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Local and Landscape Compositions Influence Stingless Bee Communities and Pollination Networks in Tropical Mixed Fruit Orchards, Thailand

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Abstract: Stingless bees are vital pollinators for both wild and crop plants, yet their communities have been affected and altered by anthropogenic land-use change. Additionally, few studies have directly addressed the consequences of land-use change for meliponines, and knowledge on how their communities change across gradients in surrounding landscape cover remains scarce. Here, we examine both how local and landscape-level compositions as well as forest proximity affect both meliponine species richness and abundance together with pollination networks across 30 mixed fruit orchards in Southern Thailand. The results reveal that most landscape-level factors significantly influenced both stingless bee richness and abundance. Surrounding forest cover has a strong positive direct effect on both factors, while agricultural and urbanized cover generally reduced both bee abundance and diversity. In the local habitat, there is a significant interaction between orchard size and floral richness with stingless bee richness. We also found that pollinator specialization in pollination networks decreased when the distance to the forest patch increased. Both local and landscape factors thus influenced meliponine assemblages, particularly the forest patches surrounding an orchard, which potentially act as a key reservoir for stingless bees and other pollinator taxa. Preservation of forest patches can protect the permanent nesting and foraging habitat of various pollinator taxa, resulting in high visitation for crop and wild plants.

Keywords: agriculture; floral resources; forest proximity; land-use change; meliponine; plant–pollinator interaction; urbanization

1. Introduction

Plant–pollinator interactions are important as most pollinators rely on flowering plants for food resources as well as angiosperms that require pollinators for pollination [1]. Land-use change is one of the most important factors of global change that influences plant–pollinator interactions [2]. Bees are considered as a key pollinator group for both wild and crop plants [3,4]; however, in an era of increasing anthropogenic land-use change, wild bee communities have been affected and altered by converting natural habitats into landscapes with reduced resource diversity and availability, particularly where land-use change is extreme [5,6]. Additionally, relatively little is known about changes in bee community composition in the tropics, where land-use change has been increasing and pollination limitation has occurred [2,7]. Food and nesting resource availabilities are considered as direct factors regulating the

bee population [8], while declines in the bee population are linked to nutritional shortages caused by land-use intensification [9]. Consequently, human disturbance of natural habitats may indirectly change pollinator communities as a result of changes in resource availability, and tropical bees may respond to land-use change differently in comparison to temperate bees.

Although many studies have examined the effects of human disturbances, such as habitat loss, grazing, agriculture, and urban development, on the richness, abundance, and community of bees, most of these studies are in temperate and Neotropical regions (e.g., [10–14]), and only a few studies have been undertaken in Southeast Asia [15–18]. Generally, natural habitats such as tropical forests are served as sources of native pollinators to surrounding areas, particularly to crops [19], that is, on farms near the natural habitat, native bee communities have been shown to provide pollination services for a crop [20–22]. Moreover, crop pollination services strongly rely on natural habitats within 1–2.5 km of farm sites [22–25]. Forest patches and proximity thus are vital for pollinator communities and crop production, and the impact of land-use change on pollinator communities remains a considerable knowledge gap that is urgently needed for pollinator management.

Stingless bees (meliponine) have been known as important pollinators for both wild and crop plants in subtropical and tropical regions [26,27]. Meliponine nests are associated primarily with remarkably large tropical forest trees, and nest density is related to pollen resource availability [28]. Either food or nesting resource availabilities or both are likely to limit the population density of stingless bees [29–31]. Some species of stingless bees are abundant in primary forests, whereas other species are abundant in disturbed forests [16] or utilize man-made structures for nesting [32]. However, only a few studies have directly addressed the consequences of land-use change for meliponines [12,13,33], mainly in the Neotropics, and there has been no study undertaken in Southeast Asia. Since “mixed fruit orchards” are typically found around traditional villages while forest patches are scattered in humid areas of Southeast Asian countries, we assume that this kind of orchard will support high biodiversity such as birds [34], bats and bees [35,36]. In addition, these orchards possibly serve as a suitable site and a sustainable way of agriculture as well as a refuge from pollution and land transition for pollinators.

Recent advances in the study of pollination networks have improved our ability to describe species interactions and explain the underlying structure of entire communities [37]. Network analysis provides a useful framework for predicting the vulnerability of pollinator–resource relationships or mutualisms to species loss [37]. The structure and complexity (e.g., specialization) of these mutualistic networks may be important in promoting community stability and function [38]. 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 [39]. The loss of more specialist species and their ecological interactions due to their high vulnerability to habitat loss may directly affect network robustness and lead to secondary extinctions, loss of interactions, and, consequently, ecosystem function disruption [40].

Hence, to understand the land-use effects on pollinators, stingless bee richness and abundance in mixed fruit orchards across a gradient of human disturbance were examined in this study. Our aims are mainly: (1) to examine both how local and landscape-level compositions as well as forest proximity influence stingless bee assemblage. We predict that abundance and richness of meliponines may be higher in orchards with greater floral resource availability and proportion of surrounding forest cover and closer to the forest; and (2) to investigate the effects of local and landscape-level compositions as well as forest proximity on the structure of pollination networks. The number of interactions and specialization of pollination networks in orchards, which are close to forest patches and surrounded by more complex landscapes (with high resource abundance), is predicted to be higher than in simple structure landscapes (with low resource abundance) (i.e., urban area). However, recent studies have revealed that social bees are fitter in more florally diverse environments such as urban gardens [41,42]. Additionally, when resources are rare, the range of food items taken by meliponines might increase. Eventually, the information in the present study could serve as a useful guide for land-use and pollinator management.

2. Materials and Methods

2.1. Study Region and Crop System

The study was conducted in Southern Thailand where the region is characterized by a mix of forest, agriculture, and urban landscape. Forests are comprised of large tropical rainforests and small fragmented patches. Most of the agricultural land consists of perennial crops, orchards, and paddy fields. According to the land use data during 2017–2018 from the Land Development Department of Thailand (LDD) [43], the plantations of rubber (*Hevea brasiliensis* Müll.Arg., 27,200 km²), oil palm (*Elaeis guineensis* Jacq., 9600 km²), and fruit trees (3200 km²) accounted for most of the agricultural area, whilst urban and built-up land covered 3200 km² in the southern part of Thailand. Overall, land-use has changed over the past ten years in the country, i.e., there have been increases in the agricultural and urban landscape, yet the forest cover has slightly decreased [43].

2.2. Study Sites

Mixed fruit orchards are commonly found in Southeast Asian traditional villages and scattered among forest patches. This orchard type plays a key role in both subsistence and cash income for farmers in the region. In Southern Thailand, mixed fruit orchards account for most of the orchard areas, while monocultural fruit orchards, such as longan (*Dimocarpus longan* Lour.), mango (*Mangifera indica* L.), and coconut (*Cocos nucifera* L.) are common in other regions of the country [43]. Generally, mixed fruit orchards contain many fruiting plants that are planted to form a multi-storied assemblage, i.e., canopy-top species are planted well-spaced, whereas subcanopy and understory species are planted between the spaces [35]. The canopy-top and subcanopy species in the present study typically included durian (*Durio zibethinus* L.), bitter beans (*Parkia speciosa* Hassk.), mangosteen (*Garcinia mangostana* L.), rambutan (*Nephelium lappaceum* L.), duku (*Lansium domesticum* Corr.), coconut, and mango, while banana (*Musa* spp.), eggplants (*Solanum* spp.), and ginger (*Zingiber* spp.) predominate in the understory.

A total of 30 mixed fruit orchards in Songkhla, Phatthalung, and Satun provinces (6°17' to 7°53' N and 100°50' to 99°50' E) were used in the study. The study orchards were located along a gradient of surrounding landscape complexity. The orchards containing more than 5 cultivated fruit species and being managed for over ten years were chosen. The size range of orchards was approximately 390–25,000 m² (Table S1). The orchards ranged from 1.5 km to 15 km approximately in geographic distance from the closest ones, and each orchard was assumed to be independent for bee sampling. Previous studies have revealed the typical homing distances of stingless bees, ranging from 300 m in small stingless bees [44] to 2 km in large stingless bees [45].

2.3. Environmental Multilevel Quantification

2.3.1. Local Conditions

The habitat scale, orchard size, floral abundance and richness, and plant diversity were selected as independent variables. Each studied mixed fruit orchard was measured by aerial photographs from Google Earth in ArcGIS 10.3 [46], while plant resource availabilities in an orchard were evaluated by ground surveys. To sample plants, line transects were used to measure flowering-plant resources and plant communities in the orchards. The length and number of transects (at 10 m intervals) depended on the size and shape of the orchards. Plant richness and abundance as well as the species and number of plant individuals in flowers rooted within 5 m of either side of the line were recorded. Floral abundance was defined as the number of flowers within sampling areas in each orchard. For the Asteraceae family, each capitulum was counted as a single flower. Plant diversity values were calculated using the Shannon–Wiener diversity index (H'). Plant species were confirmed by plant taxonomists at the Department of Biology, Division of Biological Science, Prince of Songkla University, Thailand.

2.3.2. Landscape Structure at Proximal and Broad Levels

On the landscape scale, we selected forest proximity (i.e., distance to the nearest forest) and landscape composition including proportions of three main landscape types, which were forest, agriculture, and urban around a target orchard, as independent variables. We obtained the reference land-use map from the LDD [43], which provided the shape file data with a scale of 1:25,000 digitized from satellite images resolution of 2.5 m. The three main land-use types were defined as follows: (1) forest land (FO), which mainly comprises evergreen forest, mangrove forest, and swamp forest; (2) agricultural lands (AG), which mostly consists of perennial crops, orchards, and paddy fields; (3) urbanized areas (UR), which largely include cities, towns, commercials, villages, and institutional lands. Each landscape type fraction was calculated within a 1, 2, 3, 5 and 10 km radius for each site (representing steps of spatial scales at which bees may interact with the surrounding land), and the distances to the nearest forest of each site were measured using ArcGIS 10.3 [46].

2.4. Bee Sampling

Stingless bee samplings were conducted on sunny and rain-free days. In the rainy season (November 2019–early January 2020), we merely sampled 12 sites due to the time limitation, while in the dry season (late February–June 2020), 30 sites were bee-collected. Each site was sampled two times per season. In each time, a stingless bee collection was conducted in the morning (7 am–11 am). In each site, 10 m² square plots were used. Each plot was laid along the same transects for plant sampling with 10 m apart from each other. The number of plots in each orchard was approximately proportional to the size of each orchard (more plots were conducted in larger orchard patches). The two collectors netted the stingless bees within each sampling plot for 10 min period, focusing efforts on flowering plants. The maximum vertical sampling was limited at 5 m above the ground. All individuals were collected for identification at the species level in order to investigate species abundance and richness. All specimens were pinned, labeled, and identified as species in the laboratory. The stingless bee specimens were mostly identified by the identification key of Schwarz (1939) [47]. The members of *Tetragonula* Moure, 1961, *Lepidotrigona* Schwarz, 1939 and *Lisotrigona* Moure, 1961 were identified by Sakagami (1978) [48], Attasopa et al. (2018) [49], and Engel (2000) [50], respectively. Furthermore, the body size of each stingless bee species was assessed by measuring the intertegular (IT) distance (the distance between the wing bases) by using a vernier caliper.

2.5. Constructing the Pollination Networks

The overall pollination network structures across all seasons were visualized using the bipartite package [51] implemented in R [52]. For each network, we calculated the number of interactions, connectance, and nestedness. We calculated species-level degree of specialization using d' to measure the specialization of each stingless bee species. We used the mean of d' as the overall specialization in each pollination network. This specialization index is obtained by measuring the exclusivity of interactions that each species take part in [53]. The d' was used as it is the standard measure of visitor specialization in resource choice in the visitation network, and most relevant predictor of specialization in pollination for plants in a pollination network. The d' takes into account the resource availability in the community. Resource availability was obtained from the independent measures of flower abundance at each site. d' ranges from 0 to 1, where 0 indicates high generalization (high niche overlap) and 1 high specialization (high niche segregation). Compared to other network metrics, d' is demonstrably robust to differences in species richness among networks [53].

2.6. Statistical Analyses

All analyses were performed with R, version 4.0.0 [52]. We used generalized linear mixed models (GLMM) with the MASS package [54], matrix package [55], lme4 package [56], car package [57] and lattice package [58] to determine the effects of local and landscape factors on meliponine

richness and abundance. The species richness referred to the number of species in each orchard, and species abundance was defined as the number of all species individuals in each orchard. Four local scale site-independent variables were used: orchard size, floral abundance and richness, and the Shannon–Wiener diversity index (H'), while landscape-scale independent variables included proportions of three land-use types at five different radii (defined above) and forest proximity. Season, site, and date of the survey were treated as random effects. The Poisson distribution was used for bee richness (as it was counted), while the negative binomial distribution was used for bee abundance to deal with count-based data with overdispersion [59]. To check whether the response variables were spatially autocorrelated we conducted Moran's I tests [60] with the "ape" package [61]. No significant spatial autocorrelation was found using Moran's I ($p > 0.05$ in all models).

We initially explored the correlation matrix for all independent variables using the *corr* package [62] and found that all the landscape-level variables were highly correlated (based on Pearson's correlation tests). Thus, we ran models with each landscape-level variable separately to avoid possible collinear predictor effects [18,63]. One landscape-level variable with four local variables and three interactions (the interaction between orchard size and floral richness, the interaction between orchard size and floral abundance, and the interaction between orchard size and plant richness) were initially set as a candidate model. We then minimized the number of parameters by using the Akaike's information criterion (AIC). The best single model was selected among candidate models (Table S2) using the MuMIn package [64], which provided the Akaike's information criterion corrected (AICc) and Akaike model weights (wAICc) values.

Moreover, regressions between significant parameters and both meliponine richness and abundance were plotted with the corresponding confidence interval using the *ggplot2* package [65]. The d' value was available from 10 study sites. Generalized linear models (GLM) were conducted to examine the effect of the local and landscape-level variables on d' .

3. Results

3.1. Plant Diversity

A total of 204 angiosperm plant species (29 orders, 67 families, 172 genera; Table S3) were observed across the 30 mixed fruit orchards. One hundred and three plant species in flowers representing 22 orders, 43 families, and 90 genera were observed, and 35 species of these plants were visited by stingless bees in this study. The most common plant families observed in this study were Fabaceae (18 species), Asteraceae (11 species), and Arecaceae (10 species). The five most common plant species were *Asystasia gangetica* (L.) T. Anderson (observed in 29 sites), *Durio zibethinus* L. (27 sites), *Musa* spp. (27 sites), *Garcinia mangostana* L. (25 sites), and *Lansium parasiticum* (Osbeck) K.C.Sahni & Bennet (25 sites). The six plant species that attracted the most stingless bee species and individuals were *Nephelium lappaceum* L., rambutan (10 species, 123 individuals visited), *D. zibethinus*, durian (eight species, 59 individuals), *Mangifera indica* L., mango (eight species, 65 individuals), *Cocos nucifera* L., coconut (seven species, 130 individuals), *Kyllinga brevifolia* Rottb., green kyllinga (six species, 80 individuals), and *A. gangetica*, Chinese violet (five species, 65 individuals). Moreover, we observed meliponines visited mango and jackfruit (*Artocarpus heterophyllus* Lam.) trees for resin collection.

3.2. Stingless Bee Species

A total of 746 stingless bee specimens were sampled across 30 mixed fruit orchards in Southern Thailand, representing 13 species in eight genera (Appendix A Table A1). The five most commonly observed stingless bee species in this study were *Heterotrigona itama* (Cockerell) (observed in 13 sites), *Tetragonula pagdeni* (Schwarz) (13 sites), *Tetragonula fuscobalteata* (Cameron) (11 sites), *Tetragonula laeviceps* (Smith) (seven sites), and *Geniotrigona thoracica* (Smith) (six sites). The five most abundant species found in the orchards were *Heterotrigona itama* (25.34% of all samples), *Tetragonula pagdeni* (12.60%), *Tetrigona apicalis*

(Smith) (11.66%), *Geniotrigona thoracica* (11.39%), and *Tetragonula fuscobalteata* (10.86%). In addition, the body sizes of all stingless bee species were categorized into two size classes: (1) small, 1.00–1.90 mm including *Lisotrigona cacciae* (Nures); *Lepidotrigona satun* (Attasopa & Bänziger); *Lepidotrigona terminata* (Smith); *Tetragonula pagdeni*; *Tetragonula fuscobalteata*; *Tetragonula laeviceps*; *Tetragonilla collina* (Smith); *Tetragonilla atripes* (Smith), and (2) large, 1.92–2.76 mm including *Heterotrigona itama*; *Tetrigona apicalis*; *Geniotrigona thoracica*; *Lophotrigona canifrons* (Smith); *Tetrigona melanoleuca* (Cockerell).

3.3. Environmental Multilevel Effects on Stingless Bee Richness and Abundance

The local and landscape-level structures affected stingless bee richness. The bee richness was best described by the model including orchard size, floral richness, and their interaction, and percent of forest cover within a 1 km radius (the lowest AIC, Table 1). On the habitat scale, there was a significant interaction between orchard size and floral richness, i.e., greater floral richness in the larger orchards significantly increased the richness of stingless bees but did not increase this response in the small and medium orchards (Figure 1A). On the landscape scale, greater percent of forest cover at a 1 km radius increased the number of stingless bee species (Figure 1B). In addition to the surrounding percent forest cover, the richness of stingless bees was negatively affected by the proportions of agricultural cover and urbanized cover within a 10 km radius, and the distance to the nearest forest (Table 1). Stingless bee richness declined with greater values of each of these three metrics. (Figure 1C–E).

On the other hand, the abundance of stingless bees was influenced merely by landscape factors. The abundance was effectively described by the model including the percent of forest cover within a 2 km radius (the lowest AIC, Table 1). Additionally, the abundance was significantly influenced by the percent of agricultural cover within a 2 km radius and distance to the nearest forest (Table 1). Generally, the percent of forest cover within a 2 km radius had a significantly positive effect on the abundance of bees (Figure 2A), whilst the greater percent of agricultural cover within a 2 km radius and distance to the nearest forest decreased the number of bee individuals (Figure 2B,C).

Table 1. Results of the generalized linear mixed models (GLMM) for stingless bee richness and abundance across 30 mixed fruit orchards in Southern Thailand. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Indices	Explanatory Fixed Variable	Estimate	SE	z-Value	p-Value
Richness (AIC = 249.1)	Intercept	0.059	0.003	18.56	<0.001 ***
	Orchard size	−1.929	0.003	−607.92	<0.001 ***
	Floral richness	−0.087	0.003	−27.77	<0.001 ***
	Forest cover (1 km)	0.039	0.003	14.41	<0.001 ***
	Orchard size * Floral richness	0.322	0.003	101.58	<0.001 ***
(AIC = 252.1)	Intercept	2.351	0.625	3.759	<0.001 ***
	Agricultural cover (10 km)	−0.044	0.011	−3.943	<0.001 ***
(AIC = 261.5)	Intercept	0.379	0.367	1.032	0.302
	Urbanized cover (10 km)	−0.106	0.046	−2.322	0.020 *
(AIC = 258.5)	Intercept	0.354	0.315	1.122	0.262
	Distance to forest edge	−0.0003	0.0001	−2.857	0.004 **
Abundance (AIC = 458.1)	Intercept	−0.323	0.465	−0.695	0.487
	Forest cover (2 km)	0.062	0.013	4.768	<0.001 ***
	Intercept	5.132	1.004	5.115	<0.001 ***
(AIC = 460.8)	Agricultural cover (2 km)	−0.062	0.014	−4.343	<0.001 ***
	Intercept	−0.497	1.175	−0.423	0.673
(AIC = 468)	H'	0.936	0.503	1.859	0.063
	Distance to forest edge	−5.477	2.058	−2.662	0.008 **

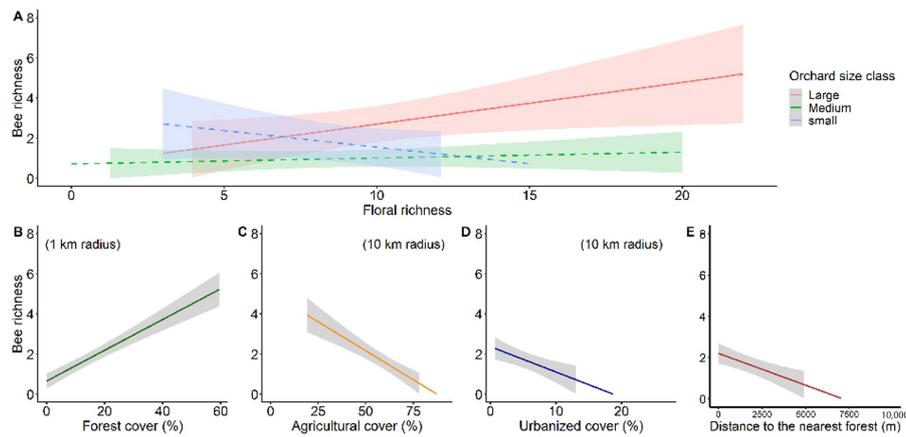


Figure 1. Effects of significant habitat and landscape factors on stingless bee richness. (A) The bee richness was influenced by a significant interaction between floral richness and orchard size, which was classified into 3 classes: blue line = small sites (300–1500 m²), green line = medium sites (2000–5000 m²), and light red line = large sites (5000–26,000 m²). Large orchard size and floral richness interaction significantly affected stingless bee richness, as shown with the solid line, while small and medium orchard sizes and floral richness interactions were not significant as shown with the dashed line. (B) Percent of forest cover within a 1 km radius had significantly positive effects on the richness, while (C–E) three landscape factors (proportions of agricultural and urbanized cover within a 10 km radius and distance to the nearest forest) had a significantly negative effect. All regressions are plotted with 95% corresponding confidence intervals.

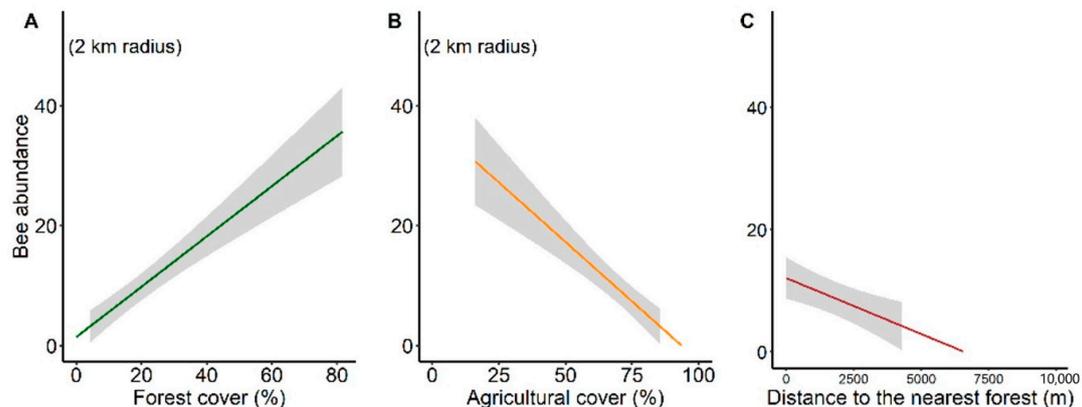


Figure 2. Effects of significant landscape factors on stingless bee abundance. (A) Percent of forest cover within a 2 km radius had a significantly positive effect on the abundance, while (B,C) two landscape factors (proportion of agricultural cover within a 2 km radius and distance to the nearest forest) had a significantly negative effect. All regressions are plotted with 95% corresponding confidence intervals.

3.4. Pollination Network

We observed 666 interactions between the 12 species of flower-visiting stingless bees and the 35 species of plant in all 30 mixed fruit orchard sites. We excluded *Lisotrigona cacciae* for the pollination network as they were captured while flying in the air. The number of interactions was quantified in all networks as visitation rate, ranging from 14 to 147 interactions. Cumulative networks of these interactions are presented in Figure 3. *Heterotrigona itama* were involved in 25% of interactions (166 interactions); *Tetrigona apicalis* in 13% (87 interactions); *Tetragonula fuscobalteata* in 12% (80 interactions); *Tetragonula pagdeni* in 11.4% (76 interactions) and *Geniotrigona thoracica* 9.9% (66 interactions). *Heterotrigona itama* and *Tetrigona apicalis* had the broadest floral host breadth. The most visited plants were *Cocos nucifera* (Palmeaceae), with 130 interactions (19.5%); *Nephelium lappaceum* (Sapindaceae), with 123 interactions (18.47%); *Kyllinga brevifolia* (Cyperaceae), with 80 interactions

(12%); *Asystasia gangetica* (Acanthaceae), with 65 interactions (9.8%) and *Durio zibethinus* (Malvaceae) with 59 interactions (8.9%). At the network level, the number of interactions, connectance, nestedness were not affected by any environmental factors. However, the mean of pollinator specialization (d') from 10 study sites was negatively influenced by distance to the forest (GLM; $F_{1,8} = 7.320$, $p = 0.027$, Figure 4).

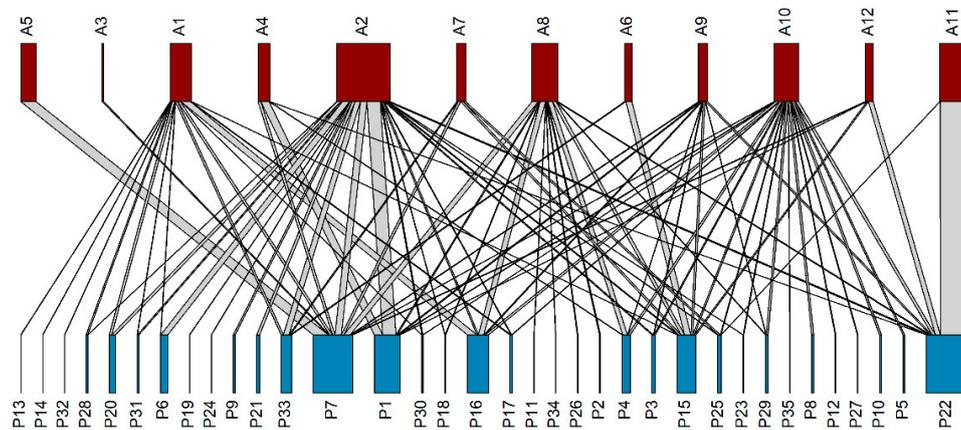


Figure 3. Pollination network of plants and stingless bees in mixed fruit orchards, Southern Thailand. The bars each represent a species and their abundance; meliponine taxa are listed along the upper bars (red), and plant taxa are listed along the lower bars (blue). Linkage width indicates the frequency of each interaction. All species names are listed in Appendix A Table A2.

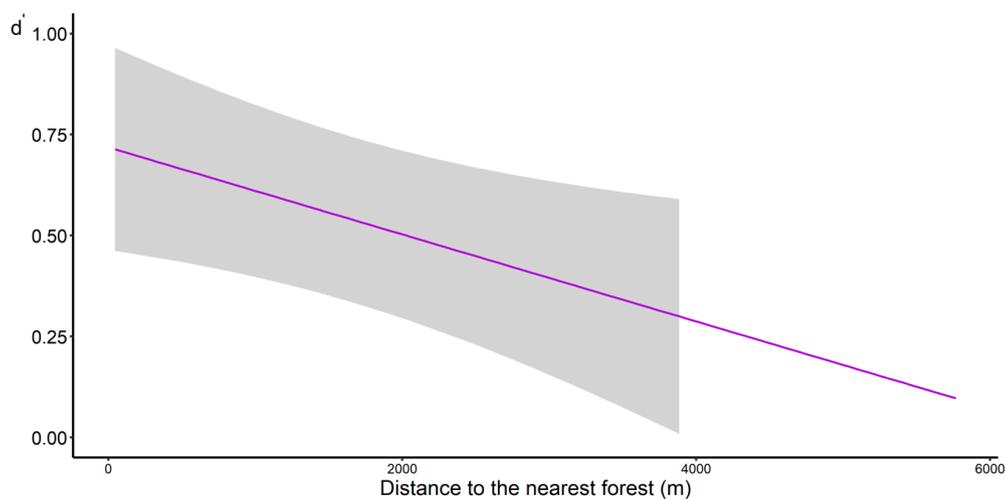


Figure 4. The specialization (d') pattern for pollination visitation network plotted against the distance to the nearest forest with 95% corresponding confidence intervals.

4. Discussion

In this study, we addressed the influence of local and landscape compositions on stingless bee communities and pollination network structure in the tropical orchards. On the local scale, there was a significant interaction between orchard size and floral richness merely affecting stingless bee richness. While, on the landscape scale, the proportion of forest cover at short distance and proximity to the forest noticeably affected both the richness and abundance of meliponine communities in mixed fruit orchards. On the other hand, there was a negative relationship between the proportion of agricultural and urbanized covers and stingless bee richness and abundance. Furthermore, the specialization decreased due to the increase in the distance to the nearest forest. We will discuss these findings in turn, ending with some thoughts on the implications for pollination conservation and agriculture.

4.1. Plant and Stingless Bee Communities

Our results highlight the roles of stingless bees visiting various plant species, especially for economic crop plants. In the present study, there were some crops, such as rambutan, durian, coconut trees, that produced a vast number of flowers (average = 4835, 32, and 77 flowers/tree, respectively), resulting in attracting various meliponine species to these crops. This is consistent with previous studies that have revealed several crops visited by diverse stingless bees [27], for example, rambutan [36], durian [66], longan [67], grapefruit [68], and coffee [19,69,70]. Although these flowering crops often provide important resources for many meliponine species, such crops support diverse and abundant pollinator communities in a short time due to their short duration of floral availability. Weeds also play an important role because of the longer duration of floral availability, i.e., green kyllinga and Chinese violet, which are introduced plants that were visited by at least five species of meliponines. These weeds provided key pollen resources as protein sources [71]. Moreover, certain crop species such as mango and jackfruit trees provided resins for stingless bees' nest construction in this study. Therefore, an orchard with diverse crops is likely more beneficial to bees than monocultural orchards, and stingless bee richness and abundance seem to depend heavily on the duration of floral availability provided by crops and weeds.

In the present study, there were more uncommon species of stingless bees observed in mixed fruit orchards since we observed along a gradient of landscape complexity. We found uncommon species (existing in 1–5 orchards) such as *Lepidotrigona satun*, *Lepidotrigona terminata*, *Lisotrigona cacciae*, *Tetragonilla atripes*, *Tetrigona apicalis*, *Tetrigona melanoleaca*, which were from wild or managed populations in orchards situated extremely near the forest (range: 45–530 m, Figure A1D). However, in previous studies, only common species of stingless bees have been found in tropical orchards in Thailand [18,36,66,72], as most studies have been conducted in monocultural orchards with few study sites. In agreement with previous studies [18,72], *Heterotrigona itama*, *Tetragonula pagdeni*, and *Tetragonula fuscobalteata* were the three most common species of stingless bees observed in our study. Two of these common species, i.e., *T. pagdeni*, and *T. fuscobalteata*, are urban-tolerant to anthropogenic landscapes as we perceived that a number of beekeepers successfully rear them in wooden boxes in cropland [32].

4.2. Response of Stingless Bee Communities to Environmental Effect at Habitat-Level

Our results highlight that meliponine species richness but not abundance was strongly influenced by habitat-level structure. In larger orchards, there was a positive correlation between floral richness and stingless bee richness, while for small and medium orchards, increasing floral richness rarely raised the bee richness. This was possibly because most large orchards were close to forest patches (average \pm SD = 844 \pm 1484 m to the nearest forest), while medium and small orchards were far from the forest patches (1860 \pm 2418 m). The distances to the nearest forest hence were considered as a confounding variable influencing stingless bee richness in the present study.

4.3. Response of Stingless Bee Communities to Environmental Effect at Landscape-Level

Our study revealed that a greater percent of forest covers around mixed fruit orchards increased both bee richness and abundance, resulting in high visitation rates for crops and other plants [25,67,73]. The landscape-level effect of forest within a 1 km radius increased stingless bee diversity, with visiting food resources in mixed crop orchards, as well as forest cover within 2 km, contributing to the rise of stingless bee abundance. Our findings are largely coincident with the few previous landscape-scale studies, indicating strong relationships between meliponines and forest cover [12,13,33]. Additionally, when the distance to the nearest forest increased, we found that both meliponine richness and abundance were reduced. Typically, natural habitats such as tropical forests are known as important reservoirs providing permanent feeding and nesting resources for wild bees, particularly for stingless bees, which primarily rely on large and hollow trees or ground cavities for nesting [28]. Thus, forest cover

surrounding an orchard within at least a 2 km radius is vital for pollination of meliponine-dependent crops and other wild plants.

We highlight that forest cover and distance to the nearest forest influenced stingless bee assemblage in mixed fruit orchards. This could be explained by bee foraging distances, which are strongly related to body size, i.e., larger bees forage farther than small ones [74]. For stingless bees, the maximum homing distances have been revealed, ranging from 712 m in the Australian stingless bee, *Tetragonula carbonaria* (small body size) [44] to 3.7 km in *Geniotrigona thoracica* (large body size) [45], yet their typical foraging distances were 333 m and 1.97 km, respectively. As a result, stingless bees with a small body size can forage typically up to 300 m from their nests, while large body stingless bees could travel further—up to 2 km. In addition to foraging distances, nesting sites influence how far stingless bees can forage into an orchard. In this study, we assumed that most observed meliponine species nest inside forest patches except for *Tetragonula pagdeni*, *Tetragonula fuscobalteata*, and *Tetragonula laeviceps* (hereafter as urban-tolerant species), which can nest in both natural and anthropogenic landscapes and are reared in wooden boxes for honey production by beekeepers in Thailand [32]. In this study, the three urban-tolerant species could be found in orchards situated at least 4 km apart from the nearest forest patch although they are categorized in small body size class. We suggest that these foragers were possibly from managed hives or their nests were nearby to our study orchards. For other stingless bee species excluding the three urban-tolerant species, we found that large meliponines (*Heterotrigona itama*, *Tetrigona apicalis*, *Geniotrigona thoracica*, *Lophotrigona canifrons*, *Tetrigona melanoleaca*) were observed in orchards far from the forest, ranging from 45 to 1465 m. While small stingless bees (*Lisotrigona cacciae*, *Lepidotrigona satun*, *Lepidotrigona terminata*, *Tetragonilla collina*, *Tetragonilla atripes*) were found in orchards closer to the forest, ranging from 0 to 533 m.

On the other hand, our results indicate that anthropogenic landscapes at short and broad spatial scales affected both richness and abundance of stingless bees. We highlight that broad landscape scales of both agricultural and urbanized areas with at least 10 km surrounding an orchard could decrease stingless bee richness, particularly uncommon species, while the proportion of agriculture at a 2 km radius but not urbanization influenced stingless bee abundance. Typically, increasing human land-use for agriculture and urbanization influences bee foraging dynamics, which are dependent on the availability of resources in the local habitat and its surrounding landscapes. Land-use change generally has affected bee assemblages [2,13,75–79]. For agricultural landscapes, different types of agriculture have differential effects on wild bees [6]. Since most of the agricultural areas in Southern Thailand are composed plantations of rubber and oil palm, nesting availability, i.e., hollow trees, seemed to be limited for stingless bees. Similarly, in urbanized landscapes, the proportion of impervious surfaces (e.g., soil covered by parking, roads, and buildings) is high in a city or town, and its negative effect on wild bee abundance and species richness were detected, particularly for uncommon species and ground-nesting bees [78]. Thus, it is possible that both anthropogenic landscapes provide limited nesting availability, i.e., hollow trees and ground cavities for stingless bees. This corresponds with our results that we could not observe uncommon meliponine species such as *Lepidotrigona satun* and *Tetragonilla atripes* in mixed fruit orchards surrounded by dominant agricultural and urbanized cover. In contrast with common species such as *Tetragonula* spp., they are responsible for the greater presence in orchards within anthropogenic landscapes. These species are more flexible in their habitat requirements and can largely utilize resource availabilities in deforested landscapes.

4.4. Pollination Network

We recorded that the specialization decreased with increasing distance to the nearest forest. Similar findings have been previously reported for both plant and bee species, whereby generalist species become more prevalent as forest cover reduced. [80]. Studies on the effects of landscape changes on plant–pollinator networks [80–82] have identified that the distance to the forest patch and forest cover can change the structure of visitation networks. This occurs because the distance to the forest patch creates environmental filters by selecting associated pollinator functional groups able to disperse to the

areas far from the forest and persist in altered landscapes [83]. These effects could be related to the loss of specialist pollinator species in mixed fruit orchards further from forest patches and/or to changes in diet breadth of pollinators in response to resource availability [39]. Although specialists seem to have been penalized by the loss of forest and no longer exist in these landscapes, generalist species may persist as the distance to the forest patch increases. In fact, floral-specialist pollinators often deliver the higher quantity of compatible pollen loads [84], while floral-generalist pollinators often carry mixed pollen from several species and transport larger amounts of heterospecific pollen grains, resulting in the prevention of stamens and causing seed set limitation in plants.

5. Implications for Conservation

Our findings in this study emphasize the landscape-level effects on meliponine diversity together with the importance of natural habitat to sustain pollinator communities, particularly stingless bees. We underline that habitat loss and fragmentation are some of the main causes of the ongoing global pollinator decline [85], creating more isolated areas and resulting in decline of both species richness and abundance of pollinators. Additionally, anthropogenic landscapes are likely to minimize pollinator movements, and it is urgently needed to understand how fragmentation, i.e., forest patches, affects meliponine assemblages in Southeast Asia. A previous study in the Neotropics revealed that larger urban forest fragments did not contain more meliponine species per unit area than smaller ones [86], so it is clear that even very small forest fragments can maintain stingless bee communities and should be conserved proficiently. Thus, tropical rainforest patches are key reservoirs for stingless bees, and other fauna as well, which support diverse pollinators for agricultural crops and other wild plants. Preservation of forests will protect the nesting and foraging habitat of many important pollinator taxa eventually.

We also highlight that floral richness at the habitat level has a positive effect on stingless bee richness, orchard management (i.e., growing/keeping attractive plant species, no herbicide application) is thus important to maintain stingless bees inside an orchard. For examples, keeping weed species in farms can provide the longer duration of floral availability, which supplement stingless bees' diet when natural habitats (tropical forests) lack floral resources and crop plants are not in their flowering time, and preserving vegetation at farm's corridors so that stingless bees can travel easily between orchards and forest patches. Importantly, planting more diverse crops in orchards is greater than monoculture as it can provide various floral resources all year round for pollinators.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/12/482/s1>, Table S1: General information about study sites, Table S2: Summary of generalized linear mixed model selection, Table S3: List of plants visited by stingless bees.

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Appendix A

Table A1. Ranked list of the 13 collected stingless bee species with abundance and percentage of the total during the study across 30 mixed fruit orchards, Southern Thailand.

No.	Meliponine Species		Abundance	Percent
1	<i>Heterotrigona</i>	<i>itama</i>	189	25.34
2	<i>Tetragonula</i>	<i>pagdeni</i>	94	12.60
3	<i>Tetrigona</i>	<i>apicalis</i>	87	11.66
4	<i>Geniotrigona</i>	<i>thoracica</i>	85	11.39
5	<i>Tetragonula</i>	<i>fuscobalteata</i>	81	10.86
6	<i>Lophotrigona</i>	<i>canifrons</i>	48	6.43
7	<i>Lepidotrigona</i>	<i>terminata</i>	37	4.96
8	<i>Tetragonula</i>	<i>laeviceps</i>	37	4.96
9	<i>Tetragonilla</i>	<i>collina</i>	31	4.16
10	<i>Tetrigona</i>	<i>melanoleuca</i>	27	3.62
11	<i>Tetragonilla</i>	<i>atripes</i>	24	3.22
12	<i>Lepidotrigona</i>	<i>satun</i>	4	0.54
13	<i>Lisotrigona</i>	<i>cacciae</i>	2	0.27

Table A2. Details of the meliponine and plant taxa used in the pollination network (Figure 3).

Label	Plant Species	Label	Meliponine Species
P1	<i>Kyllinga brevifolia</i> Rottb.	A1	<i>Geniotrigona thoracica</i>
P2	<i>Scoparia dulcis</i> L.	A2	<i>Heterotrigona itama</i>
P3	<i>Musa</i> spp.	A3	<i>Lepidotrigona satun</i>
P4	<i>Ocimum tenuiflorum</i> L.	A4	<i>Lepidotrigona terminata</i>
P5	<i>Artocarpus heterophyllus</i> Lam.	A5	<i>Lophotrigona canifrons</i>
P6	<i>Melastoma malabathricum</i> L.	A6	<i>Tetragonilla atripes</i>
P7	<i>Nephelium lappaceum</i> L.	A7	<i>Tetragonilla collina</i>
P8	<i>Artocarpus integer</i> (Thunb.) Merr.	A8	<i>Tetragonula fuscobalteata</i>
P9	<i>Bidens pilosa</i> L.	A9	<i>Tetragonula laeviceps</i>
P10	<i>Tagetes erecta</i> L.	A10	<i>Tetragonula pagdeni</i>
P11	<i>Etlingera elatior</i> (Jack) R.M. Sm.	A11	<i>Tetrigona apicalis</i>
P12	<i>Ruellia tuberosa</i> L.	A12	<i>Tetrigona melanoleuca</i>
P13	<i>Averrhoa bilimbi</i> L.		
P14	<i>Calopogonium mucunoides</i> Desv.		
P15	<i>Durio zibethinus</i> L.		
P16	<i>Asystasia gangetica</i> (L.) T. Anderson		
P17	<i>Elaeis guineensis</i> Jacq.		
P18	<i>Cleome rutidosperma</i> DC.		
P19	<i>Leucas aspera</i> (Willd.) Link		
P20	<i>Benincasa hispida</i> (Thunb.) Cogn.		
P21	<i>Solanum virginianum</i> L.		
P22	<i>Cocos nucifera</i> L.		
P23	<i>Mangifera foetida</i> Lour.		
P24	<i>Solanum ferox</i> L.		
P25	<i>Mimosa pudica</i> L.		
P26	<i>Xanthostemon chrysanthus</i> (F. Müll.) Benth.		
P27	<i>Hippeastrum johnsonii</i> (Gowen) Herb.		
P28	<i>Oxalis barrelieri</i> L.		
P29	<i>Garcinia atroviridis</i> Griff. ex T. Anderson		
P30	<i>Salacca magnifica</i> Moge		
P31	<i>Ageratum conyzoides</i> (L.) L.		
P32	<i>Chromolaena odorata</i> (L.) R.M. King & H. Rob.		
P33	<i>Urena lobata</i> L.		
P34	<i>Eulalia</i> sp.		
P35	<i>Ocimum basilicum</i> L.		

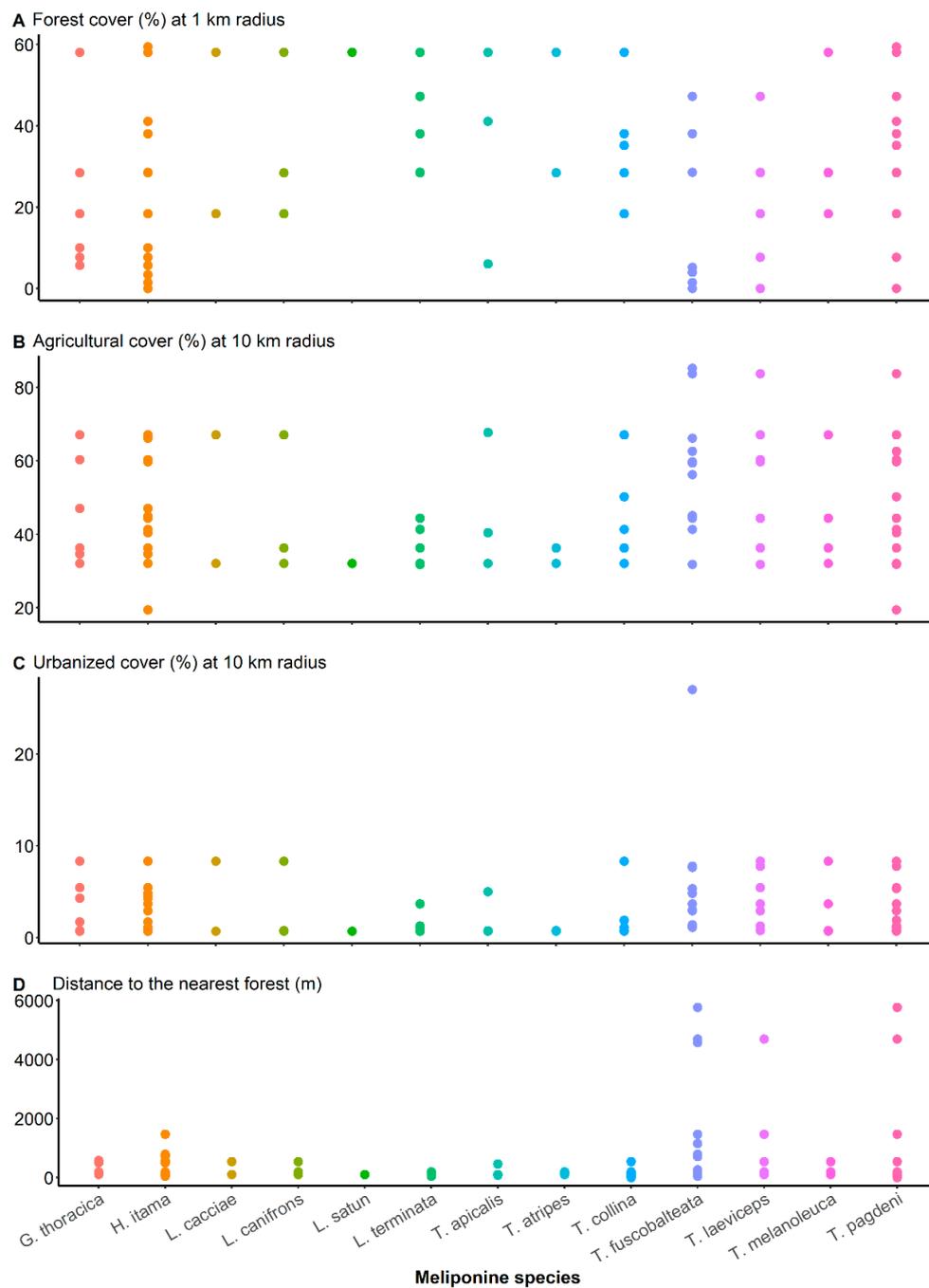


Figure A1. Effects of landscape-scale factors on stingless bee richness. Each dot represents each orchard where the meliponine species were collected. **(A)** Forest cover (%) at 1 km radius. **(B)** Agriculture cover (%) at 10 km radius. **(C)** Urbanized cover (%) at 10 km radius. **(D)** Distance to the nearest forest (m).

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