



Original Research Article

The role of bats in pollination networks is influenced by landscape structure

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ABSTRACT

Nectarivorous bats are essential to the functioning to both agricultural and natural ecosystems in the tropics, yet these pollinator communities are declining as a result of habitat loss and hunting. Temporal variation and habitat changes lead to both roost and floral resource loss, which is the major driver of bat pollination decline. This study aims to determine how the bat pollination networks in mixed-fruit orchards are affected by flowering seasons and different land-use types. We estimated the abundance of nectarivorous and frugivorous bats using video observations to determine floral visitation rates from 18 mixed-fruit orchards in Southern Thailand. Pollination networks were then created based on network level indices (number of interactions and specialisation) and species level indices (strength–dependence of plant on each bat, and generalised degree—the number of interactions per species divided by the number of possible interacting partners) for each bat group at each orchard. We found that specialisation in low season networks was higher than those from peak season. Nectarivorous bats showed higher levels of normalised degree, and strength than frugivorous bats. The normalised degree of frugivorous bats, but not nectarivorous bats increased with the proportion of urban area within 30 km radius. The strength of bats was positively correlated with the proportion of plantations within a 2 km radius. Our results show that both bat guilds are strongly integrated into pollination networks where they occur and provide evidence that increasing the area of plantation and urban alters the degree of generalization of pollinators which can significantly impact pollination success of plants.

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1. Introduction

Pollinators provide a wide range of benefits to society in terms of contributions to food security, farmer livelihoods, social and cultural values, as well as the maintenance of wider biodiversity and ecosystems (Potts et al., 2016). In the tropics, plant-animal mutualisms are vital for ecosystem function (Wright, 2002). In addition to insects, some bat and bird species also play

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important roles as pollinators in tropical habitats. Bat pollination occurs in over 528 species in 67 families and 28 orders of angiosperms worldwide (Kunz et al., 2011). In the Old World tropics, several studies have examined the pollination effectiveness of bat pollinators (Bumrungsri et al., 2008, 2009; Acharya et al., 2015; Nor Zalipah et al., 2016; Aziz et al., 2017; Stewart and Dudash, 2017); pteropodid bats, for instance, are known to pollinate flowers of about 168 species in 100 genera and 41 families (Kunz et al., 2011). Bats within the family Pteropodidae are classified into two feeding guilds: obligate nectarivores (nectarivorous) and frugi-nectarivores (frugivorous). These two bat guilds have been demonstrated to have different foraging times (Stewart et al., 2014), and nectarivorous bats show higher effectiveness as pollinators (Stewart and Dudash, 2017). Most studies on bat pollination interactions have been limited to a single species in a single site, i.e. local interactions of single bats species with local fruits, mostly including data from only one site (Bumrungsri et al., 2008; Nor Zalipah et al., 2016; Sritongchuay et al., 2008; Wayo et al., 2018). Consequently, little is known about the community structure of bat pollination interactions, with very few exceptions (Sritongchuay and Bumrungsri, 2016; Stewart and Dudash, 2017).

Many bats face several threats in concert (e.g., habitat loss, bushmeat hunting, and climate change) (Frick et al., 2019; Tanalgo et al., 2018). Changes in land-use results in species extinctions (Wilson et al., 2016). Moreover, landscape fragmentation, habitat loss and degradation often disrupt mutualistic or other species interactions (Ashworth et al., 2004; Pimm and Raven, 2000). Many studies have focused on the effects of anthropogenic habitat modification on the diversity of pollinators and their host plants as well as plant–pollinator community composition (e.g. Angold et al., 2006; McKinney, 2008; Winfree et al., 2011). Recent advances in the study of pollination networks have improved our ability to describe plant–pollinator interactions and the underlying structure (Vizentin-Bugoni et al., 2018). Network analysis provides a useful framework for predicting vulnerability of resource relationships or mutualisms to species loss (Montoya et al., 2006). The structure and complexity (e.g. linkage density) of these mutualistic networks may be important in promoting community stability and functioning (Bastolla et al., 2009; Tylianakis et al., 2010; Kaiser-Bunbury and Blüthgen, 2015). Species activities due to variations in the environment, related to resource limitation and changes in species interaction (Wright, 2002). The effects of land-use change and local habitat on plants and pollinators are also likely to influence their mutualistic interactions, thereby impacting the architecture of their networks (Fortuna and Bascompte, 2006; Ferreira et al., 2013; Weiner et al., 2014). The degree of generalization of pollinator species is also likely to vary in response to perturbations. Furthermore, variation in diet breadth has been shown to impact the stability and functioning of food webs (Kondoh, 2003). For instance, urban flower visitors were found to be more generalistic in their diet. Baldock et al. (2015) suggesting that in urban areas, the same pollinators may become less effective due to augmented transfer of heterospecific pollen (Kremen et al., 2007; Leong et al., 2014). Moreover, such climatic seasonality affect plant phenology even in the tropics (Morellato et al., 2016). Not all bat floral resources are available year round. Previous studies revealed that higher availability of floral resources is associated with a higher diversity of pollinators, leading them to specialize on specific flower species so that specialization in high flowering season tend to be higher than low flowering season (Bender et al., 2017; Fontaine et al., 2006; Ghazoul, 2006; Magrath et al., 2017).

Understanding the degree of variation in the generalization of entire community and pollinator groups may thus provide important new insights into plant–pollinator communities. However, despite the growing number of studies of impact of landscape changes on visitation networks providing information about resource use by flying insects, little is known to date about how landscape context influences bat pollination network structure (Sritongchuay and Bumrungsri, 2016). In this study, we investigated changes in plant–bat pollinator interactions in mixed-fruit orchards between flowering seasons and along the gradient of increasing land-use intensity by specifically determining whether: 1) flowering seasons influence pollination network structure, especially specialization; 2) landscape contexts affect bat pollination networks in mixed-fruit orchards; and 3) surrounding land-use types affects bat pollination networks at the species level. We predicted that higher floral resource availability in the high flowering season would lead to greater partitioning of a floral niche by pollinators, i.e. higher specialization. Moreover, the number of interactions in orchards surrounded by more complex landscapes with high resource abundance (i.e. lowland mosaic, montane mosaic) is higher than in simple structure landscapes with low resource abundance (i.e. urban). Additionally, when resources are rare, the diet breadth of pollinators tends to increase (MacArthur and Pianka, 1966; Fontaine et al., 2008). Since frugivorous bats (generalists) are capable of exploiting a wider range of resources, including fruits and flowers, they are likely to be less sensitive to landscape changes (Hadley and Betts, 2012). Therefore, we predicted that shifting towards higher generalism in nectarivorous bats is affected by landscape changes in smaller scales whereas the shifting of generalism degree in frugivorous bats is influenced by broader scales.

2. Materials and methods

2.1. Site selections

This study was conducted in 18 mixed-fruit orchards at various sites in Southern Thailand (Songkhla, Phattalung, Satun, and Nakhon Si Thammarat provinces, 6°20' to 8°20' S and 99°40' to 110°00' E) between September 2012 to June 2013. The elevation ranged from 167 to 276 m above sea level. The main landscape types in this region are tropical rainforests, rubber plantations, oil-palm plantations, mixed-fruit orchards, and urban areas. Mixed-fruit orchards consist of planted fruit crops and native tree species, as well as, herb and shrub species. The main fruit trees include durian (*Durio zibethinus* L.), bitter bean (*Parkia speciosa* Hassk.), mangosteen (*Garcinia mangostana* L.), domestic jackfruit (*Artocarpus integer* (Thunb.) Merr.),

rambutan (*Nephelium lappaceum* L.) and mango (*Mangifera indica* L.). We selected the orchards that were managed without pesticide use and all orchards were at least 10 km apart (Fig. 1).

We used 1:133,400 scale photographic imagery from Landsat Thematic Mapper data in Arcmap 10.2 to create a map of landcover. Eight landcover classes were used, including water, mangrove, lowland evergreen forest (forest at elevation up to 750 m above sea level), lower montane evergreen forest (forest in elevation above 750 m, up to 1500 m asl), upper montane evergreen forest (forest at elevation above 1500 m asl), lowland mosaic (vegetated areas in elevation up to 750 m asl, typically consists of tree gardens, agricultural fields, forest, regrowth or plantations), montane mosaic (same as lowland mosaic, but occurring in elevation above 750 m asl), montane open (Clearings and other open areas in elevation above 750 m asl), urban, and plantation (closed canopy oil-palm and rubber plantations larger than 1 km²). The landcover classes were established

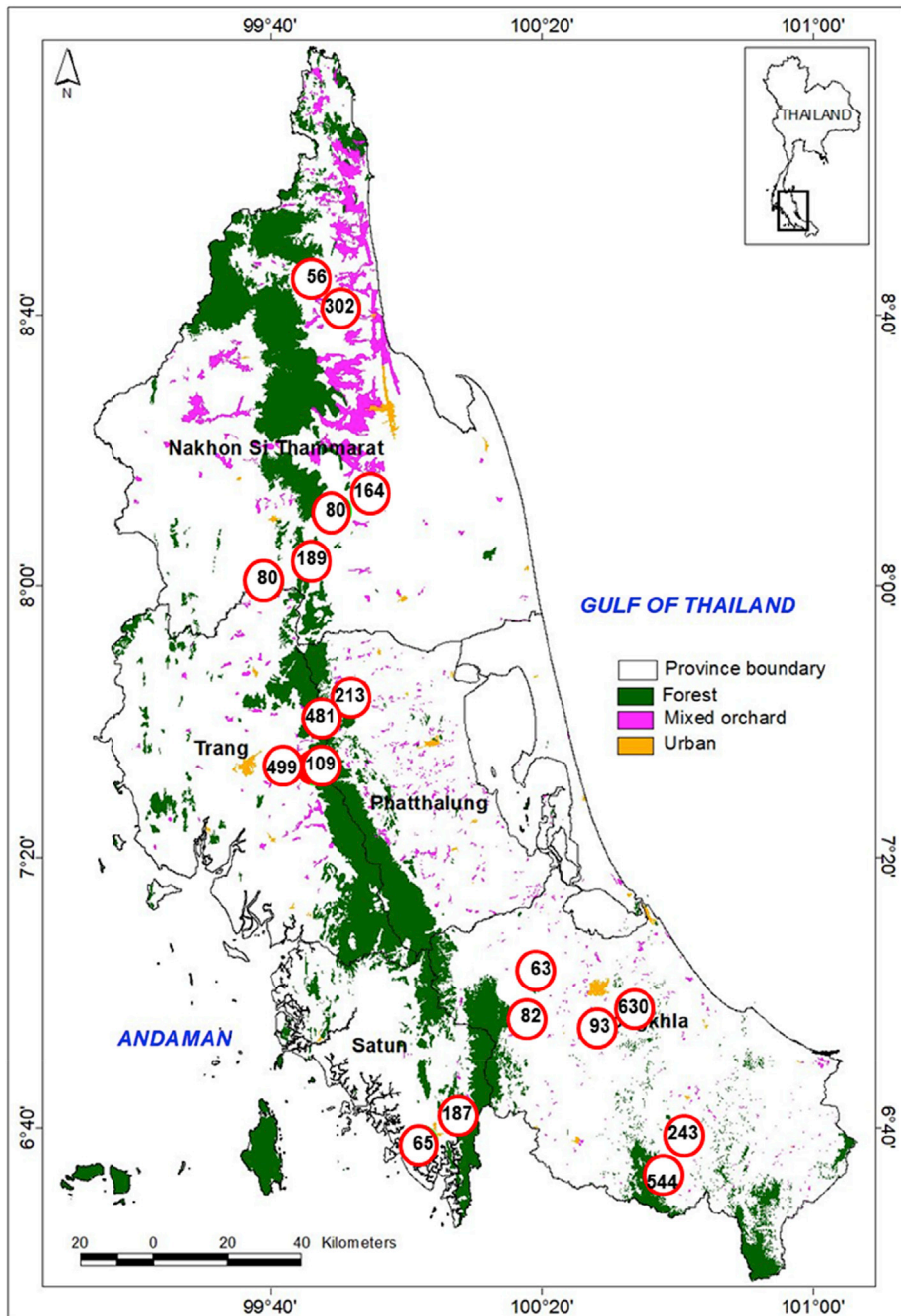


Fig. 1. Map of study area. Visitors were observed from 18 orchards at varying distances from 10 forest patches and surrounded by different land-use types in southern Thailand. Number in the circle represents total of bat visitation frequencies in each study-site.

following (Miettinen et al., 2016) and we calculated the proportion of each landscape class fraction within 50 m, 500 m, 1 km, 2 km, 10 km, 20 km, and 30 km radius at each site. The organisms' perception of their environment can vary among species, therefore to study the effect of landscape on biological communities, a multi-level scale is necessary (Moreira et al., 2015). The landscape structure may affect foraging behaviour and the number of pollinators at the proximal level and the population's dynamics at a broader landscape level. It is also necessary to select the best scale of estimation for each level. For example, given that nectarivorous *Rousettus* bats can forage a mean distance of 1.7–6.9 km for (Bonaccorso et al., 2014), and the mean foraging range is 6 km for the Cave nectar bat, *Eonycteris spelaea* (Acharya et al., 2015), the appropriate scale for estimating the proximal level was between 50 m and 10 km. The landscape at the broad level (from 20 km to 30 km) comprise areas large enough to hold a sufficient number of individuals to influence their population dynamics and distribution (Fahrig, 2013). At this level, the landscape could promote concentration or dispersal of populations, as well as relatively high beta diversity, which can reduce the effect of local factors on the structure of communities. We also collect data on the number of bat-pollinated plant species trees at a scale of 150 m radius at each site.

2.2. Flowering phenology

In each studied orchard, we marked a 100 × 100 m plot and monitored the flowering phenology of every individual tree of chiropterophilous plant species every month from January 2012 to June 2013. We chose night-blooming plant taxa reported to be bats pollinated species: *Ceiba pentandra* (L.) Gaertn., *Durio zibethinus* L., *Musa acuminata* Colla, *Oroxylum indicum* (L.) Kurz, *Parkia speciosa* Hassk., *Parkia timoriana* (DC.) Merr. (Sritongchuay et al., 2016; Stewart and Dudash, 2017). Mass (Peak) flowering season of bat-pollinated plant species is between November and April whereas low flowering season is between May and October (Stewart and Dudash, 2017). We counted the number of floral units (either individual flowers or capitula) for each bat-pollinated plant species. We determined the mean number of flowers in a capitulum from 20 capitula. We estimated the number of individuals of each plant species in each orchard by multiplying plant density (determined from the marked plot) by the total area of the orchard. Additionally, we calculated the total number of flowers by multiplying the number of individual plants by the mean number of open flowers for each plant.

2.3. Data collection

At each 100 × 100 m plot, we observed nightly visitation rates by placing camera traps (Moultrie game spy d55-IRXT infrared flash camera) c. 5–10 m from the inflorescence of every flowering trees. Camera traps were set for motion detector mode to record 15 s video and still pictures for 15 min every hour from 1900 h to 0500 h in all twenty plots. In each flowering tree of *Ceiba pentandra* (L.) Gaertn., *Durio zibethinus* L., *Parkia speciosa* Hassk., *Parkia timoriana* (DC.) Merr., three camera traps were placed at the top, middle, and bottom of canopy, and aimed to three inflorescences whereas in *Musa acuminata* Colla, and *Oroxylum indicum* (L.) Kurz, one camera trap was aimed to inflorescence per tree. The number of camera traps set at each study site was presented in Table S3. Since it is difficult to identify bats to species from camera traps, we also mist-netted at each site to identify the local species, allowing us to confirm our video identification. The mist nets were placed close to the flowering trees to avoid capturing the bats that visited other fruit trees in the same orchard. Bats were identified to species following Francis (2008), mainly from external morphology and size. We categorized fruit bats into two groups, nectarivorous (*Eonycteris spelaea* (Dobson), *Macroglossus minimus* (Geoffroy), *M. sobrinus* (Andersen)) and frugivorous (*Cynopterus brachyotis* (Muller), *C. horsfieldi* (Gray), *C. sphinx* (Vahl) and *Rousettus leschenaultii* (Desmarest)), following criteria in Stewart et al. (2014).

2.4. Constructing flower-visitation networks

For community levels, we calculated a number of interactions as well as network specialisation (H_2' index). H_2' index shows the degree of specialisation in the entire network whether species restrict their interactions from those randomly expected based on a partner's availability (Blüthgen et al., 2006). H_2' ranges between 0 (no specialisation) and 1 (complete specialisation). At the species level, to investigate the visitation frequency of each bat guild (nectarivorous vs frugivorous), we summed all bats captured by camera traps at each plant species. We calculated the normalised degree, and network strength. Normalised degree is the number of interactions per bat guild divided by the number of possible interacting plant species, which controls for differences in network size. Normalised degree estimates how generalist/specialist a species is relative to other species in the same trophic level of the community in which it occurs. For network strength, the index aims at quantifying the dependence of the plant community on a given pollinator (Jordano, 1987). The strength values represent the dependence of each plant on each bat guild as the proportion of visits the plant receives from each bat guild. High strength indicates a high relevance of bat guild for the plants in the system. Formally, if a_{ij} is the number of visit pollinator j pays to plant i , then the dependence for this combination is given by $p_{ij} = a_{ij} / \sum a_{ij}$. The strength of species j is then: $s_j = \sum p_{ij}$ (Bascompte et al., 2006).

2.5. Statistical analyses

Firstly, a probability distribution that best fits the response variables were identified. We verified that assumptions of normality and heteroscedasticity were met, and that Poisson models were not overdispersed. To determine the effect of flowering season and land-use classes on specialization (H_2'), we used generalized linear mixed modeling (GLMM) with a normal distribution and a log link function. Flowering seasons, flower abundance, number of flower species and proportion of each land-use class surrounding each study sites at 7 different scales (50 m, 500 m, 1 km, 2 km, 10 km, 20 km, and 30 km) were included as explanatory variables. Study site was included as a random effect as every study site does not show significant spatial autocorrelation and effect on average of response variables. We used generalized linear mixed models (GLMM) to investigate the effect of density of bat-pollinated-plant trees in 150 m radius and proportion of each land-use class surrounding each study sites on the number of interactions with a Poisson distribution and a log link function. We also used generalized linear mixed models (GLMM) to investigate the effect bat guilds and land-use classes on pollination network structure in species level (normalised degree and network strength) with a gamma error distribution and a log link function. Bat guilds and proportion of each land-use class surrounding each study sites at 7 different scales were included as explanatory variables. Study site was included as a random effect. We used sample size corrected Akaike Information Criterion (AICc) to determine the best candidate model and Akaike weights (wAICc) to quantify the probability by which a given model is the best within the candidate models set (Table S2). GLMMs were analysed using the package lme4. For visitation frequency and number of plant species visited by each bat species, we compared differences among all of the bat species and flowering seasons by estimating bootstrapped 95% confidence intervals (95% CIs). No significant spatial autocorrelation was found using Moran's I ($P > 0.005$ in all models). Spatial autocorrelation was checked by using Moran's I (Gittleman and Kot, 1990) with the "ape" package (Paradis et al., 2004). The overall pollination networks were visualized using the *bipartite* package. All analyses were conducted in R 3.4.4 (R Core Team, 2018).

3. Results

3.1. Overall characteristics of networks

We observed 4311 interactions between the seven species of flower-visiting bats and the six species plant in all 18 mixed-fruit orchard sites. The number of interactions was quantified in all networks as visitation rate, ranging from 56 to 630 interactions. Cumulative networks of these interactions are presented in S1. *E. spelaea* were involved in 71.81% of interactions (3096 interactions, Mean \pm SD = 155 \pm 136); *C. sphinx* in 12.36% (533 interactions, 28.1 \pm 37.0); *M. sobrinus* in 8.6% (371 interactions, 40.7 \pm 48.9); *C. brachyotis* in 3.55% (153 interactions, 9.56 \pm 11.2); *C. horsfieldii* in 1.74% (75 interactions, 8.33 \pm 10.5); *R. leschenaulti* in 1.06% (46 interactions, 5.75 \pm 5.18); *M. minimus* in 0.85% (37 interactions, 6.17 \pm 9.33) (Fig. 2). *Eonycteris spelaea* and *Macroglossus sobrinus* had the broadest floral host breadth. The most visited plants were *Musa* spp. (Musaceae), with 1344 visits (31.18%); *Parkia speciosa* (Fabaceae), with 930 visits (21.58%) and *Durio zibethinus* (Bombaceae), with 767 visits (17.80%). The studied orchards contained 6 plant species visited by nectar-feeding bats.

3.2. Network structure and resource availability across seasons

Specialisation (H_2') varied across seasons (GLMM; $F_{1, 118} = 39.552$, $P < 0.001$). Specialisation in low season networks (mean \pm SD = 0.550 \pm 0.205) was higher than those from peak season (0.441 \pm 0.201) across all communities (Fig. 3 A). *Eonycteris spelaea* visited to significantly higher number of plant species in high season than low season (Fig. 3 B). In contrast to specialization, greater floral resource availability was higher in peak flowering season compared to low flowering season (flowering plant species richness: low season = 3.047 \pm 0.2133 and peak season = 4.634 \pm 0.540; $t = -25.022$, $P < 0.001$; abundance of flowers: low season = 249.281 \pm 77.793 and peak season = 712.747 \pm 347.969; $t = -16.674$, $P < 0.001$). Specialization was strongly negatively influenced by flower abundance (GLMM; $F_{1, 117} = 36.74148$, $P < 0.001$) but was not affected by number of flower species in the network (GLMM; $F_{1, 117} = 3.53067$, $P = 0.063$).

3.3. Response of pollination networks to environmental effects at multiple levels

At the network level, the number of interactions was not affected by density of bat pollinate-plant species within 150 m radius (GLMM: $Z = 0.379$, $P = 0.705$), proportion of low mosaic (GLMM: $Z = 1.535$, $P = 0.874$) and proportion of plantation ($Z = 0.651$, $P = 0.515$) in proximal scale (within 2 km radius) and urban area ($Z = 0.334$, $P = 0.738$) in broader scale (within 30 km radius). However, for specialization, there was significant interaction between seasons and proportion of urban area (GLMM; $t = -3.141$, $P = 0.002$). The specialization from low season networks was significantly affected by proportion of urban area within 30 km radius whereas the proportion of urban areas surrounding orchards did not have effect on specialization of networks from peak season (Fig. 4, Table 2). The bipartite pollination network from orchard surrounded by less than 25%, 25% - 50%, and more than 50% of urban areas were presented in Fig. S1. In contrast, at the bat guild level, the normalised degree of nectarivorous bats (0.874 \pm 0.11) was significantly greater higher than frugivorous bats (0.45 \pm 0.19) (GLMM, $t = -9.678$, $P < 0.001$, Table 3, Fig. 5). The normalised degree of both bat guilds was not affected by landscape area within a proximal scale. However, at a broader scale, there was significant interaction between bat guilds and proportion of urban area (GLMM;

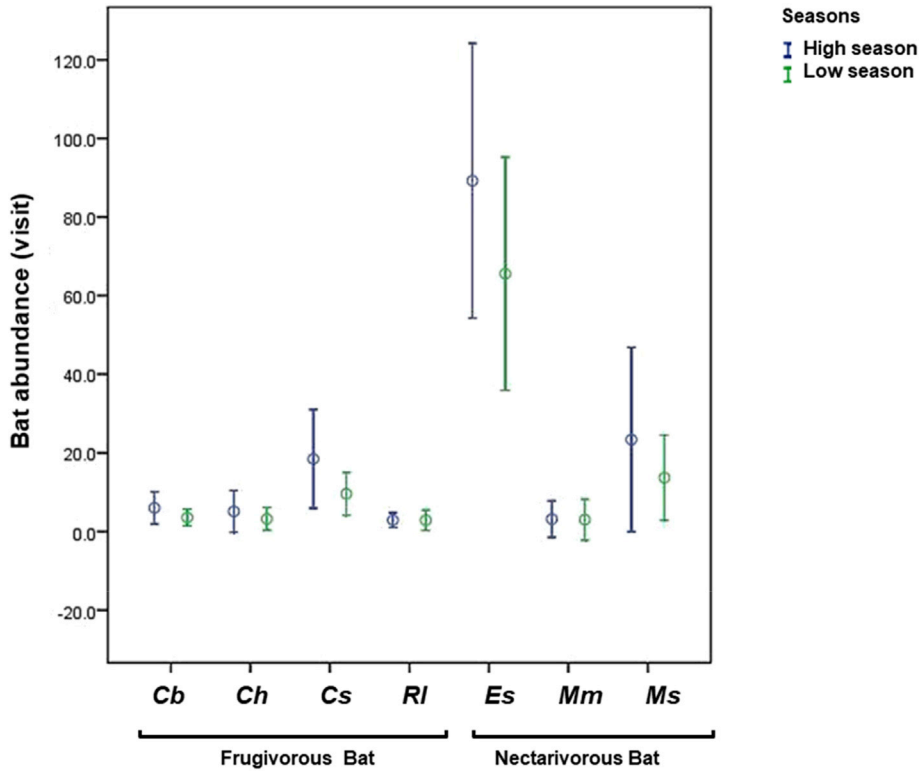


Fig. 2. The frequency of each bat species in different flowering seasons. Bootstrapped means and 95% confidence intervals were generated for number of frequency of each bat species. Non-overlapping 95% confidence intervals indicate significantly different bat species along x-axes (left to right): frugivorous bat, *Cynopterus brachyotis*, *Cynopterus horsfieldii*, *Cynopterus sphinx*, *Rousettus leschenaultii*; nectarivorous bat, *Eonycteris spelaea*, *Macroglossus minimus*, *Macroglossus sobrinus*.

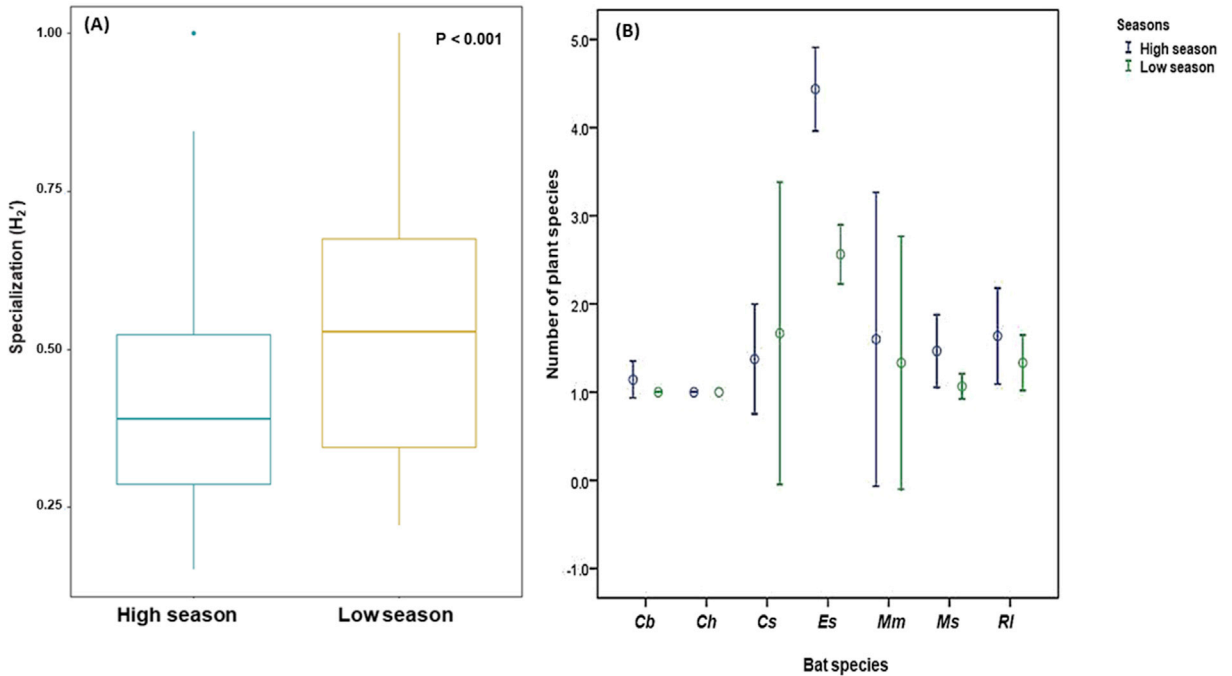


Fig. 3. A) The specialization between peak flowering season and steady flowering season. B) Number of plant species visited by each bat species in different flowering seasons. Bootstrapped means and 95% confidence intervals were generated for number of plant species. Non-overlapping 95% confidence intervals indicate significantly different of number of plant species between high and low flowering seasons.

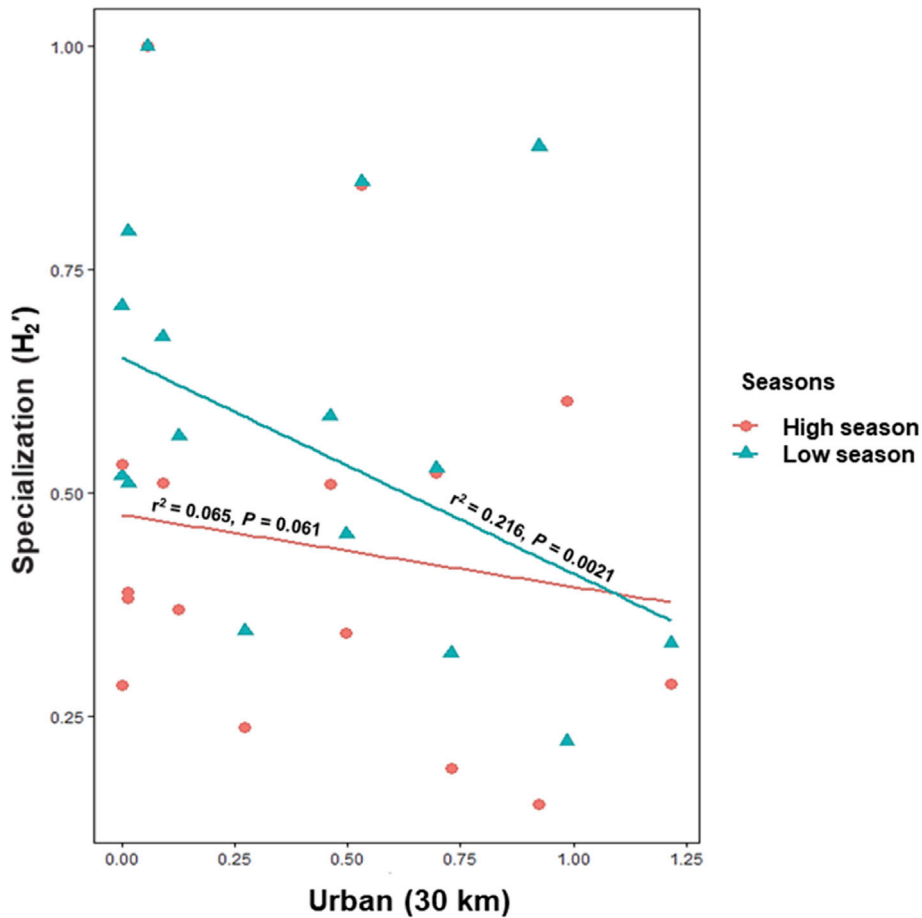


Fig. 4. The specialization (H_2') from steady season network (green triangles) was significantly affected by proportion of urban area within 30 km radius whereas the proportion of urban areas surrounding orchards did not have effect on specialization of networks from peak season (red circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Species level pollination network parameters for each bat species of nectarivorous bats^(a) and frugivorous bats^(b).

Bat species	# Interactions	Degree	Normalised degree	Strength
<i>Eonycteris spelaea</i> ^a	154.80 ± 32.40	4.8 ± 1.17	0.86 ± 0.15	4.07 ± 1.24
<i>Macroglossus sobrinus</i> ^a	40.67 ± 46.11	2.11 ± 1.20	0.37 ± 0.22	0.56 ± 0.31
<i>Macroglossus minimus</i> ^a	6.17 ± 8.51	1	0.17 ± 0.02	0.25 ± 0.35
<i>Cynopterus brachyotis</i> ^b	9.56 ± 10.85	1.25 ± .56	0.24 ± 0.13	0.48 ± 0.50
<i>Cynopterus horsfieldii</i> ^b	8.33 ± 9.93	1.22 ± 0.42	0.21 ± 0.12	0.30 ± 0.37
<i>Cynopterus sphinx</i> ^b	28.05 ± 36.06	1.47 ± 0.75	0.27 ± 0.12	0.60 ± 0.60
<i>Rousettus leschenaultii</i> ^b	5.75 ± 4.84	1.25 ± 0.43	0.20 ± 0.07	0.38 ± 0.56

Table 2

Results of generalized linear mixed models for specialization of bat pollination network structure in mixed fruit orchards in southern Thailand. The explanatory variables are seasons (steady and peak flowering seasons), proportion of urban area within 30 km radius.

	Explanatory fixed variable	Estimate	SE	DF	t-value	P-value
Specialization (AIC = -146.834)	Intercept	0.497	0.070	117	7.057	<0.001***
	Season (high)	0.181	0.027	117	6.732	<0.001***
	Urban (30 km)	-0.096	0.124	14	-0.777	0.450
	Season (high) *	-0.146	0.046	117	-3.141	0.0021**
	Urban (30 km)					

Table 3

Results of generalized linear mixed models for degree, normalised degree, and interaction strength of bat pollination network structure in mixed fruit orchards in southern Thailand. The explanatory variables are bat guilds, proportion of plantation, and proportion of lowland mosaic within a 2 km radius and proportion of urban area within 30 km radius.

Indice	Explanatory fixed variable	Estimate	SE	t-value	P-value
Normalised degree (AIC = -43.106)	Intercept	0.129	0.089	1.442	0.015
	Bat group (frugivorous)	-1.139	0.117	-9.678	<0.001***
	Urban (30 km)	-0.001	0.002	-0.072	0.942
	Bat group * Urban (30 km)	0.011	0.002	4.877	<0.001***
Strength (AIC = 104.99)	Intercept	1.307	0.221	5.904	<0.001***
	Bat group (frugivorous)	-1.532	0.200	-7.664	0.001***
	Plantation (2 km)	0.038	0.008	3.912	<0.001***
	Urban (30 km)	0.001	0.003	0.232	0.817
	Bat group * Urban (30 km)	0.010	0.004	2.397	0.0165 *

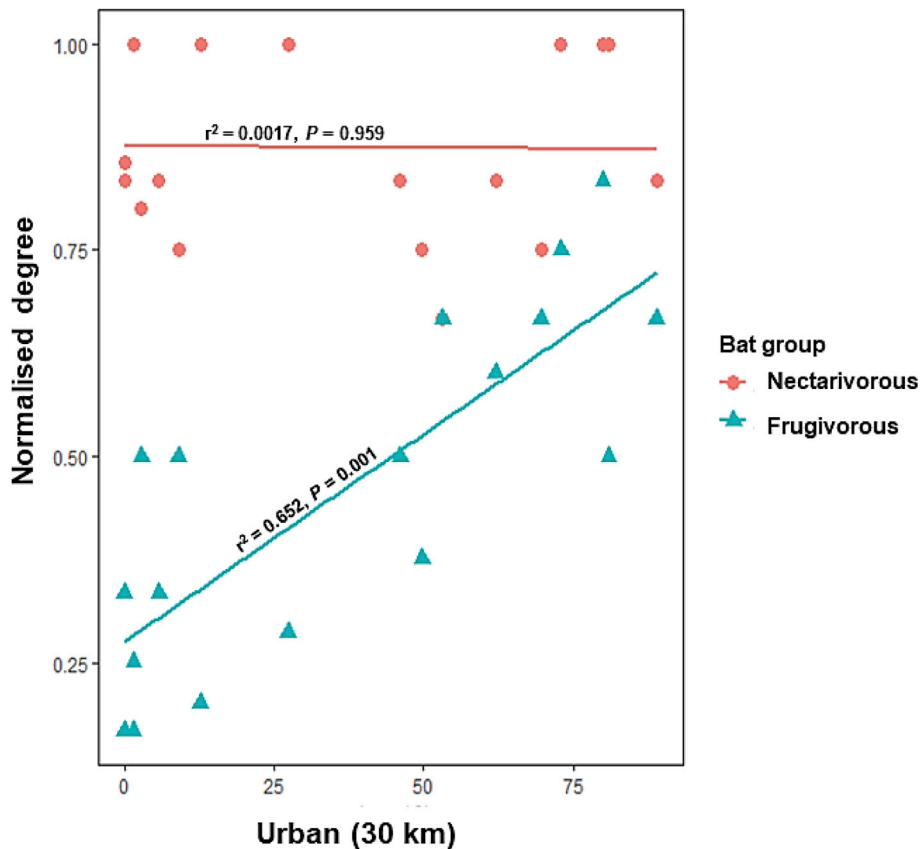


Fig. 5. The normalised degree of nectarivorous bats (red circles) and frugivorous bats (green triangles) plotted against the proportion of urban area within 30 km radius around each site. Each point represents a single fruit orchard in southern Thailand. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

$t = 4.877, P < 0.001$, Table 3). The normalised degree of frugivorous bat, but not nectarivorous bats increased with the proportion of urban area within 30 km radius ($P = 0.0003$, Fig. 5).

The network strength was strongly influenced by bat guilds (nectarivorous bat: 4.36 ± 1.30 ; frugivorous bats: 1.30 ± 0.80 , GLMM, $t = -7.664, P < 0.001$, Table 3) and proportion of plantation in proximal landscape scale (GLMM, $t = 3.912, P < 0.001$, Table 3). Since there is no significant effect of bat guilds and proportion of plantation interaction, we analysed all bats together. The network strength of bats was positively correlated with proportion of plantation within a 2 km radius (Fig. 6A). The network strength was also affected by the interaction of bat guild and the proportion of urban area within 30 km (GLMM, $t = 0.010, P = 0.016$, Table 3). The network strength of frugivorous bats was positively impacted by the proportion of urban ($P = 0.25$, Fig. 6B) but the network strength of nectarivorous bats was not significantly affected by proportion of urban area ($P = 0.844$, Fig. 6B).

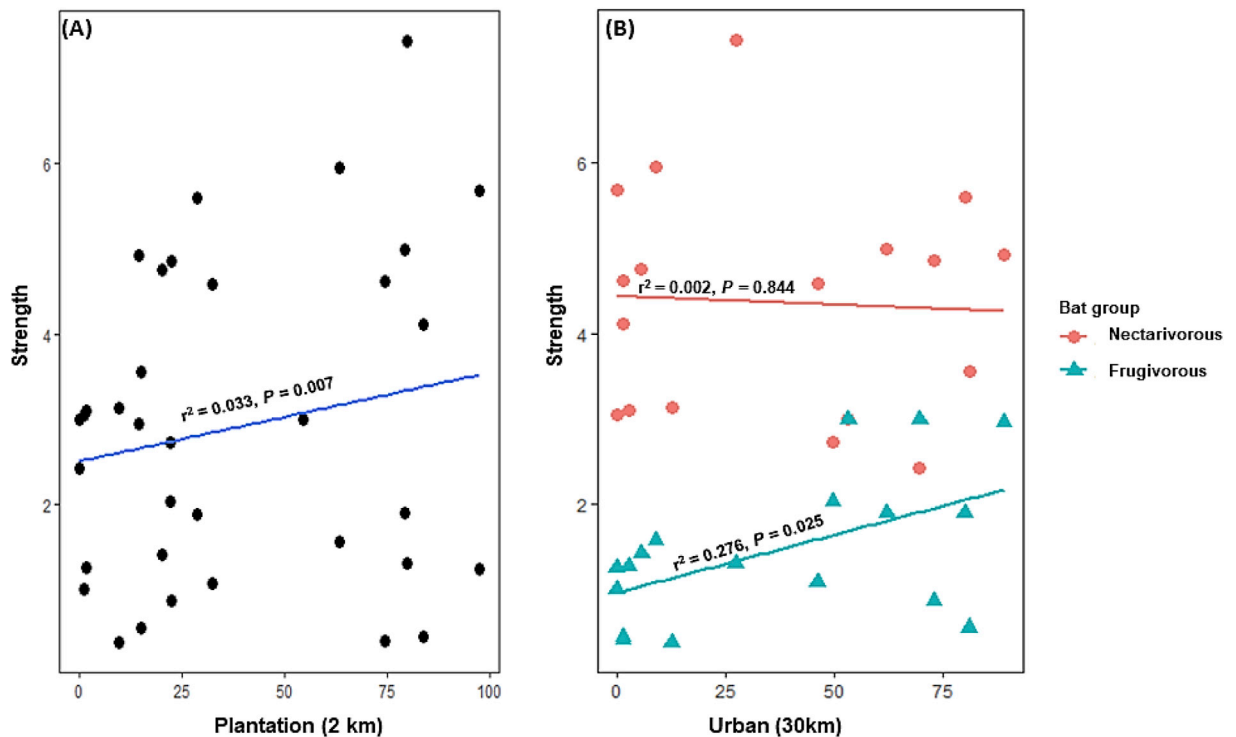


Fig. 6. A) The strength of bats plotted against proportion of plantation area within 2 km radius B) The interaction strength of nectarivorous bats (red circles) and frugivorous bats (green triangles) plotted against proportion of urban area within 30 km radius. Each point represents a single fruit orchard in southern Thailand. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

To our knowledge, this is the first study to investigate the impact of flowering season and landscape context on plants and bats pollinators with a particular focus on their interactions and the resulting structure of pollination networks. We investigated pollination network structure between low and maximum flowering season. We also explored the impact of bats guilds (nectarivorous and frugivorous bats) and the quality of surrounding habitats on bats communities and pollination network structure. There are two important results; firstly bat guilds (nectarivorous and frugivorous bats) differ in their impact on bat–pollination networks across seasons. Second, the network parameters at the species level of these two groups are differentially affected by the proportion of plantation and urban areas. We will discuss these two findings in turn, ending with some thoughts on the implications for pollination conservation and agriculture.

4.1. Network structure and resource availability across seasons

As resource availability varies across a year, contrary to our expectations, we found bat pollination networks were more specialised during low flowering season, when floral resource was less available. Similar findings have been reported for greater specialization in dry periods with lower related to lower floral availability and richness of plant species flowering (Souza et al., 2018). Other studies showed that higher levels of tree may be expected when resource availability is higher (Fontaine et al., 2006; Ghazoul, 2006). Nevertheless, the higher specialization in the low flowering season recorded here is associated with lower floral availability of plants. It is possible that resource availability can lead to changes in specialization of species by effecting competition among species. Increase in competitive interactions may have caused the increase in specialization when floral resources are low (Tinoco et al., 2017).

4.2. Roles of bat guilds in pollination networks

Our results clearly show that both bat guilds are strongly integrated in pollination network where they occur. These groups are dominated by *E. spelaea* for nectarivorous bats and *C. sphinx* for frugivorous bats. However the number of interactions performed by nectarivorous bats was higher than frugivorous bats, leading to higher network strength in nectarivorous bats. Results also show that nectarivorous bats visited flowers on more species of plants than frugivorous bats. From the roles estimated here, high network strength define the core of network (i.e. those generalists that interact with both specialists and

generalists) and enhance network robustness (Sole and Montoya, 2001; Dunne et al., 2002). This pattern may result from foraging strategies; nectar bats only forage on floral resources, while frugivorous bats predominantly forage on fruit resources (Stewart et al., 2014). Additionally, species-specific morphological traits may constrain the opportunity for interactions between bats and flowers. Nectar-specialist *Eonycteris* and *Macroglossus* species have elongated rostrums and tongues. In contrast, the other (frugivorous) bats species have relatively robust rostrums and short tongues (Marshall, 1983, 1985; Hodgkison et al., 2004; Francis, 2008; Bumrungsri et al., 2008, 2013). Consequently, tubular flowers (e.g. *Musa*, *Oroxylum*) are more likely to be visited by nectar-specialist bats (Sritongchuay et al., 2008; Fleming et al., 2009; Stewart et al., 2014), while frugivorous bats may be more likely to visit flowers with “shaving brush” morphologies (e.g. *Parkia*) because tubular shaped corollas limit frugivorous bats access to nectar given broader muzzles and shorter tongues.

4.3. Response of bat guilds to environmental effects

Along the landscape gradient, we recorded the specialization decreased with proportion of urban areas within 30 km radius in low flowering period when floral resource was low. However, we did not detect any impact of the landscape context on the number of interactions. This indicates that analyzing solely the number of interactions in network did not enable us to detect any changes in network structure along our landscape gradient. Our results also shows that the degree of generalism in nectarivorous bats diets changed positively with the proportion of plantation area at a proximal scale (within 2 km radius), suggesting that in location with high plantation area, the same nectarivorous bats visit to more plant species and may become less effective as pollinators. Typically, plantations consist of contiguous closed canopy oil-palm and rubber plantations larger than 1 km² where local plant richness and density are low. Although (Acharya et al., 2015) demonstrated that the nectar-specialist *E. spelaea* generally has strong fidelity to its' particular foraging plant and visit to the same area each night, however, pollinator dietary breadth is often context dependent; pollinators have been shown to switch from floral specialist to generalist strategies, when local floral resources decrease (Chittka and Schürkens, 2001; Fontaine et al., 2011). Pollinator foraging strategy is a critical for pollination success since floral-specialist pollinators typically deliver higher quality conspecific pollen loads (Ashman et al., 2004), whereas floral-generalist pollinators typically transport mixed pollen from several species and deliver larger amounts of incompatible pollen. This might block stamens and limit seed set in bats pollinated plants.

Similarly, at a species level, we also showed that the degree of generalism in frugivorous bat diets increased with proportion of urban areas within 30 km radius. At broad level, the positive effect of proportion of urban area is most likely associated with the food and roost availability. The dominant frugivorous bats are *Cynopterus* spp are tolerant of high levels of human disturbance (Campbell et al., 2006; Lim et al., 2018). These species use a wide variety of roost plant in habitats ranging from mature secondary forest to suburban gardens, and also exploit the eaves of buildings (Campbell et al., 2006), and roost under leaves of palm trees (*Livistona* sp., S. Bumrungsri pers. obs.). Frugivorous bats species have robust rostrums, short tongues, and consume both floral and fruit resources (Hodgkison et al., 2004; Bumrungsri et al., 2008, 2013; Francis, 2008; Stewart et al., 2014). Since the alimentary canals of frugivorous bats are short, the digestion is rapid, passage taking about 20–40 min which is short time to digest pollen (Marshall, 1983). In areas with a low proportion of urban area there are greater areas of lowland evergreen forest and lowland mosaic which typically consists of tree gardens, fruit orchards, agricultural fields, and forest, providing more fruit resources (Miettinen et al., 2016), consequently, frugivorous bats may rely on fruit resources as they are easier to digest. When there are fewer fruit resources in urban areas, frugivorous bats often shift to consume more nectar from more plant species in backyard gardens leading to higher generalism of frugivorous bats in the areas with higher proportions of urban landcover (Bumrungsri et al., 2007; Parry-Jones and Augee, 2001; Williams et al., 2006). The generalism and strength of frugivorous bats was not affected by landscape structure at smaller scales may be the consequence of wide range of feeding capabilities. Frugivorous bats can feed on both fruits and flowers, thus this bat guild are likely to perceive landscape as having larger amount of habitat (Hadley and Betts, 2012).

4.4. Limitations to research

There are three main limitations with our study. First, bat pollination networks were constructed using visitation rates alone and not pollination effectiveness. To improve measurements of pollinator performance underlying such predictions, we suggest surveying visitation frequency, pollinator effectiveness (pollen deposition ability) and pollinator importance (a measure combines of both visitation frequency and pollen deposition ability) of flower visitors in each study site. Second, we did not collect data on reproductive success (seed set and fruit set) of our plant species. As not all pollen grains deposited on a stigma are compatible or conspecific, seed and fruit production is not always directly related to pollen deposition. Mature fruit set is a very important proxy of pollinator effectiveness for studying in ecosystem services and conservation. Third, our study only examined bat pollination networks in study areas involving the smaller pteropodids, and have not accounted for the role of larger pteropodids i.e. flying foxes which are important in ensuring the reproductive success of economic crops such as durian (Aziz et al., 2017).

4.5. Agricultural and conservation implications

Bats provide essential ecosystem services, however, their populations are threatened by both anthropogenic and land-use changes (O'Shea et al., 2016; Sherwin et al., 2013), thus it is important to understand their role to the ecosystem in order to develop effective land-use management and thus maintain service provision. Our findings emphasise how plant-bat interactions within mixed-fruit orchards may undergo significant changes due to landscape context. Moreover, our study provides solid evidence that increasing the area of plantation and urban areas changes the role of pollinators. The dietary shifts of bats pollinators such as the increase in generalism of nectarivorous and frugivorous bats with proportion of plantation and urban respectively can result in changes in visitation rates, all of which can significantly impact pollination success in plants (Ghazoul, 2005). Because bat visitors are crucial for the pollination of many crops, the patterns found in this study have important implications for the conservation of pollination services and can contribute to landscape design and management, which may directly affect the productivity of agricultural crops. For instance, previous studies in this habitat found that the visitation rate of bats and reproductive success of durian was enhanced substantially enhanced by the proximity to the caves (Sritongchuay et al., 2016; Sritongchuay and Bumrungsri, 2016).

In quantifying the impact of landscape on pollination networks, our results can provide potential conservation recommendations concerning both plants and animals. Conservation practices aiming to preserve plant-pollinator interactions should promote the maintenance of both groups of bats and specialist plant species (e.g., *Oroxylum indicum*). Moreover, to maintain pollinators in orchards, we recommend including plant species that flower year-round, such as *Musa*. An approach which integrates agricultural areas, semi-natural habitats and planned urban ecosystems may improve pollination services efficiency. The maintenance of natural habitats surrounding agricultural areas may improve pollination services in the crops. Disseminating information about the ecological and economic significance of pollination services to farmers can help raise awareness about landscape management and the important roles of nectarivorous bats.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00702>.

References

- Acharya, P.R., Racey, P.A., Sotthibandhu, S., Bumrungsri, S., 2015. Home-range and foraging areas of the dawn bat *Eonycteris spelaea* in agricultural areas of Thailand. *Acta Chiropterol.* 17, 307–319. <https://doi.org/10.3161/15081109ACC2015.17.2.006>.
- Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K., Small, E., Wood, B., Wadsworth, R., Sanderson, R., Thompson, K., 2006. Biodiversity in urban habitat patches. *Sci. Total Environ.* 360, 196–204. <https://doi.org/10.1016/j.scitotenv.2005.08.035>.
- Ashman, T.-L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J., Morgan, M.T., Wilson, W.G., 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85, 2408–2421. <https://doi.org/10.1890/03-8024>.
- Ashworth, L., Aguilar, R., Galetto, L., Aizen, M.A., 2004. Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *J. Ecol.* 92, 717–719. <https://doi.org/10.1111/j.0022-0477.2004.00910.x>.
- Aziz, S.A., Clements, G.R., McConkey, K.R., Sritongchuay, T., Pathil, S., Abu Yazid, M.N.H., Campos-Arceiz, A., Forget, P.-M., Bumrungsri, S., 2017. Pollination by the locally endangered island flying fox (*Pteropus hypomelanus*) enhances fruit production of the economically important durian (*Durio zibethinus*). *Ecol. Evolut.* 7, 8670–8684. <https://doi.org/10.1002/ece3.3213>.
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc. Biol. Sci.* 282, 20142849–20142849. <https://doi.org/10.1098/rspb.2014.2849>.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433. <https://doi.org/10.1126/science.1123412>.
- Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020. <https://doi.org/10.1038/nature07950>.
- Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., Hensen, I., Kühn, I., Wiegand, T., Dehling, D.M., Schleuning, M., 2017. Functionally specialised birds respond flexibly to seasonal changes in fruit availability. *J. Anim. Ecol.* 86, 800–811. <https://doi.org/10.1111/1365-2656.12683>.
- Blüthgen, Nico, Menzel, F., Blüthgen, Nils, 2006. Measuring specialization in species interaction networks. *BMC Ecol.* 6, 9. <https://doi.org/10.1186/1472-6785-6-9>.

- 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 [WWW Document]. <https://doi.org/10.3161/150811014X683255>.
- 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. *J. Trop. Ecol.* 24, 467–475. <https://doi.org/10.1017/S0266467408005191>.
- 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 Chiropterol.* 15, 95–104. <https://doi.org/10.3161/150811013X667894>.
- Bumrungsri, S., Leelapaibul, W., Racey, P.A., 2007. Resource partitioning in sympatric Cynopterus bats in lowland tropical rain forest, Thailand. *Biotropica* 39, 241–248. <https://doi.org/10.1111/j.1744-7429.2006.00245.x>.
- Bumrungsri, S., Sripaoraya, E., Chongsiri, T., Sridith, K., Racey, P.A., 2009. The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. *J. Trop. Ecol.* 25, 85–92. <https://doi.org/10.1017/S0266467408005531>.
- Campbell, P., Reid, N.M., Zubaid, A., Adnan, A.M., Kunz, T.H., 2006. Comparative roosting ecology of *Cynopterus* (chiroptera: Pteropodidae) fruit bats in peninsular Malaysia. *Biotropica* 38, 725–734. <https://doi.org/10.1111/j.1744-7429.2006.00203.x>.
- Chittka, L., Schürkens, S., 2001. Successful invasion of a floral market. *Nature* 411, 653–653. <https://doi.org/10.1038/35079676>.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>.
- Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663. <https://doi.org/10.1111/jbi.12130>.
- Ferreira, P.A., Boscolo, D., Viana, B.F., 2013. What do we know about the effects of landscape changes on plant–pollinator interaction networks? *Ecol. Indic.* 31, 35–40. <https://doi.org/10.1016/j.ecolind.2012.07.025>.
- Fleming, T.H., Geiselman, C., Kress, W.J., 2009. The evolution of bat pollination: a phylogenetic perspective. *Ann. Bot.* 104, 1017–1043. <https://doi.org/10.1093/aob/mcp197>.
- Fontaine, C., Collin, C.L., Dajoz, I., 2008. Generalist foraging of pollinators: diet expansion at high density: flexibility of pollinator generalization. *J. Ecol.* 96, 1002–1010. <https://doi.org/10.1111/j.1365-2745.2008.01405.x>.
- Fontaine, C., Dajoz, I., Méridet, J., Loreau, M., 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol.* 4, 804–808. <https://doi.org/10.1371/journal.pbio.0040001>.
- Fontaine, C., Guimarães, P.R., Kéfi, S., Loeuille, N., Memmott, J., Putten, W.H. van der, Veen, F.J.F. van, Thébault, E., 2011. The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14, 1170–1181. <https://doi.org/10.1111/j.1461-0248.2011.01688.x>.
- Fortuna, M.A., Bascompte, J., 2006. Habitat loss and the structure of plant–animal mutualistic networks: mutualistic networks and habitat loss. *Ecol. Lett.* 9, 281–286. <https://doi.org/10.1111/j.1461-0248.2005.00868.x>.
- Francis, C.M., 2008. *A Field Guide to the Mammals of Thailand and South-East Asia*. Asia Books Company, Limited, Thailand, Peninsular Malaysia, Singapore, Myanmar, Laos, Vietnam, Cambodia.
- Frick, W.F., Kingston, T., Flanders, J., 2019. A review of the major threats and challenges to global bat conservation. In: *Annals of the New York Academy of Sciences*. <https://doi.org/10.1111/nyas.14045>.
- Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. *J. Ecol.* 94, 295–304. <https://doi.org/10.1111/j.1365-2745.2006.01098.x>.
- Ghazoul, J., 2005. Pollen and seed dispersal among dispersed plants. *Biol. Rev.* 80, 413. <https://doi.org/10.1017/S1464793105006731>.
- Gittleman, J.L., Kot, M., 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Syst. Zool.* 39, 227–241. <https://doi.org/10.2307/2992183>.
- Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biol. Rev.* 87, 526–544. <https://doi.org/10.1111/j.1469-185X.2011.00205.x>.
- Hodgkinson, R., Balding, S.T., Zubaid, A., Kunz, T.H., 2004. Temporal variation in the relative abundance of fruit bats (megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. *Biotropica* 36, 522–533. <https://doi.org/10.1111/j.1744-7429.2004.tb00347.x>.
- Jordano, P., 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *Am. Nat.* 129, 657–677. <https://doi.org/10.1086/284665>.
- Kaiser-Bunbury, C.N., Blüthgen, N., 2015. Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants* 7, plv076. <https://doi.org/10.1093/aobpla/plv076>.
- Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299, 1388–1391. <https://doi.org/10.1126/science.1079154>.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10, 299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>.
- Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T., Fleming, T.H., 2011. *Ecosystem services provided by bats*. *Europe* 31, 32.
- Leong, M., Kremen, C., Roderick, G.K., 2014. Pollinator interactions with yellow starthistle (*centaurea solstitialis*) across urban, agricultural, and natural landscapes. *PLoS One* 9, e86357. <https://doi.org/10.1371/journal.pone.0086357>.
- Lim, V.-C., Clare, E.L., Littlefair, J.E., Ramli, R., Bhassu, S., Wilson, J.-J., 2018. Impact of urbanisation and agriculture on the diet of fruit bats. *Urban Ecosyst.* 21, 61–70. <https://doi.org/10.1007/s11252-017-0700-3>.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100, 603–609.
- Magrath, A., González-Varo, J.P., Boiffier, M., Vilà, M., Bartomeus, I., 2017. Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nat. Ecol. Evol.* 1, 1299–1307. <https://doi.org/10.1038/s41559-017-0249-9>.
- Marshall, A.G., 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zool. J. Linn. Soc.* 83, 351–369. <https://doi.org/10.1111/j.1096-3642.1985.tb01181.x>.
- Marshall, A.G., 1983. Bats, flowers and fruit: evolutionary relationships in the Old World. *Biol. J. Linn. Soc.* 20, 115–135. <https://doi.org/10.1111/j.1095-8312.1983.tb01593.x>.
- McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>.
- Miettinen, J., Shi, C., Liew, S.C., 2016. 2015 Land cover map of Southeast Asia at 250 m spatial resolution. *Rem. Sens. Lett.* 7, 701–710. <https://doi.org/10.1080/2157074X.2016.1182659>.
- Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. *Nature* 442, 259–264. <https://doi.org/10.1038/nature04927>.
- Moreira, E.F., Boscolo, D., Viana, B.F., 2015. Spatial heterogeneity regulates plant–pollinator networks across multiple landscape scales. *PLoS One* 10, e0123628. <https://doi.org/10.1371/journal.pone.0123628>.
- Morellato, L.P.C., Alberton, B., Alvarado, S.T., Borges, B., Buisson, E., Camargo, M.G.G., Cancian, L.F., Carstensen, D.W., Escobar, D.F.E., Leite, P.T.P., Mendoza, I., Rocha, N.M.W.B., Soares, N.C., Silva, T.S.F., Staggemeier, V.G., Streher, A.S., Vargas, B.C., Peres, C.A., 2016. Linking plant phenology to conservation biology. *Biol. Conserv.* 195, 60–72. <https://doi.org/10.1016/j.biocon.2015.12.033>.
- Nor Zalipah, M., Shahrl Anuar, M.S., Jones, G., 2016. The potential significance of nectar-feeding bats as pollinators in mangrove habitats of Peninsular Malaysia. *Biotropica* 48, 425–428. <https://doi.org/10.1111/btp.12335>.
- O’Shea, T.J., Cryan, P.M., Hayman, D.T.S., Plowright, R.K., Streicker, D.G., 2016. Multiple mortality events in bats: a global review: multiple mortality events in bats. *Mamm. Rev.* 46, 175–190. <https://doi.org/10.1111/mam.12064>.
- Parry-Jones, K.A., Augée, M.L., 2001. Factors affecting the occupation of a colony site in Sydney, New South Wales by the grey-headed flying-fox *Pteropus poliocephalus* (Pteropodidae): FLYING-FOX USAGE OF AN URBAN COLONY SITE. *Austral Ecol.* 26, 47–55. <https://doi.org/10.1111/j.1442-9993.2001.01072.pp.x>.

- Pimm, S.L., Raven, P., 2000. Biodiversity: extinction by numbers. *Nature* 403, 843–845. <https://doi.org/10.1038/35002708>.
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229. <https://doi.org/10.1038/nature20588>.
- Sherwin, H.A., Montgomery, W.I., Lundy, M.G., 2013. The impact and implications of climate change for bats: bats and climate change. *Mamm. Rev.* 43, 171–182. <https://doi.org/10.1111/j.1365-2907.2012.00214.x>.
- Sole, R.V., Montoya, M., 2001. Complexity and fragility in ecological networks. *Proc. Biol. Sci.* 268, 2039–2045. <https://doi.org/10.1098/rspb.2001.1767>.
- Souza, C.S., Maruyama, P.K., Aoki, C., Sigris, M.R., Raizer, J., Gross, C.L., de Araujo, A.C., 2018. Temporal variation in plant-pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. *J. Ecol.* 106, 2409–2420. <https://doi.org/10.1111/1365-2745.12978>.
- Sritongchuay, T., Bumrungsri, S., Sripao-raya, E., 2008. The pollination ecology of the late-successional tree, *Oroxylum indicum* (Bignoniaceae) in Thailand. *J. Trop. Ecol.* 24, 477–484. <https://doi.org/10.1017/S026646740800521X>.
- Sritongchuay, T., Bumrungsri, S., 2016. Specialized and facultative nectar-feeding bats have different effects on pollination networks in mixed fruit orchards, in southern Thailand. *J. Pollinat. Ecol.* 19, 98–103. [https://doi.org/10.26786/1920-7603\(2016\)7](https://doi.org/10.26786/1920-7603(2016)7).
- Sritongchuay, Tuanjit, Kremen, C., Bumrungsri, S., 2016. Effects of forest and cave proximity on fruit set of tree crops in tropical orchards in Southern Thailand. *J. Trop. Ecol.* 32, 269–279. <https://doi.org/10.1017/S0266467416000353>.
- Stewart, A.B., Dudash, M.R., 2017. Flower-visiting bat species contribute unequally toward agricultural pollination ecosystem services in southern Thailand. *Biotropica* 49, 239–248. <https://doi.org/10.1111/btp.12401>.
- 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. *J. Trop. Ecol.* 30, 249–257. Cambridge. <https://doi.org/10.1017/S0266467414000042>.
- Tanalgo, K.C., Tabora, J.A.G., Hughes, A.C., 2018. Bat cave vulnerability index (BCVI): a holistic rapid assessment tool to identify priorities for effective cave conservation in the tropics. *Ecol. Indicat.* 89, 852–860.
- Tinoco, B.A., Graham, C.H., Aguilar, J.M., Schleuning, M., 2017. Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos* 126, 52–60. <https://doi.org/10.1111/oik.02998>.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Conserv.* 143, 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>.
- Vizentin-Bugoni, J., Maruyama, P.K., de Souza, C.S., Ollerton, J., Rech, A.R., Sazima, M., 2018. Plant-pollinator networks in the tropics: a review. In: Dáttilo, W., Rico-Gray, V. (Eds.), *Ecological Networks in the Tropics*. Springer International Publishing, Cham, pp. 73–91. https://doi.org/10.1007/978-3-319-68228-0_6.
- Wayo, K., Phankaew, C., Stewart, A.B., Bumrungsri, S., 2018. Bees are supplementary pollinators of self-compatible chiropterophilous durian. *J. Trop. Ecol.* 34, 41–52. <https://doi.org/10.1017/S0266467418000019>.
- Weiner, C.N., Werner, M., Linsenmair, K.E., Blüthgen, N., 2014. Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines. *Ecology* 95, 466–474. <https://doi.org/10.1890/13-0436.1>.
- Williams, N.S.G., McDonnell, M.J., Phelan, G.K., Keim, L.D., Van Der Ree, R., 2006. Range expansion due to urbanization: increased food resources attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecol.* 31, 190–198. <https://doi.org/10.1111/j.1442-9993.2006.01590.x>.
- Wilson, M.C., Chen, X.-Y., Corlett, R.T., Didham, R.K., Ding, P., Holt, R.D., Holyoak, M., Hu, G., Hughes, A.C., Jiang, L., Laurance, W.F., Liu, J., Pimm, S.L., Robinson, S.K., Russo, S.E., Si, X., Wilcove, D.S., Wu, J., Yu, M., 2016. Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landsc. Ecol.* 31, 219–227. <https://doi.org/10.1007/s10980-015-0312-3>.
- Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Systemat.* 42, 1–22. <https://doi.org/10.1146/annurev-ecolsys-102710-145042>.
- Wright, J.S., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130, 1–14. <https://doi.org/10.1007/s004420100809>.