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

Kanuengnit Wayo 1, Tuanjit Sritongchuay 2, Bajaree Chuttong 3, Korrawat Attasopa 3 and Sara Bumrungsri 1,*

1 Department of Biology, Division of Biological Science, Faculty of Science, Prince of Songkla University, Hat Yai, Songkhla 90110, Thailand; kanuengnit025@gmail.com
2 Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla 666303, China; t.sritongchuay@gmail.com
3 Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand; bajaree.c@cmu.ac.th (B.C.); k.attasopa@gmail.com (K.A.)

* Correspondence: sara.b@psu.ac.th; Tel.: +66-7428-8537

Received: 31 October 2020; Accepted: 15 December 2020; Published: 17 December 2020

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 m$^2$ 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 Lisotrigna 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
Diversity 2020, 12, 482

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 corrr 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 Areaceae (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 fuscohaleata (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 acciae (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; Tetrigna 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.

| 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. |
|---------|---------------------------------------------------------------------------------------------------|
| Index   | 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 *** |
| (AIC = 460.8) | Intercept                                                      | 5.132    | 1.004 | 5.115   | <0.001 *** |
|          | 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 m\(^2\)), green line = medium sites (2000–5000 m\(^2\)), and light red line = large sites (5000–26,000 m\(^2\)). 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.

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* (Palmaceae), with 130 interactions (19.5%); *Nephelium lappaceum* (Sapindaceae), with 123 interactions (18.47%); *Kyllinga brevifolia* (Cyperaceae), with 123 interactions (18.47%); *Kyllinga brevifolia* (Cyperaceae), with 123 interactions (18.47%);
(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).

![Pollination network of plants and stingless bees in mixed fruit orchards, Southern Thailand.](image1)

**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.

![Pollination visitation network plotted against the distance to the nearest forest with 95% confidence intervals.](image2)

**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 ± SD = 844 ± 1484 m to the nearest forest), while medium and small orchards were far from the forest patches (1860 ± 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.

Author Contributions: Conceptualization, K.W., T.S., B.C. and S.B.; methodology, K.W., T.S., B.C. and S.B.; formal analysis, K.W. and T.S.; investigation, K.W., T.S., B.C., K.A. and S.B.; resources, K.W., T.S., B.C. and S.B.; data curation, K.W.; writing—original draft preparation, K.W.; writing—review and editing, T.S., B.C., K.A. and S.B.; visualization, K.W.; supervision, T.S., B.C. and S.B.; project administration, K.W., T.S., B.C. and S.B.; funding acquisition, K.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Thailand Agricultural Research Development Agency (ARDA) and Science Achievement Scholarship of Thailand (SAST).

Acknowledgments: Our special thanks are extended to all the mixed fruit orchardists in Songkhla, Phatthalung and Satun provinces who permitted us to conduct fieldwork in their lands. This project could not have been completed without the help and fieldwork assistance provided by Arthorn Wayo, Sittisak Wayo, and members of the Department of Biology, Division of Biological Science, Prince of Songkla University. We also thank the editors and reviewers whose suggestions improved this work.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Animal Ethics: Permission to work with the animals of this research project (project number 2562-01-073) was granted by Institutional Animal Care and Use Committee, Prince of Songkla University.
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   | Heterotrigona itama      | 189       | 25.34   |
| 2   | Tetragonula pagdeni      | 94        | 12.60   |
| 3   | Tetrigona apicalis       | 87        | 11.66   |
| 4   | Geniotrigona thoracica   | 85        | 11.39   |
| 5   | Tetragonula fuscosalteata| 81        | 10.86   |
| 6   | Lophotrigona canifrons   | 48        | 6.43    |
| 7   | Lepidotrigona terminata  | 37        | 4.96    |
| 8   | Tetragonula laeviceps    | 37        | 4.96    |
| 9   | Tetragonilla collina     | 31        | 4.16    |
| 10  | Tetrigona melanoleuca    | 27        | 3.62    |
| 11  | Tetragonilla atripes     | 24        | 3.22    |
| 12  | Lepidotrigona satun      | 4         | 0.54    |
| 13  | Lisotrigona cacciae      | 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    | Kylinga brevifolia Rottb. | A1    | Geniotrigona thoracica   |
| P2    | Scoparia dulcis L.    | A2    | Heterotrigona itama      |
| P3    | Musa spp.            | A3    | Lepidotrigona satun      |
| P4    | Ocimum lenuiflorum L. | A4    | Lepidotrigona terminata  |
| P5    | Artocarpus heterophyllus Lam. | A5   | Lophotrigona canifrons   |
| P6    | Melastoma malabatricum L. | A6   | Tetragonilla atripes     |
| P7    | Nepheleum lappacenum L. | A7    | Tetragonilla collina     |
| P8    | Artocarpus integer (Thunb.) Merr. | A8   | Tetragonula fuscosalteata|
| P9    | Bidens pilosa L.      | A9    | Tetragonula laeviceps    |
| P10   | Tagetes erecta L.     | A10   | Tetragonula pagdeni      |
| P11   | Etlingera elatior (Jack) R.M. Sm. | A11  | Tetrigona apicalis       |
| P12   | Ruellia tuberosa L.   | A12   | Tetrigona melanoleuca    |
| P13   | Averrhoa bilimbi L.    |       |                          |
| P14   | Calopogonium micuncoides Desv. |       |                          |
| P15   | Durio zibethinus L.    |       |                          |
| P16   | Asystasia gangetica (L.) T. Anderson |       |                          |
| P17   | Elaeis guineensis Jacq. |       |                          |
| P18   | Cleome rutidosperma DC. |       |                          |
| P19   | Leucas aspera (Wild.) Link |       |                          |
| P20   | Benincasa hispida (Thunb.) Cogn. |       |                          |
| P21   | Solanum virginianum L. |       |                          |
| P22   | Cocos nucifera L.      |       |                          |
| P23   | Mangifera foetida Lour. |       |                          |
| P24   | Solanum ferox L.       |       |                          |
| P25   | Mimosa pudica L.       |       |                          |
| P26   | Xanthostemon chrysanthus (F. Müll.) Benth. |       |                          |
| P27   | Hippastrum johnsonii (Gowen) Herb. |       |                          |
| P28   | Oxalis barleri L.      |       |                          |
| P29   | Garcinia atroviridis Griff. ex T. Anderson |       |                          |
| P30   | Salacia magnifica Mogea |       |                          |
| P31   | Ageratum conyzoides (L.) L. |       |                          |
| P32   | Chromolaena odorata (L.) R.M. King & H. Rob. |       |                          |
| P33   | Luren lobata L.        |       |                          |
| P34   | Eulalia sp.            |       |                          |
| P35   | Ocimum basilicum 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).

References
1. Ollerton, J.; Winfree, R.; Tarrant, S. How many flowering plants are pollinated by animals? *Oikos* 2011, 120, 321–326. [CrossRef]
2. Dalsgaard, B. Land-use and climate impacts on plant–pollinator interactions and pollination services. *Diversity* 2020, 12, 168. [CrossRef]
3. Rech, A.R.; Dalsgaard, B.; Sandel, B.; Sonne, J.; Svenning, J.C.; Holmes, N.; Ollerton, J. The macroecology of animal versus wind pollination: Ecological factors are more important than historical climate stability. *Plant Ecol. Divers.* 2016, 9, 253–262. [CrossRef]
4. Klein, A.M.; Vaissière, B.E.; Cane, J.H.; Steffan-Dewenter, I.; Cunningham, S.A.; Kremen, C.; Tscharntke, T. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 2007, 274, 303–313. [CrossRef]

5. Winfree, R.; Aguilar, R.; Vazquez, D.P.; Lebuhn, G.; Aizen, M.A. A meta-analysis of bees’ responses to anthropogenic disturbance. *Ecology* 2009, 90, 2068–2076. [CrossRef]

6. Winfree, R.; Bartomeus, I.; Cariveau, D.P. Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst.* 2011, 42, 1–22. [CrossRef]

7. Ollerton, J. Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annu. Rev. Ecol. Evol. Syst.* 2017, 48, 353–376. [CrossRef]

8. Roulston, T.H.; Goodell, K. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 2011, 56, 293–312. [CrossRef]

9. Vaudo, A.D.; Tooker, J.F.; Grozinger, C.M.; Patch, H.M. Bee nutrition and floral resource restoration. *Curr. Opin. Insect Sci.* 2015, 10, 133–141. [CrossRef]

10. Brosi, B.J.; Daily, G.C.; Ehrlich, P.R. Bee community shifts with landscape context in a tropical countryside. *Ecol. Appl.* 2007, 17, 418–430. [CrossRef]

11. Brosi, B.J.; Daily, G.C.; Shih, T.M.; Oviedo, F.; Durán, G. The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* 2008, 45, 773–783. [CrossRef]

12. Brosi, B.J. The complex responses of social stingless bees (Apidae: Meliponini) to tropical deforestation. *For. Ecol. Manag.* 2009, 258, 1830–1837. [CrossRef]

13. Lichtenberg, E.M.; Mendenhall, C.D.; Brosi, B. Foraging traits modulate stingless bee community disassembly under forest loss. *J. Anim. Ecol.* 2017, 86, 1404–1416. [CrossRef]

14. Miljanic, A.S.; Loy, X.; Gruenewald, D.L.; Dobbs, E.K.; Gottlieb, I.G.W.; Fletcher, R.J.; Brosi, B.J. Bee communities in forestry production landscapes: Interactive effects of local-level management and landscape context. *Landsc. Ecol.* 2018, 1–18. [CrossRef]

15. Liow, L.H.; Sodhi, N.S.; Elmqvist, T. Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *J. Appl. Ecol.* 2001, 38, 180–192. [CrossRef]

16. Samejima, H.; Marzuki, M.; Nagamitsu, T.; Nakasizuka, T. The effects of human disturbance on a stingless bee community in a tropical rainforest. *Biol. Conserv.* 2004, 120, 577–587. [CrossRef]

17. Stewart, A.B.; Sritongchuay, T.; Teartisup, P.; Kaewsomboon, S.; Bumrungsri, S. Habitat and landscape factors influence pollinators in a tropical megacity, Bangkok, Thailand. *PeerJ* 2018, 6, e5335. [CrossRef]

18. Tangtorwongsakul, P.; Warrit, N.; Gale, G.A. Effects of landscape cover and local habitat characteristics on visiting bees in tropical orchards. *Agric. For. Entomol.* 2018, 20, 28–40. [CrossRef]

19. Ricketts, T.H. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.* 2004, 18, 1262–1271. [CrossRef]

20. Boonithee, A.; Juntawong, N.; Pechhacker, H.; Hüttenger, E. Floral visits to select crops by four *Apis* species and *Trigona* sp. in Thailand. *Acta Hortic.* 1991, 288, 74–80. [CrossRef]

21. Kremen, C.; Williams, N.M.; Thorp, R.W. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA* 2002, 99, 16812–16816. [CrossRef]

22. Ricketts, T.H.; Daily, G.C.; Ehrlich, P.R.; Michener, C.D. Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci. USA* 2004, 101, 12579–12582. [CrossRef]

23. Kremen, C.; Williams, N.M.; Bugg, R.L.; Fay, J.P.; Thorp, R.W. The area requirements of an ecosystem service: Crop pollination by native bee communities in California. *Ecol. Lett.* 2004, 7, 1109–1119. [CrossRef]

24. Hülsmann, M.; von Wehrden, H.; Klein, A.M.; Leonhardt, S.D. Plant diversity and composition compensate for negative effects of urbanization on foraging bumble bees. *Apidologie* 2015, 46, 760–770. [CrossRef]

25. Garibaldi, L.A.; Steffan-Dewenter, I.; Kremen, C.; Morales, J.M.; Bonmarco, R.; Cunningham, S.A.; Carvalheiro, L.G.; Chaffo, N.P.; Dudenhofer, J.H.; Greenleaf, S.S.; et al. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 2011, 14, 1062–1072. [CrossRef]

26. Momose, K.; Yumoto, T.; Nagamitsu, T.; Kato, M.; Nagamasu, H.; Sakai, S.; Harrison, R.D.; Itoika, T.; Hamid, A.A.; Inoue, T. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. *J. Anim. Ecol.* 2011, 80, 1477–1501. [CrossRef]

27. Heard, T.A. The role of stingless bees in crop pollination. *Annu. Rev. Entomol.* 1999, 44, 183–206. [CrossRef]
Diversity 2020, 12, 482

28. Eltz, T.; Bruhl, C.A.; Imiyabir, Z.; Linsenmair, K.E. Nesting and nest trees of stingless bees (Apidae: Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, with implications for forest management. For. Ecol. Manag. 2003, 172, 301–313. [CrossRef]

29. Hubbell, S.P.; Johnson, L. Competition and nest spacing in a tropical stingless bee community. Ecology 1997, 58, 949–963. [CrossRef]

30. Inoue, T.; Nakamura, K.; Salmah, S.; Abbas, I. Population dynamics of animals in unpredictably-changing tropical environments. J. Biosci. 1993, 18, 425–455. [CrossRef]

31. Eltz, T.; Bruhl, C.A.; Van der Kaars, S.; Eduard Linsenmair, K. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia 2002, 131, 27–34. [CrossRef] [PubMed]

32. Chuttong, B.; Chanbang, Y.; Burgett, M. Meliponiculture—Stingless bee beekeeping in Thailand. Bee World 1997, 78, 101–108.

33. Brown, J.C.; Albrecht, C. The effect of tropical deforestation on stingless bees of the genus Melipona (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. J. Biogeogr. 2001, 28, 623–634. [CrossRef]

34. Round, P.D.; Gale, G.A.; Brockelman, W.Y. A comparison of bird communities in mixed fruit orchards and natural forest at Khao Luang, southern Thailand. Biodivers. Conserv. 2006, 15, 2873–2891. [CrossRef]

35. Bumrungsri, S.; Sripaoraya, E.; Chongsiri, T.; Sridith, K.; Racey, P.A. The pollination ecology of durian (Durio zibethinus, Bombaceae) in southern Thailand. J. Trop. Ecol. 2009, 25, 85–92. [CrossRef]

36. Weiner, C.N.; Werner, M.; Linsenmair, K.E.; Blüthgen, N. Land-use impacts on plant-pollinator networks: Interaction strength and specialization predict pollinator declines. Ecology 2014, 95, 466–474. [CrossRef]

37. Montoya, J.M.; Pimm, S.L.; Solé, R.V. Ecological networks and their fragility. Nature 2006, 442, 259–264. [CrossRef]

38. Kaiser-Bunbury, C.N.; Blüthgen, N. Integrating network ecology with applied conservation: A synthesis and guide to implementation. AoB Plants 2015, 7, 1–15. [CrossRef]

39. Weiner, C.N.; Werner, M.; Linsenmair, K.E.; Blüthgen, N. Land-use impacts on plant-pollinator networks: Interaction strength and specialization predict pollinator declines. Ecology 2014, 95, 466–474. [CrossRef]

40. Blüthgen, N.; Klein, A.M. Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. Basic Appl. Ecol. 2011, 12, 282–291. [CrossRef]

41. Kaluza, B.F.; Wallace, H.; Heard, T.A.; Klein, A.M.; Leonhardt, S.D. Urban gardens promote bee foraging over natural habitats and plantations. Ecol. Evol. 2016, 6, 1304–1316. [CrossRef] [PubMed]

42. Kaluza, B.F.; Wallace, H.M.; Heard, T.A.; Minden, V.; Klein, A.; Leonhardt, S.D. Social bees are fitter in more biodiverse environments. Sci. Rep. 2018, 8, 1–10. [CrossRef] [PubMed]

43. Land Development Department. GIS Data on Land Use Resources; Land Development Department: Bangkok, Thailand, 2019.

44. Smith, J.P.; Heard, T.A.; Beekman, M.; Gloag, R. Flight range of the Australian stingless bee Tetragonula carbonaria (Hymenoptera: Apidae). Austral Entomol. 2017, 56, 50–53. [CrossRef]

45. Wahala, S.; Huang, P. Foraging distance in the stingless bee Melipona emeryi (Hymenoptera: Apidae) in lowland dipterocarp forests in Sabah, Malaysia. J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. 1978, 21, 165–247.

46. Environmental Systems Research Institute (ESRI) ArcGIS Desktop Help 10.3 Geostatistical Analyst. 2014. Available online: https://desktop.arcgis.com/en/arcmap/10.3/get-started/quick-start-guides/arcgis-desktop-get-start-guide.htm (accessed on 30 August 2020).

47. Schwarz, H.F. The Indo-Malayan species of Trigona. Bull. Am. Museum Nat. Hist. 1939, 76, 83–141.

48. Sakagami, S.F. Tetragonula Stingless Bees of the Continental Asia and Sri Lanka (Hymenoptera, Apidae). J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. 1973, 30, 229–247.

49. Attasopa, K.; Bänziger, H.; Disayathanoowat, T.; Packer, L. A new species of Lepidotrigona (hymenoptera: Apidae) from Thailand with the description of males of L. flavibasis and L. doipaensis and comments on asymmetrical genitalia in bees. Zootaxa 2018, 4442, 63–82. [CrossRef]

50. Engel, M.S. A review of the Indo-Malayan meliponine genus Lisotrigona, with two new species (Hymenoptera: Apidae). Orient. Insects 2000, 34, 229–237. [CrossRef]

51. Dormann, C.F.; Fruend, J.; Gruber, B.; Beckett, S.; Devoto, M.; Felix, G.; Iriondo, J.; Opsahl, T.; Pinheiro, R.; Strauss, R.; et al. Package ‘Bipartite’: Visualizing Bipartite Networks and Calculating Some (Ecological) Indices. Available online: https://cran.r-project.org/web/packages/bipartite/bipartite.pdf (accessed on 30 August 2020).
52. R Core Team. *R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2020.*

53. Blüthgen, N.; Menzel, F.; Blüthgen, N. Measuring specialization in species interaction networks. *BMC Ecol.* 2006, 6, 1–12. [CrossRef]

54. Ripley, B.D.; Venables, W.N.; Bates, D.M.; Hornik, K.; Gebhardt, A.; Firth, D. Package ‘MASS’. Available online: http://www.statsox.ac.uk/pub/MASS4 (accessed on 30 August 2020).

55. Bates, D.; Maechler, M. Matrix: Sparse and Dense Matrix Classes and Methods. Available online: https://cran.r-project.org/package=Matrix (accessed on 30 August 2020).

56. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Linear Mixed-Effects Models using “Eigen” and S4. Available online: https://cran.r-project.org/package=lme4 (accessed on 30 August 2020).

57. Fox, J.; Weisberg, S.; Price, B.; Adler, D.; Bates, D.; Baud-Bovy, G.; Bolker, B.; Ellison, S.; Firth, D.; Friendly, M.; et al. Package ‘Car’. Available online: https://cran.r-project.org/package=car (accessed on 30 August 2020).

58. Sarkar, D.; Andrews, F.; Wright, K.; Klepeis, N.; Murrell, P. Package ‘Lattice’. Available online: http://lmdvr.r-forge.r-project.org (accessed on 30 August 2020).

59. O’Hara, R.B.; Kotze, D.J. Do not log-transform count data. *Methods Ecol. Evol.* 2010, 1, 118–122. [CrossRef]

60. Gittleman, J.L.; Kot, M. Adaptation: Statistics and a null model for estimating phylogenetic effects. *Syst. Zool.* 1990, 39, 227–241. [CrossRef]

61. Paradis, E.; Blomberg, S.; Bolker, B.; Brown, J.; Claramunt, S.; Claude, J.; Cuong, H.S.; Desper, R.; Didier, G.; Durand, B.; et al. Package ‘Ape’. Available online: http://ape-package.ird.fr/ (accessed on 10 December 2020).

62. Kuhn, M.; Jackson, S.; Cimentada, J. Corrr: Correlations in R. Available online: https://cran.r-project.org/package=corrr (accessed on 30 August 2020).

63. Blanche, K.R.; Ludwig, J.A.; Cunningham, S.A. Proximity to rainforest enhances pollination and fruit set in chiropterophilous durian. *J. Trop. Ecol.* 2018, 34, 41–52. [CrossRef]

64. Wayo, K.; Phankaew, C.; Stewart, A.B.; Bumrungsri, S. Bees are supplementary pollinators of self-compatible premontane subtropical forest. *J. Appl. Ecol.* 2006, 43, 1182–1187. [CrossRef]

65. Chaco, N.P.; Aizen, M.A. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J. Appl. Ecol.* 2006, 43, 18–27. [CrossRef]

66. Klein, A.M.; Steffan-Dewenter, I.; Tscharntke, T. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B Biol. Sci.* 2003, 270, 955–961. [CrossRef]

67. Blanche, K.R.; Ludwig, J.A.; Cunningham, S.A. Proximity to rainforest enhances pollination and fruit set in orchards. *J. Appl. Ecol.* 2006, 43, 1182–1187. [CrossRef]

68. Frias, B.E.D.; Barbosa, C.D.; Lourengo, A.P. Pollen nutrition in honey bees (*Apis mellifera*): Impact on adult health. *Apidologie* 2016, 47, 15–25. [CrossRef]

69. Hansen, K.; Sritongchhuay, T.; Bumrungsri, S.; Simmons, B.I.; Strange, N.; Dalsgaard, B. Landscape-level effects of forest on pollinators and fruit set of guava (*Psidium guajava*) in orchards across southern Thailand. *Diversity* 2020, 12, 259. [CrossRef]

70. Ricketts, T.H.; Regitz, J.; Steffan-Dewenter, I.; Cunningham, S.A.; Kremen, C.; Bogdanski, A.; Gemmill-Herren, B.; Greenleaf, S.S.; Klein, A.M.; Mayfield, M.M.; et al. Landscape effects on crop pollination services: Are there general patterns? *Ecol. Lett.* 2008, 11, 499–515. [CrossRef]

71. Greenleaf, S.S.; Williams, N.M.; Winfree, R.; Kremen, C. Bee foraging ranges and their relationship to body size. *Oecologia* 2007, 153, 589–596. [CrossRef]

72. Winfree, R.; Griswold, T.; Kremen, C. Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.* 2007, 21, 213–223. [CrossRef]

73. Gutierréz-Chacón, C.; Dormann, C.F.; Klein, A.M. Forest-edge associated bees benefit from the proportion of tropical forest regardless of its edge length. *Biol. Conserv.* 2018, 220, 149–160. [CrossRef]
77. Cariveau, D.P.; Winfree, R. Causes of variation in wild bee responses to anthropogenic drivers. *Curr. Opin. Insect Sci.* 2015, 10, 104–109. [CrossRef] [PubMed]

78. Geslin, B.; Le Féon, V.; Folschweiller, M.; Flacher, F.; Carmignac, D.; Motard, E.; Perret, S.; Dajoz, I. The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecol. Evol.* 2016, 6, 6599–6615. [CrossRef] [PubMed]

79. Wenzel, A.; Grass, I.; Belavadi, V.V.; Tscharntke, T. How urbanization is driving pollinator diversity and pollination—A systematic review. *Biol. Conserv.* 2020, 241, 108321. [CrossRef]

80. Ferreira, P.A.; Boscolo, D.; Lopes, L.E.; Carvalheiro, L.G.; Biesmeijer, J.C.; da Rocha, P.L.B.; Viana, B.F. Forest and connectivity loss simplify tropical pollination networks. *Oecologia* 2020, 192, 577–590. [CrossRef]

81. Sritongchuay, T.; Hughes, A.C.; Memmott, J.; Bumsrusri, S. Forest proximity and lowland mosaic increase robustness of tropical pollination networks in mixed fruit orchards. *Landscape Urban Plan.* 2019, 192, 103646. [CrossRef]

82. Sritongchuay, T.; Hughes, A.C.; Bumsrusri, S. The role of bats in pollination networks is influenced by landscape structure. *Glob. Ecol. Conserv.* 2019, 20, 1–13. [CrossRef]

83. Aizen, M.A.; Sabatino, M.; Tylianakis, J.M. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science* 2012, 335, 1486–1489. [CrossRef]

84. Ashman, T.; 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.; et al. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology* 2004, 85, 2408–2421. [CrossRef]

85. Potts, S.G.; Biesmeijer, J.C.; Kremen, C.; Neumann, P.; Schweiger, O.; Kunin, W.E. Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* 2010, 25, 345–353. [CrossRef] [PubMed]

86. Antonini, Y.; Martins, R.P.; Aguiar, L.M.; Loyola, R.D. Richness, composition and trophic niche of stingless bee assemblages in urban forest remnants. *Urban Ecosyst.* 2013, 16, 527–541. [CrossRef]

**Publisher’s Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).