, the future survival of this crop is dependent on the survival of these bats.

Hunting of fruit bats such as *E. spelaea* has led to serious declines in bat populations throughout South-East Asia, including in Thailand (Mickleburgh *et al.* 1992, S. Bumrungsri, pers. obs.). As a consequence, the likelihood of pollination failure in durian may increase. *Eonycteris spelaea* (Bumrungsri 1997, Start 1974) is also known as the major pollinator of other economically and ecologically important plants including *Oroxylum indicum*, *Parkia speciosa*, *P. timoriana*, *Sonneratia* spp. and *Duabanga grandiflora* (Bumrungsri *et al.* 2008, 2009, 2013; Hopkins 1994, Start & Marshall 1974, Srithongchuay *et al.* 2008). Mixed planting of these species can promote the visitation of bat pollinators to fruit orchards year-round, particularly since a recent study found that *E. spelaea* exhibits strong fidelity to foraging areas (Acharya *et al.* 2015). Maintaining crop yields and ecological complexity requires a combination of conservation measures, including protecting both pollinators (e.g. insects and bats) and their habitats (e.g. forests and caves). Moreover, maintaining small forest patches and limestone karsts may provide stepping stones across fragmented landscapes, and attract greater numbers of pollinators to agricultural areas (Klein *et al.* 2014).

Our approach still has some key limitations that will need to be addressed in future studies. We estimated plant reproductive success by measuring fruit set 2 wk after flower opening and we studied the effect of natural habitats on three plant species. However, we still lack knowledge about how natural habitat proximity can affect ecological interaction networks (and plant-pollinator networks in particular) within the whole community. Thus, future studies should focus on how adjacency to natural habitat affects both structure and function in pollination networks.

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## LITERATURE CITED

- ACHARYA, P. R., RACEY, P. A., SOTTHIBANDHU, S. & BUMRUNGSRI, S. 2015. Feeding behaviour of the dawn bat (*Eonycteris spelaea*) promotes cross pollination of economically important plants in Southeast Asia. *Journal of Pollination Ecology* 15: 44–50.
- ARAÚJO, E. D., COSTA, M., CHAUD-NETTO, J. & FOWLER, H. G. 2004. Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. *Brazilian Journal of Biology* 64:563–568.
- BAWA, K. S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21:399–422.
- BLANCHE, K. R., LUDWIG, J. A. & CUNNINGHAM, S. A. 2006. Proximity to rainforest enhances pollination and fruit set in orchards. *Journal of Applied Ecology* 43:1182–1187.
- BLANCHE, R. & CUNNINGHAM, S. A. 2005. Rain forest provides pollinating beetles for Atemoya crops. *Journal of Economic Entomology* 98:1193–1201.
- BLÜTHGEN, N. & KLEIN, A.-M. 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology* 12:282–291.
- BONACCORSO, F. J., WINKELMANN, J. R., TODD, C. M. & MILES, A. C. 2014. Foraging movements of epauletted fruit bats (Pteropodidae) in relation to the distribution of sycamore figs (Moraceae) in Kruger National Park, South Africa. *Acta Chiropterologica* 16:41–52.
- BROWN, J. C. & ALBRECHT, C. 2001. The effect of tropical deforestation on stingless bees of the genus *Melipona* (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. *Journal of Biogeography* 28:623–634.
- BUMRUNGSRI, S. 1997. *Roost selection of cave dwelling bats in Songkla and Satun Provinces*. M.Sc. thesis, Kasetsart University, Bangkok, 79 pp. [In Thai with English abstract]
- BUMRUNGSRI, S., HARBIT, A., BENZIE, C., CARMOUCHE, K., SRIDITH, K. & RACEY, P. 2008. The pollination ecology of two species of *Parkia* (Mimosaceae) in Southern Thailand. *Journal of Tropical Ecology* 24:467–475.
- BUMRUNGSRI, S., SRIPAORAYA, E., CHONGSIRI, T., SRIDITH, K. & RACEY, P. A. 2009. The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in Southern Thailand. *Journal of Tropical Ecology* 25:85–92.
- BUMRUNGSRI, S., LANG, D., HARROWER, C., SRIPAORAYA, E., KITPIPIT, K. & RACEY, P. A. 2013. The dawn bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae) feeds mainly on pollen of economically important food plants in Thailand. *Acta Chiropterologica* 15:95–104.
- BURNHAM, K. P. & ANDERSON, D. R. 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304.
- CARVALHEIRO, L. G., SEYMOUR, C. L., VELDTMAN, R. & NICOLSON, S. W. 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology* 47:810–820.
- DAG, A. & GAZIT, S. 2000. Mango pollinators in Israel. *Journal of Applied Horticulture (Lucknow)* 2:39–43.
- ELTZ, T., BRÜHL, C. A., VANDER KAARS, S. & LINSENMAIR, K. E. 2002. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. *Oecologia* 131:27–34.
- FORTUNA, M. A. & BASCOMPTE, J. 2006. Habitat loss and the structure of plant–animal mutualistic networks. *Ecology Letters*, 9: 281–286.
- FRANCIS, C. M. & BARRETT, P. 2008. *A field guide to the mammals of Thailand and South-East Asia*. Asia Books, London. 393 pp.
- GATHMANN, A. & TSCHARNTKE, T. 2002. Foraging ranges of solitary bees. *Ecology* 71:757–764.
- GIRÃO, L. C., LOPES, A. V., TABARELLI, M. & BRUNA, E. M. 2007. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. *PLoS ONE* 2: e908.
- GREENLEAF, S. S. & KREMEN, C. 2006a. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences USA* 103:13890–13895.
- GREENLEAF, S. S. & KREMEN, C. 2006b. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133:81–87.
- GREENLEAF, S. S., WILLIAMS, N. M., WINFREE, R. & KREMEN, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- HALCROFT, M. T., SPOONER-HART, R., HAIGH, A. M., HEARD, T. A. & DOLLIN, A. 2013. The Australian stingless bee industry: a follow-up survey, one decade on. *Journal of Apicultural Research* 52:1–7.
- HEARD, T. A. 1994. Behaviour and pollinator efficiency of stingless bees and honey bees on macadamia flowers. *Journal of Apicultural Research* 33:191–198.
- HEARD, T. A. 1999. The role of stingless bees in crop pollination. *Annual Review of Entomology* 44:183–206.
- HEARD, T. A. & EXLEY, E. M. 1994. Diversity, abundance, and distribution of insect visitors to macadamia flowers. *Environmental Entomology* 23:91–100.
- HEARD, T. A. & DOLLIN, A. E. 2000. Stingless bee keeping in Australia: snapshot of an infant industry. *Bee World* 81:116–125.
- HOLLING, C. S. 1994. Cross-scale morphology, geometry, and dynamics of ecosystems. Pp. 351–423 in Samson, F. B. & Knopf, F. L. (eds). *Ecosystem management*. Springer, New York.
- HONSHO, C., SOMSRI, S., TETSUMURA, T., YAMASHITA, K. & YONEMORI, K. 2007. Effective pollination period in durian (*Durio zibethinus* Murr.) and the factors regulating it. *Scientia Horticulturae* 111:193–196.
- HOPKINS, H. C. F. 1994. The Indo-Pacific species of *Parkia* (Leguminosae: Mimosoideae). *Kew Bulletin* 1:181–234.
- JHA, S. & DICK, C. W. 2010. Native bees mediate long-distance pollen dispersal in a shade coffee landscape mosaic. *Proceedings of the National Academy of Sciences USA* 107:13760–13764.
- KLEIN, A.-M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 2003a. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology* 40: 837–845.
- KLEIN, A.-M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 2003b. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London B: Biological Sciences* 270:955–961.

- KLEIN, A. M., BOREUX, V., BAUHUS, J., CHAPPELL, M. J., FISCHER, J. & PHILPOTT, S. M. 2014. Forest islands in an agricultural sea. Pp. 79–95 in Kettle, C. J. & Koh, L. P. (eds). *Global forest fragmentation*. CPI, Croydon.
- KREMEN, C., WILLIAMS, N. M. & THORP, R. W. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences USA* 99:16812–16816.
- KREMEN, C., WILLIAMS, N. M., BUGG, R. L., FAY, J. P. & THORP, R. W. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters* 7:1109–1119.
- KUSUMANINGTYAS, R., KOBAYASHI, S. & TAKEDA, S. 2006. Mixed species gardens in Java and the transmigration areas of Sumatra, Indonesia: a comparison. *Journal of Tropical Agriculture* 44: 15–22.
- LENNARTSSON, T. 2002. Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. *Ecology* 83:3060–3072.
- LIM, A. L. 1984. The reproductive biology of rambutan, *Nephelium lappaceum* L. (Sapindaceae). *Gardens' Bulletin Singapore* 37: 181–192.
- MEMMOTT, J. & GODFRAY, H. C. J. 1993. Parasitoid webs. Pp. 217–234 in Lasalle, J. & Gauld, I. D. (eds). *Hymenoptera and biodiversity*. CAB, Wallingford.
- MICHON, G. & MARY, F. 1994. Conversion of traditional village gardens and new economic strategies of rural households in the area of Bogor, Indonesia. *Agroforestry Systems* 25:31–58.
- MICKLEBURGH, S. P., HUTSON, A. M. & RACEY, P. A. 1992. *Old World fruit bats. An action plan for their conservation*. IUCN, Gland. 252 pp.
- MOELLER, D. A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301.
- MORANDIN, L. A. & WINSTON, M. L. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agriculture, Ecosystems and Environment* 116:289–292.
- MORANDIN, L. A., WINSTON, M. L., ABBOTT, V. A. & FRANKLIN, M. T. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic and Applied Ecology* 8:117–124.
- NATHAN, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. *Diversity and Distributions* 11:125–130.
- OLLERTON, J., WINFREE, R. & TARRANT, S. 2010. How many flowering plants are pollinated by animals? *Oikos* 120: 321–326.
- QUESADA, M., STONER, K. E., ROSAS-GUERRERO, V., PALACIOS-GUEVARA, C. & LOBO, J. A. 2003. Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera: Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree *Ceiba grandiflora*. *Oecologia* 135: 400–406.
- QUESADA, M., STONER, K. E., LOBO, J. A., HERRERIAS-DIEGO, Y., PALACIOS-GUEVARA, C., MUNGUÍA-ROSAS, M. A., O.-SALAZAR, K. A. & ROSAS-GUERRERO, V. 2004. Effects of forest fragmentation on pollinator activity and consequences for plant reproductive success and mating patterns in bat-pollinated Bombacaceous trees. *Biotropica* 36:131–138.
- RITCHIE, M. E. & OLFF, H. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400:557–560.
- RICKETTS, T. H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology* 18: 1262–1271.
- 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. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11: 499–515.
- RINCÓN-RABANALES, M., ROUBIK, D. W., GUZMÁN, M. A., SALVADOR-FIGUEROA, M., ADRIANO-ANAYA, L. & OVANDO, I. 2015. High yields and bee pollination of hermaphroditic rambutan (*Nephelium lappaceum* L.) in Chiapas, Mexico. *Fruits* 70: 23–27.
- SHARMA, D. K. & SINGH, R. N. 1970. Self-incompatibility in mango (*Mangifera indica* L.). *Horticultural Research* 10: 108–118.
- SHIVARAMU, K., SAKTHIVEL, T. & REDDY, P. V. 2012. Diversity and foraging dynamics of insect pollinators on rambutan (*Nephelium lappaceum* L.). *Pest Management in Horticultural Ecosystems* 18:158–160.
- SINGH, S., DHYANI, D. & AHUJA, P. S. 2011. Apomixis in plants – embryology, genetics and molecular basis. *Journal of Cell and Plant Sciences* 2:24–31.
- SRITHONGCHUAY, T., BUMRUNGSRI, S. & SRIPAO-RAYA, E. 2008. The pollination ecology of the late-successional tree, *Oroxylum indicum* (Bignoniaceae) in Thailand. *Journal of Tropical Ecology* 24:477–484.
- START, A. N. 1974. *The feeding biology in relation to food sources of nectarivorous bats (Chiroptera: Macrogloninae) in Malaysia*. Unpublished PhD Thesis, University of Aberdeen. 247 pp.
- START, A. N. & MARSHALL, A. G. 1974. Nectarivorous bats as pollinators of trees in West Malaysia. Pp. 141–150 in Burley, J. & Styles, B. T. (eds). *Tropical trees: variation, breeding and conservation in tropical forest trees*. Academic Press, London.
- STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121:432–440.
- STEWART, A. B., MAKOWSKY, R. & DUDASH, M. R. 2014. Differences in foraging times between two feeding guilds within Old World fruit bats (Pteropodidae) in southern Thailand. *Journal of Tropical Ecology* 30:249–257.
- STONER, K. E., QUESADA, M., ROSAS-GUERRERO, V. & LOBO, J. A. 2002. Effects of forest fragmentation on the colima long-nosed bat (*Musonycteris harrisoni*) foraging in tropical dry forest of Jalisco, Mexico. *Biotropica* 34:462–467.
- TSCHARNTKE, T., KLEIN, A. M., KRUESS, A., STEFFAN-DEWENTER, I. & THIES, C. 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters* 8:857–874.
- VAN WELZEN, P. C., LAMB, A. & WONG, W. W. W. 1988. Edible Sapindaceae in Sabah. *Nature Malaysiana* 13:10–25.

- WAHALA, S. & HUANG, P. 2005. Foraging distance in the stingless bee *Trigona thoracica*. Pp. 71–74 in Harrison, R. D. (eds). *Proceedings of the CTFS-AA International Field Biology Course 2005*. Center for Tropical Forest Science–Arnold Arboretum Asia Program, National Parks, Wildlife and Plant Conservation Department, Khao Chong, Thailand.
- WHITEHEAD, C. 1959. The rambutan, a description of the characteristics and potential of the more important varieties. *Malayan Agricultural Journal* 42:53–75.
- WINFREE, R., WILLIAMS, N. M., DUSHOFF, J. & KREMEN, C. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters* 10:1105–1113.