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Forest proximity and lowland mosaic increase robustness of tropical pollination networks in mixed fruit orchards.

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Abstract

More than 30% of global crop plants rely on pollinators to set fruit or seed. While several studies have documented the negative effects of habitat degradation and distance from natural habitats on pollinator diversity in tropical areas, such studies have focused on single crops in particular areas without examining entire plant-pollinator communities. Here, we compared the plant-pollinator network structure between mixed fruit orchards that were near to (<1 km) and far from (>7 km) tropical forests and further investigated the effect of landscape composition in surrounding areas on plant-pollinator network structure. Our ten pairs of orchards were in Thailand and grew a range of tropical fruits pollinated by insects, birds and bats. The average number of visitor-flower interactions was higher at sites near the forest. Similarly, network robustness (the resistance of the network to losing species as a result of primary species removal) and interaction evenness (evenness of interactions among species) were higher at the sites closer to the forest. Robustness was strongly positively influenced by the proportion of lowland mosaic within a 1 km radius, while interaction evenness was positively affected by the proportion of urban area and montane mosaic within a 4 km radius of each site. Conservation of (semi-) natural habitats is therefore important for maintaining the diversity of wild pollinators and agricultural production.

Key words: forest proximity, interaction evenness, landscape composition, mixed fruit orchard, pollination network, robustness

1. Introduction

Landscape fragmentation, habitat loss and degradation resulting from human activity often have detrimental effects on biodiversity, often disrupting mutualistic and other species interactions (Ashworth, Aguilar, Galetto, & Aizen, 2004; Pimm & Raven, 2000). Decreasing habitat availability at the landscape level can isolate patches of suitable habitat, leading to reduced dispersal rates and changing the spatial distribution of resources (Holyoak, Leibold, & Holt, 2005). Additionally, landscape changes (particularly increased patch isolation) can significantly alter pollinator diversity, abundance, and movement patterns, thus directly impacting on the services they provide (Brosi & Briggs, 2013; Greenleaf & Kremen, 2006; Zurbuchen et al., 2010). Habitat degradation strongly influences communities of plants, their pollinators, and related services based on the increased spatial isolation of populations and decreased supplies of floral resources and nesting site availability (Viana et al., 2012). Moreover, landscape composition (i.e. agricultural and urban areas) may affect pollinator communities because of landscape functional heterogeneity in which different landcover types provide different resources and are identified based on differences on resource dependencies of species groups. The negative effects of isolation from natural habitat on the pollination ecology, species richness and abundance of pollinators of a single crop species have been intensively considered (Bailey et al., 2014; Chacoff & Aizen, 2006; Klein, Steffan-Dewenter, & Tscharntke, 2003; Kremen, Williams, & Thorp, 2002; Monasterolo, Musicante, Valladares, & Salvo, 2015; Ricketts, 2004; Zelaya, Chacoff, Aragón, & Blendinger, 2018). The impact of distance to the forest on pollination success generally varies according to plant species and depends on the main flower visitors of each plant species (Blanche, Ludwig, & Cunningham, 2006; Chacoff, Aizen, & Aschero, 2008; Sritongchuay, Kremen, & Bumrungsri, 2016).

Recent advances in the study of ecological networks, such as pollination, parasitoid, and seed dispersal networks, have improved our ability to describe species interactions and

explain the underlying structure, function, and stability of entire communities (Montoya, Pimm, & Solé, 2006). Network indices are especially useful in comparing pollination networks sampled from different environments. In particular, network robustness [a measure of resistance to secondary extinctions following successive single species removals from the web (Dunne, Williams, & Martinez, 2002; Memmott, Waser, & Price, 2004; Solé & Montoya, 2001)] has been used to understand the real threat of species loss on ecosystem services and functioning (Pocock, Evans, & Memmott, 2012). Although some network research has been conducted on how variation in habitat quality can result in the loss of interactions from tropical networks (e.g. Aizen, Sabatino, & Tylianakis, 2012; Tylianakis, Tscharntke, & Lewis, 2007), habitat loss can affect pollination networks in many ways, and more work is needed to reveal the depth of these impacts. In general, habitat destruction tends to decrease connectance and nestedness (Spiesman & Inouye, 2013) while increasing modularity (Spiesman & Inouye, 2013). However in this study we focus on robustness and evenness, because robustness and evenness are independent of species richness (Tylianakis et al., 2007). Species interactions can be lost very quickly, even under low levels of habitat destruction or disturbance (Fortuna & Bascompte, 2006; Keitt, 2009). Habitat loss not only disrupts pollination interaction networks, but it can also have strong impacts on network stability (Krause, Frank, Mason, Ulanowicz, & Taylor, 2003; McCann, Rasmussen, Umbanhowar, & Humphries, 2005; Pimm, 1979). The loss of more than half of the most-connected species can cause a sudden and rapid collapse of the entire network (Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch, 2010). Moreover, the loss of the most abundant pollinator species can also reduce plant reproductive function at the community level (Brosi & Briggs, 2013).

The vast majority of studies examining pollination networks have been conducted in temperate, arctic or high-altitude habitats. Furthermore, most pollination studies in tropical areas have focused on a small subset of the community in particular areas. Understanding the

consequences of forest proximity and landscape changes on the structure of plant-pollinator interaction networks at the community level in tropical regions should thus complement and extend our previous knowledge. In this paper, we explore the structure of the plant-pollinator networks in a tropical agricultural habitat and to ask how proximity to natural habitat and changes in landscape composition in surrounding areas affect both the structure and function of plant-pollinator networks. Our focal habitats are mixed fruit orchards and we include the non-crop plants growing in this habitat in our study, as these plants can sustain pollinators when the crops are not flowering. There are 3 objectives to our study: (1) To determine how forest proximity affects morphotype composition of pollinator communities in mixed fruit orchards. We predict that abundance and morphotype richness of pollinators will be higher in farms closer to the forest; (2) To use visitation networks to quantify how forest proximity influences pollination network structure, focusing on robustness (a measure of resistance to secondary extinctions following single species successively removed from the web (Dunne et al., 2002; Memmott et al., 2004; Solé & Montoya, 2001)) and interaction evenness (evenness of interaction among species), these being good estimators of changes in network structure (Tylianakis et al., 2007); (3) To investigate the effects of landscape composition in the area surrounding the orchards on pollination network structure (robustness and interaction evenness). We expect a higher robustness and interaction evenness in orchards closer to the forest and surrounded by higher proportion of structurally-rich landscape (i.e. lowland mosaic, montane mosaic), rather than structurally poor landscape (i.e. urban). Given that earlier studies indicate that pollinators with narrow habitat requirements and low mobility tend to be more sensitive to habitat loss than generalist species and those with larger home-ranges (Aizen et al., 2012; Biesmeijer, 2006; Gathmann & Tschardtke, 2002), differential responses to habitat degradation could promote shifts in interaction network characteristics, potentially affecting the robustness and interaction evenness of pollination networks.

2. Materials and method

2.1. Study sites

Mixed fruit orchards are common in Southeast Asian traditional villages, supplying products both for household use and local markets. Orchard patches typically range from 0.03 to 100 ha. Each orchard consists of planted fruit crops, selected native tree species (with high production values), herbs, and shrubs, resulting in a multi-storied assemblage. Some fruit orchards have operated for over 100 years. The main fruit trees typically include durian (*Durio zibethinus* L.), bitter beans (*Parkia speciosa* Hassk.), mangosteen (*Garcinia mangostana* L.), domestic jackfruit (*Artocarpus integer* (Thunb.) Merr.), rambutan (*Nephelium lappaceum* L.), banana (*Musa acuminata* Colla) and mango (*Mangifera indica* L.). Within this study, we selected pairs of orchards that were managed without pesticide or herbicide use.

The study took place from January 2012 to June 2013, in 10 pairs of mixed fruit orchards situated at varying distances from 10 tropical rainforests in southern Thailand (Nakhon Si Thammarat, Phattalung, Trang, Satun and Songkhla provinces, 6°20' to 8°20'N and 99°40' to 110°00'E - shown in appendix S1). The ten patches of forest ranged in area from 360 ha to 65,000 ha and in elevation from 230 m to 1090 m. Deforestation has been driven by agricultural conversion into rubber and oil palm plantations, and fruit orchards. We used 1:133,400 scale photographic imagery from Landsat Thematic Mapper data with a geographic information system (ARCGIS 10.2) to create a map of land use. Eight land-use classes were used, including 1) mangrove; 2) lowland evergreen forest (forest at elevations up to 750 m asl); 3) lower montane evergreen forest (forest in elevations above 750 m, up to 1500 m asl); 4) lowland mosaic (vegetated areas in elevations up to 750 m asl, typically consisting of tree gardens, agricultural fields, forest, regrowth or plantations); 5) montane mosaic (same as

lowland mosaic, but occurring at elevations above 750 m asl); 6) montane open (clearances and other open areas at elevations above 750 m asl); 7) urban; 8) large-scale closed canopy palm plantations. The land use classes were established following Miettinen, Shi, & Liew (2016) and we calculated the proportion of each landscape class fraction within a 50m, 100m, 250m, 500m, 1km, 2km, 4km, 6km, 8km, 10km, 15km, 20km, and 30km radius at each site (Appendix S2).

2.2. Sampling protocols

To determine the effect of distance to the forest on pollination networks, we compared mixed fruit orchards that were “near” to the forest (<1 km from the closest forest edge) to orchards that were “far” from the forest (>7 km from the closest forest edge). We chose these distances based on pollinator foraging distances; a stingless bee species (*Geniotrigona thoracica* (Smith, 1857)) can forage in disturbed areas a mean distance of 1.973 km from the forest (Wahala & Huang, 2013), whereas the mean foraging range is 1.7 to 6.9 km for nectarivorous *Rousettus* bats (Bonaccorso, Winkelmann, Todd, & Miles, 2014) and 6 km for the Cave nectar bat, *Eonycteris spelaea* (Dobson) (Acharya, Racey, Sotthibandhu, & Bumrungsri, 2015).

For each of the ten forest fragments, a pair of orchards near and far from the forest was selected using the following criteria: 1) mixed fruit orchards with more than 10 cultivated fruit species (all contained *Parkia*, *Durian*, *Rambutan*, and *Mangosteen* trees); 2) they had been managed as mixed fruit orchards for over 10 years, ensuring that all fruit plants were well-established and producing flowers; 3) pairs of orchards were spaced at least 10 km apart (this distance ensured that all pairs were independent of one another, as it exceeds the reported foraging distances of the pollinator species in our study area). The distance from each study orchard to caves where bats may roost ranged from 0.7 to 29 km (data on bat roosting caves was from (Bumrungsri, 1997); <http://www.thailandcaves.shepton.org.uk>).

2.2.1. Sampling the plant communities

In each study orchard, we marked a 50 x 150 m plot in which we set up 5 parallel 150-m transects at 10 m intervals. To determine plants species abundance, we surveyed the plant communities from January 2012 to June 2013 by recording every individual of all flowering species in the study orchards every two weeks. We counted the number of floral units (either individual flowers or capitula) for each plant. We determined the mean number of flowers in a capitulum from 20 capitula. We estimated the number of individuals of each plant species in each orchard by multiplying plant density (determined from the marked plot) by the total area of the orchard. Additionally, we calculated the total number of flowers by multiplying the number of individual plants by the mean number of open flowers for each plant. Phenological observations were conducted by recording the first flowering date, 10% flowering date, (when flowers included 10% of observed plants), and 50% flowering date (when flowers included 50% of observed plants). We identified the plant species that were visited by a potential pollinator and then built the interaction networks. When possible, plants were identified to species or genus in the field, and difficult-to-identify taxa were compared to the reference collection in the Prince of Songkla University Herbarium. Rarefied plant richness was calculated by using the rarefy function of the vegan package in R (Oksanen, 2013).

2.2.2. Sampling the flower-visitors

To identify flower visitors and understand how the network of interactions is affected by landscape and distance to the forest, flower visitor observations were conducted monthly from April 2012 to June 2013. This was done in fair weather (i.e. sunny and without rain, with the temperature ranging from 31° C to 38° C). In each orchard, we observed flower visitors while walking the five 150 m transects described above. Sampling took place between 0800 to 1100 and 1500 to 1830, recording both visitor frequency and visitor richness. We only collected

data on insects when they came into contact with the reproductive parts of the flower. For each plant species, we observed pollinators focally facing each of the four cardinal directions of the tree (north, south, east, and west) using 15-min observation sessions.

Insects were collected with a long-handled net up to a height of 4 m and transferred to a euthanizing bottle containing ethyl-acetate. Insects were identified from field guides or by a professional taxonomist (see Acknowledgements). Recorded taxa are listed in appendix S4. We use the term morphotypes to describe pollinator taxa. Although identifying insects to species would have been ideal, the difficulty of identifying pollinators to the species level under field conditions prompted us to identify insects to the morphotype level and this is an accepted approach recommended by Kremen et al., (2002). For nocturnal pollinators, such as bats and moths, we placed camera traps (Moultrie game spy d55-IRXT infrared flash camera) c. 5-10 m from the inflorescence of nocturnal flowering trees (three inflorescences per tree) set to record 15-second videos and still pictures for 15 minutes every hour in all twenty plots. Because it is difficult to identify bats and moths to species from camera traps, we also used mist-nets and sweep nets for specimen collection at each site to identify the local species of bats and moths, allowing us to confirm our video identifications. The mist nets were placed close to the flowers of durian and visiting bats were identified to species following (Francis, 2008), mainly based on external morphology and size.

2.3. *Constructing the flower-visitation networks*

The overall pollination network structures across all seasons were visualized using the bipartite package implemented in R. For each network, we calculated connectance, interaction evenness based on Tylianakis et al. (2007)'s method, and robustness (Memmott et al. 2004). To generate secondary extinction curves, we randomly removed plant and pollinator morphotype from the network without replacement, where a species was considered to be

extinct if it was left without plant hosts or animal pollinators, similar to Dunne et al. (2002) and Memmott et al. (2004).

2.4. Statistical analyses

All analyses were conducted in R 3.4.4 (R Core Team, 2018). Firstly, a probability distribution that best fits the response variables was identified. Generalized linear mixed models (GLMMs) were conducted with the nlme package. We verified that assumptions of normality and heteroscedasticity were met and that Poisson models were not overdispersed. Distance to the forest was included as an explanatory variable. Pairs of study sites (orchards near and far from the same forest patch) were included as a random effect, as every pair of study sites does not show a significant effect on the average of response variables. A normal distribution and a log link function were used to determine the effect of distance to the forest on plant rarefied richness, number of plant-animal interactions, and connectance. The Poisson distribution and log link function were used for following variables: plant abundance, pollinator abundance (number of individuals per hour) and pollinator richness, stingless bee and nocturnal insect frequency (as all response variables were counts).

To test the effect of distance to the forest and landscape structure on pollination network structure, the response variables (robustness and evenness) were examined using a GLMM with a normal distribution and a log link. Distance to the forest and the proportion of each land use class surrounding each study site at 13 different scales (50m, 100m, 250m, 500m, 1km, 2km, 4km, 6km, 8km, 10km, 15km, 20km, and 30km) were included as explanatory variables. Pairs of study sites (orchards near and far from the same forest patch) were included as a random effect. The interactions between explanatory variables that contribute at least marginally to the model ($P < 0.10$) were also added. To determine the best model, the GLMM with lowest Akaike's information criterion (AIC) was selected (Table S3).

We also used generalized linear mixed models (GLMMs) to test the effect number of plant species in each study site on evenness. Dissimilarity in plant and pollinator composition between each pair was calculated with the Bray-Curtis dissimilarity index (Bray & Curtis, 1957) with the `vegdist` function of the `vegan` R-package (Oksanen, 2013). The Bray-Curtis dissimilarity is between 0 and 1, where 0 means the two sites share all their species, and 1 means the two sites do not share any species.

We used structural equation modelling (SEM) to investigate the relationships between environmental variables (land use and forest proximity) and pollinator community composition (richness and abundance) and prevalence on pollination network structure (robustness and interaction evenness). SEM can be used for identifying direct and indirect correlations between variables within a defined mechanistic path that incorporates logically-plausible causal links. Based on the results of the previous sections, we used distance to the forest, percent lowland mosaic and urban areas as indicators of land use and pollinator abundance and richness as indicators of pollinator community composition on pollination network. We constructed SEMs, considering different causal paths among the response variables. First, we considered links from environmental variables to pollinator community composition affecting the pollination network structure. Second, we considered environmental variables directly affecting both pollinator community composition and pollination network structure. The SEMs were evaluated through Chi-square tests, comparative fit index (CFI), and the Root Mean Square Error of Approximation (RMSEA) following Sonne et al. (2016). The Chi-square value indicates the divergence between the sample and the fitted structures in the data; a non-significant result ($P > 0.05$) indicates a good model fit. The CFI compares the Chi-square of the model with the Chi-square value of an independent model assuming no correlation among all variables while accounting for sample size. With a range from 0 to 1, we accepted models with CFIs > 0.09 . Lastly, the RMSA was considered because of its sensitivity to the number of

estimated parameters in the model. Here, $RMSEA < 0.07$ were used as an indication of a good model fit. By stepwise refitting, we simplified the SEMs, removing non-significant links conditional on the model fit, i.e. assessed by the Chi-square test, CFI, and RMSEA, being satisfied. To fit the structural equations, we used the “sem” function in the R package Lavaan (Rosseel, 2012).

3. Results

Overall, we recorded 95,871 plant-animal interactions among 61 species of plant with 316 morphotypes of insect, 3 species of bird and 7 species of bat. Insects made up 98.9% of visits, birds 0.3% of visits and bats 0.8% of visits.

3.1. *The plant community*

The 20 orchards contained 31 species of crop plants and 30 species of non-crop plants; the number of plant species showed no consistent patterns in the two types of orchards. There was no significant difference in the number of rarefied plant species in orchards to forest (mean $\pm$ SD: 35.141 ± 3.495 species) and orchards far from forest (32.386 ± 3.887 species) (GLMM; $F_{1,9} = 0.855$ $P = 0.379$) or in the abundance of plants in orchards near close to forest (62.6 ± 7.644) and orchards far to forest (57.2 ± 7.222) (GLMM; $F_{1,9} = 0.513$ $P = 0.492$). The Bray-Curtis dissimilarity was high for plant species composition (0.762 ± 0.108). Thirty-one plant species (50.8% of all plant species) flowered year-round, 27 species (44.3%) flowered between March and May, and three species flowered between August and October. Both types of orchards were dominated by a few common plant species, namely *Musa sapientum* L. (Musaceae), *Nephelium lappaceum* L. (Sapindaceae), *Azadirachta excelsa* (Jack) Jacobs (Meliaceae), and *Sandoricum koetjape* Merr. (Meliaceae). *Musa sapientum* L. was also the species most commonly visited by nocturnal pollinators, including nectar and fruit bats.

3.2. *The flower-visiting animal community*

The morphotype richness of pollinators in the orchards to forest (113.3 ± 22.24) was significantly higher than in the orchards far from the forest (67.9 ± 18.25) (GLMM; $F_{1,9} = 3.457$ $P < 0.001$) (Figure 1A). Total pollinator abundance (number of individuals per hour) in orchards to forest (57.834 ± 2.174) was also significantly higher than in the orchards far from the forest (43.807 ± 1.863) (GLMM; $F_{1,9} = 15.615$ $P = 0.033$) (Figure 1B). The Bray-Curtis dissimilarity was moderate in animal visitor morphotype composition (0.495 ± 0.118). Hymenoptera were common visitors to both orchards near and far from the forest; within this order, thirty-two morphotypes belonged to the Apoidea. Bees were the most abundant flower visitors in both orchard types (Figure 2), accounting for 22% of all individuals observed. Stingless bees were significantly more abundant in sites near to forest (1660.8 ± 370.26 vs 987.7 ± 95.73 , Figure 2) (GLMM; $F_{1,9} = 96.865$ $P < 0.001$). The visit frequency of bees correlated with plant phenology. The peak of bee visit frequency was from March to June, when most plants were flowering (Figure 3A).

Three species of bird (*Cinnyris jugularis* (Linnaeus), *Anthreptes malacensis* (Scopoli), *Arachnothera longirostra* (Latham)) interacted with six plant species (*Musa sapientum* L., *Cassia siamea* Lamk., *Barringtonia acutangula* (L.) Gaerth., *Syzygium malaccense* Merr & Perry, *Etlingera elatior* (Jack.) R.M. Smith., *Cocos nucifera* L.). Bird visits contributed 0.3% of all animal visits, and percentages were similar at orchards both near and far from forests. During the nocturnal observations, we recorded thirty-two pollinator morphotypes (1.5 % of all visits) visiting five species of plant (*Ceiba pentandra* (L.) Gaertn., *Durio zibethinus* L., *Musa acuminata* Colla, *Oroxylum indicum* (L.) Kurz, *Parkia speciose* Hassk.). Seven species of bat (Pteropodidae, *Eonycteris spelaea* (Dobson), *Macroglossus minimus* (Geoffroy), *M. sobrinus* (Andersen)), *Cynopterus brachyotis* (Muller), *C. horsfieldi* (Gray), *C. sphinx* (Vahl) and *Rousettus leschenaultii* (Desmarest)) visited flowers within the study orchards. Thirteen

morphotypes in order Coleoptera, four morphotypes in order Lepidoptera, and *Apis dorsata* (Fabricius) were observed during the night (Appendix S4). The frequency of nocturnal insects in the orchards near to forest (91.6 ± 39.19) was similar to the orchards far from the forest (103.5 ± 24.61) (GLMM; $F_{1,9} = 0.661$ $P = 0.4371$).

3.3 Response of pollination networks to environmental effects

The bipartite networks are given in Figure 4. The number of plant-animal interactions in the orchards to forest (3665.0 ± 815.747) was significantly higher than in the orchards far from the forest (2569.9 ± 578.036) (GLMM; $F_{1,9} = 19.2542$ $P = 0.0018$) (Figure 1 C). Connectance in orchards near to forest (0.116 ± 0.024) was also significantly higher than in the orchards far from forest (0.097 ± 0.013) (GLMM; $F_{1,9} = 5.741$ $P = 0.040$) (Figure 1 D). Network robustness was negatively influenced by distance to the forest (GLMM; $F_{1,7} = 4.55$ $P = 0.040$) and positively affected by the proportion of lowland mosaic within a 1 km radius around each site (GLMM; $F_{1,7} = 75.69$ $P = 0.0001$) (Figure 5 A). When examining robustness, random removal of pollinators led to a decline of plant species after 80% - 90% of all pollinator morphotypes had been removed.

The GLMM analysis shows that interaction evenness was positively affected by proportion of montane mosaic (GLMM; $F_{1,6} = 8.900$ $P = 0.0245$) within a 4 km radius of each site (Figure 5 B) and there was a significant interaction between distance to the forest and proportion of urban area (GLMM; $F_{1,6} = 11.120$ $P = 0.015$). The interaction evenness of orchards near to forest was significantly affected by the proportion of urban area ($t = 6.423$, $P < 0.001$), whereas the proportion of urban areas surrounding orchards far from forest did not have an effect on interaction evenness (Figure 5 C, Table 1). There was a significant positive relationship between the number of plant species in the pollination network and interaction evenness (GLMM; $F_{1,9} = 5.198$ $P = 0.049$, Figure S5). Within the orchards near the forest,

more than half (55.56%) of plants were generalists, whereas, from the orchards far from forest, fewer plant species were generalists (21.43%) (categorized here as species associated with more than one pollinator morphotype).

For the SEM, we found a direct positive effect from the proportion of urban area (standardized coefficient; $\beta = 0.44$, figure 6) and a direct negative effect from distance to the forest ($\beta = -0.45$) on interaction evenness. We found a direct negative effect from distance to the forest ($\beta = -0.03$) and a positive effect from the proportion of lowland mosaic ($\beta = 0.42$) on robustness. A positive association was found between pollinator abundance and robustness ($\beta = 0.76$). We found that pollinator abundance was negatively associated with distance to the forest ($\beta = -1.26$) and proportion of urban area ($\beta = -0.18$), and positively associated with the proportion of lowland mosaic ($\beta = 0.99$). There was a positive correlation between pollinator richness and abundance ($r = 0.760$, $P = 0.007$). All correlations between variables are reported in the supplementary material (Table S6).

4. Discussion

In this study, we explored the influence of distance to the forest and the surrounding landscape composition on pollinator communities and pollination network structure in the tropics. Proximity to the forest affects the morphotype richness of pollinator communities in mixed fruit orchards, corresponding with our previous study that suggested pollinator function (i.e. the reproductive success of insect-pollinated plants) decreases as distance to the forest increases (Sritongchuay et al., 2016). Additionally, there was a negative relationship between distance to the forest and both network robustness and interaction evenness. Thus, as the distance to the forest increases, these two important network parameters decrease.

4.1. Plant and Pollinator communities

In our study, about 50% of plant species are not domesticated crops and flower year-round, for instance, *Cassia siamea* Lamk., *Alpinia galanga* (L.) Willd., *Musa acuminata* Colla, and *Oroxylum indicum* (L.) Kurz (figure 3). Continuous flowering in non-crop plants ensures efficient pollination of plants differing in flower phenology by providing inter-season continuity of food resources, thereby supporting pollinator diversity and abundance in mixed fruit orchards (Mayfield & Belaradi, 2008; Ponisio et al., 2014). In contrast to mixed fruit orchards, crop monocultures reduce the overall habitat resources for pollinators, by failing to provide resources when crop plants are not flowering. With few species of floral resources in intensively managed fields, the temporal availability of pollen and nectar from few crops mean that the benefits to pollinator are limited to the duration of crop flowering (Blitzer et al., 2012).

Hymenoptera (Apoidea), especially stingless bees, were the most abundant flower visitors. Bees are well known as important pollinators of both crop and wild plant species (Garibaldi et al., 2013; Garibaldi, Requier, Rollin, & Andersson, 2017; Klein et al., 2007; Ollerton, Winfree, & Tarrant, 2011). Bees showed higher visitation frequencies at orchards close to the forest compared with orchards far from the forest; this has previously been related to bee pollination success in agroforestry systems in Thailand (Sritongchuay et al., 2016) and Indonesia (Klein et al., 2003). *Apis cerana* (Fabricius) bees observed in the study were from both wild and managed populations. However, large-scale beekeeping operations utilizing *A. cerana* can be found in the northern and eastern parts of Thailand, where large longan, lychee, and coffee monocultures have been cultivated, but beekeeping is still rare in southern Thailand (Chantawannakul, 2018). The reason for higher visitation frequencies at orchards close to the forest may be due to the availability of nest cavities in big trees near forests (Brown & Albrecht, 2001; Eltz, Brühl, van der Kaars, & Linsenmair, 2002) and constraints on the dispersal capacity of pollinators, as service provision is likely to be related to resources important for bee survival.

Moths (Lepidoptera) and beetles (Coleoptera) are the major nocturnal insect pollinators, and moths are important pollinators in tropical regions. In several studies, moths were considered to be second in importance only to bees, in terms of pollination provision (Johnson et al., 2017; Ollerton, 2017). Forest proximity did not significantly influence the visitation rates of nocturnal insects. Since moths and beetles were the most frequent nocturnal visitors, it seems likely that their abundance might be more sensitive to additional factors. For instance, previous studies have demonstrated that moths were affected by artificial night light (Macgregor, Pocock, Fox, & Evans, 2015).

Although bat and bird visitation is not as high as insect visitation, from our study, we found that five plant species (*Ceiba pentandra* (L.) Gaertn., *Durio zibethinus* L., *Musa acuminata* Colla, *Oroxylum indicum* (L.) Kurz, *Parkia speciose* Hassk.) depend on bat pollinators. Seven species of bat (Pteropodidae, *Eonycteris spelaea* (Dobson), *Macroglossus minimus* (Geoffroy), *M. sobrinus* (Andersen)), *Cynopterus brachyotis* (Muller), *C. horsfieldi* (Gray), *C. sphinx* (Vahl) and *Rousettus leschenaultii* (Desmarest)) played important roles in our pollination networks. Previous studies have also found that both bat abundance and network strength were negatively affected by distance to the nearest cave and to the forest, habitats that are important sources for bat pollinators (Sritongchuay & Bumrungsri, 2016). In addition, we found that many plant species require bird pollinators, as birds are key pollinators of several plant families, especially plants in the family Zingiberaceae (Sakai, Kawakita, Ooi, & Inoue, 2013).

4.2. The response of pollination networks to environmental effects

Network robustness was higher in orchard networks closer to forest and positively influenced by the proportion of lowland mosaic, which includes tree gardens, agricultural fields, plantations, and forests. Our results agree with our prediction that the pollination

network in orchards close to the forest in heterogeneous landscapes support higher interaction robustness. This may be because both plants and insects in orchards near forest are more diverse, providing higher redundancy and resilience to the loss of small numbers of pollinators. It has been suggested that robustness and evenness may be associated with pollination network stability (Martin, Feit, Requier, Friberg, & Jonsson, 2019; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010).

We found that interaction evenness increased with the proportion of montane mosaic in the surrounding area which typically consists of forest above 750m asl. This finding is consistent with our prediction, and, in host-parasitoid food webs interactions, evenness has been found to decline with habitat disturbance (Albrecht, Duelli, Schmid, & Müller, 2007; Tylianakis et al., 2007). Moreover, higher interaction evenness could be associated with the overall sustainability of plant-pollinator communities (Tylianakis et al., 2010). We also found a positive correlation between interaction evenness and the proportion of urban areas. Similar findings have been reported for pollinators in experimental plant communities in urban and agricultural areas, where interaction evenness was higher in urban compared to agricultural areas (Geslin, Gauzens, Thébault, & Dajoz, 2013; Theodorou et al., 2017). The positive correlation between interaction evenness and proportion of urban areas could be a consequence of a predominance of generalist pollinators in orchards in urban areas. Previous studies suggest that in urban areas, the same pollinators may become less effective due to the augmented transfer of heterospecific pollen (Baldock et al., 2015; Claire Kremen et al., 2007; Leong, Kremen, & Roderick, 2014). We also found that interaction evenness increased with increasing plant species richness in pollination networks and the number of plant species relates to the proportion of urban areas. Similarly, Tylianakis et al. (2007) showed that interaction evenness was positively related to the diversity and abundance of species from lower trophic levels.

4.3. Agricultural and conservation implications

Our findings demonstrate how plant-pollinator interactions within mixed fruit orchards change as they become isolated. Moreover, our study provides evidence that increasing the distance to pollinator sources reduces the morphotype richness of pollinators and decreases robustness and interaction evenness. Because flower visitors are crucial for the pollination of many crops, our findings have important implications for conserving pollination services and can contribute to landscape design directives, which may directly affect the productivity of many agricultural crops. Several studies have previously shown that pollination services are greater in crops adjoining forest patches or other seminatural habitats (Bailey et al., 2014; Geslin et al., 2016; Hass et al., 2018; Joshi, Otieno, Rajotte, Fleischer, & Biddinger, 2016; Potts et al., 2016; Sritongchuay et al., 2016; Tibesigwa, Siikamäki, Lokina, & Alvsilver, 2019). In addition to forests, caves also play an important role as pollinator sources in some countries. Previous studies in these habitats found that the visitation rate of bats and reproductive success of durian was substantially increased by greater proximity to caves (Sritongchuay & Bumrungsri, 2016; Sritongchuay et al., 2016). We found evidence that local vegetation (species richness) also strongly influenced the structure of pollination networks (interaction evenness).

4.4. Limitations to research

Our approach has two limitations which should be addressed in future studies. First, the lack of identification to the species level for insects must be viewed with caution concerning the generalisation of our conclusions. We do not know whether changes in network structure along with landscape gradient are caused by changes in species composition within flower visitor morphotypes or changes in species foraging behaviour of the morphotypes. The issue is particularly apparent in groups such as stingless bees, which we can only identify to morphotype due to the large number of similar species. Studying pollination networks at the species level along landscape gradients should improve our understanding of these systems. Moreover, molecular barcoding can provide a possible method for species identification, but

may be challenging due to both lack of reference material and the ability to capture and remove a leg from rapidly moving pollinators without disrupting their activity. Second, the possibility of network rewiring should be incorporated into the robustness assessment (Kaiser-Bunbury et al., 2010). When species lose all its partners, a species does not necessarily become extinct. In some circumstances, it may reconnect (rewire) to other species. Rewiring allows species to increase their tolerance to perturbations in the systems and increases the robustness of networks. Although our robustness approach did not include the option of rewiring, the relative robustness of the two types of orchard remains informative for comparison between conditions.

In conclusion, our study suggests that plant-pollinator interactions within mixed fruit orchards change with distance from natural habitats and with landscape structure at a proximal scale. Our results show a similar pattern to plant-pollinator networks in an Afrotropical landscape where the local landscape structure supports flower-visitor networks (Hagen & Kraemer, 2010), and in Argentina where the proximity to habitat influences the number of links in pollination networks (Sabatino, Maceira, & Aizen, 2010). Thus, the improved management of natural habitats in orchards can promote higher ecosystem function. This finding enhances our understanding of how overall pollination networks become less stable, thereby decreasing ecosystem functions as a result of structural landscape changes. Sustainable conservation policies and practices can be adopted to ensure the preservation of natural habitats within tropical landscapes to maintain the provision of pollination services in tropical fruit orchards. Our results show that preserving forest remnants and restoring natural landscape will likely facilitate greater nesting and roosting sites for pollinators and provide superior, more consistent floral resources throughout the entire year.

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657 Table 1 Results of generalized linear mixed models for the pollination network structure in
 658 mixed fruit orchards in southern Thailand. For robustness, the explanatory variables are the
 659 distance to the forest edge, the proportion of plantation, and proportion of lowland mosaic
 660 within a 1 km radius. For evenness, the explanatory variables are the distance to the forest edge,
 661 the proportion of urban area and montane mosaic within a 4 km radius.

Indice	Explanatory fixed variable	Estimate	SE	t-value	P-value
Robustness	Intercept	0.7852	0.0169	46.2642	<0.001***
(AIC = -46.939)	Distance to forest edge (Far)	-0.0669	0.0102	-6.5555	0.0003 **
	Plantation	-0.0003	0.0002	-1.6525	0.1424
	Low.mosaic (1 km)	0.0009	0.0002	4.8928	0.0018**
Evenness	Intercept	0.9127	0.0130	70.32	<0.001***
(AIC = -39.476)	Distance to forest edge (Far)	-0.0262	0.0153	-1.7058	0.1389
	Urban (4 km)	0.0541	0.0196	2.7569	0.0330*
	Montane mosaic	0.0018	0.0007	2.6089	0.0402*
	Distance to forest edge × Urban (4 km)	-0.0522	0.0245	-2.1315	0.0402*

662

663

Figure legend

Figure 1 (A) The pollinator richness and (B) pollinator abundance (C) number of links in networks and (D) connectance from mixed fruit orchards near and far forest edge.

Figure 2 The percentage of the five most abundant pollinator species accounted in pollination network from every orchard.

Figure 3 A) Monthly bee visit frequency all year round observed in mixed fruit orchards in Southern Thailand B) the bar graph shows flowering phenology calendar of 14 most common plant species based on frequencies of occurrences in our 20 study sites. The selected crop plant species are shown as red bars, and non-crop plant species are shown as blue bars.

Figure 4 Quantitative pollination network (A) at a pair of mixed fruit orchards near to the forest edge and (B) at orchards far from the forest edge (for each web, the bars each represent a species and their abundance; the lower bars represent plant species and the upper bars represent animal species. Linkage width indicates the frequency of each interaction.

Figure 5 (A) The robustness following random removal of animal species of pollination networks near to the forest (blue circles) and pollination networks far from the forest (green circle) plotted against the proportion of lowland mosaic within a 1 km radius. The evenness of pollination networks near to the forest (blue circles) and pollination networks far from the forest (green circle) plotted against (B) proportion montane mosaic (C) proportion of urban area within a 4 km radius.

Figure 6 Result from the structural equation model showing the direct and indirect links of environmental variables (land use and distance to the forest) and pollinator community composition (richness and abundance) prevalence on pollination network structure

(robustness and interaction evenness). Black arrows indicate positive relationships, red arrows indicate negative relationships; the thickness of each arrow illustrates the strength, i.e. standardized path coefficients.

Supplementary S1 Map of the study area. Visitors were observed from 20 orchards at varying distances from 10 forest patches in southern Thailand. Pies show the composition of the landscape at 4 km radius around focal fields.

Supplementary S5 The interaction evenness plotted against a number of pollinator species.

Table legend

Table 1 Results of generalized linear mixed models for the pollination network structure in mixed fruit orchards in southern Thailand. For robustness, the explanatory variables are the distance to the forest edge, the proportion of plantation, and proportion of lowland mosaic within a 1 km radius. For evenness, the explanatory variables are the distance to the forest edge, the proportion of urban area and montane mosaic within a 4 km radius.

S2 The proportion of each landscape structure in different radius scales.

S3 Summary of model selection for each dependent variable

S4 The species code number and morphotype species of insect pollinators

S6 Results from the structural equation model showing regression, covariance, and variance to predict the relationships between environmental variables (land use and forest proximity) and pollinator community composition (richness and abundance) prevalence on pollination network structure (robustness and interaction evenness).

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Forest Proximity

A1	Cerambycidae	P1	<i>Musa sapientum</i> L. (Musaceae)
A2	Chrysomelidae	P2	<i>Sandoricum koetjape</i> (Burm.f.) Merr. (Meliaceae)
A3	Elateridae	P3	<i>Theobroma cacao</i> L. (Malvaceae)
A4	Lycidae	P4	<i>Artocarpus heterophyllus</i> Lam. (Moraceae)
A5	Cantharidae	P5	<i>Alpinia galanga</i> (L.) Willd. (Zingiberaceae)
A6	Scarabaeidae	P6	<i>Cassia siamea</i> Lamk. (Caesalpiniaceae)
A7	Staphylinidae	P7	<i>Nephelium lappaceum</i> L. (Sapindaceae)
A8	Asilidae	P8	<i>Artocarpus integer</i> (Thumb.) Merr. (Moraceae)
A9	Calliphoridae	P9	<i>Syzygium malaccense</i> Merr & Perry (Myrtaceae)
A10	Dolichopodidae	P10	<i>Edlingera elatior</i> (Jack.) R.M. Smith. (Zingiberaceae)
A11	Drosophilidae	P11	<i>Dipterocarpus</i> sp. (Dipterocarpaceae)
A12	Stratiomyidae	P12	<i>Fragaria fragrans</i> Roxd. (Gentianaceae)
A13	Syrphidae	P13	<i>Durio tibethinus</i> L. (Bombacaceae)
A14	Tephritidae	P14	<i>Celba pentandra</i> (L.) Gaerth. (Malvaceae)
A15	Coreidae	P15	<i>Capsicum frutescens</i> L. (Solanaceae)
A16	Pentatomidae	P16	<i>Microcos tomentosa</i> Smith. (Malvaceae)
A17	Scutelleridae	P17	<i>Oroxylum indicum</i> Vent. (Bignoniaceae)
A18	Anthophorini	P18	<i>Tamarindus indica</i> L. (Fabaceae)
A19	Apidae	P19	<i>Solanum torvum</i> SW. (Solanaceae)
A20	Halicidae	P20	<i>Citrus aurantifolia</i> Swingle. (Rutaceae)
A21	Megachilidae	P21	<i>Cocos nucifera</i> L. (Arecaceae)
A22	Mutillidae	P22	<i>Mangifera foetida</i> Lour. (Anacardaceae)
A23	Scoliidae	P23	<i>Mangifera indica</i> L. (Anacardaceae)
A24	Arctidae	P24	<i>Carica papaya</i> L. (Caricaceae)
A25	Danidae	P25	<i>Garcinia mangostana</i> L. (Clusiaceae)
A26	Lycanidae	P26	<i>Morinda citrifolia</i> (Rubiaceae)
A27	Mantidae	P27	<i>Lansium domesticum</i> L. (Meliaceae)
A28	Nectarivorous bat	P28	<i>Manilkara zapota</i> (L.) Van Royen. (Sapotaceae)
A29	Frugivorous bat	P29	<i>Citrus</i> (Rutaceae)
		P30	<i>Zalacca edulis</i> Reinw. (Arecaceae)
		P31	<i>Azadirachta indica</i> A. Juss. (Meliaceae)
		P32	<i>Parkia speciosa</i> Hassk. (Fabaceae)
		P33	<i>Ananas comosus</i> (L.) Merr. (Bromeliaceae)
		P34	<i>Areca catechu</i> L. (Arecaceae)
		P35	<i>Clausena cambodiana</i> Guill. (Rutaceae)
		P36	<i>Syzygium samarangense</i> (Myrtaceae)

A1	Cerambycidae	P1	<i>Musa sapientum</i> L. (Musaceae)
A2	Scarabaeidae	P2	<i>Sandoricum koetjape</i> (Burm.f.) Merr. (Meliaceae)
A3	Asilidae	P3	<i>Artocarpus heterophyllus</i> Lam. (Moraceae)
A4	Calliphoridae	P4	<i>Alpinia galanga</i> (L.) Willd. (Zingiberaceae)
A5	Drosophilidae	P5	<i>Cassia siamea</i> Lamk. (Caesalpiniaceae)
A6	Stratiomyidae	P6	<i>Nephelium lappaceum</i> L. (Sapindaceae)
A7	Syrphidae	P7	<i>Syzygium malaccense</i> Merr & Perry (Myrtaceae)
A8	Pentatomidae	P8	<i>Durio tibethinus</i> L. (Bombacaceae)
A9	Anthophorini	P9	<i>Annona squamosa</i> L. (Annonaceae)
A10	Apidae	P10	<i>Psidium guajava</i> L. (Myrtaceae)
A11	Lycanidae	P11	<i>Capsicum frutescens</i> L. (Solanaceae)
A12	Papilionidae	P12	<i>Citrus hystrix</i> DC. (Rutaceae)
A13	Nectarivorous bat	P13	<i>Tamarindus indica</i> L. (Fabaceae)
A14	Frugivorous bat	P14	<i>Solanum torvum</i> SW. (Solanaceae)
		P15	<i>Citrus aurantifolia</i> Swingle. (Rutaceae)
		P16	<i>Bouea microphylla</i> Griff. (Anacardiaceae)
		P17	<i>Cocos nucifera</i> L. (Arecaceae)
		P18	<i>Baccaurea ramiflora</i> Lour. (Euphorbiaceae)
		P19	<i>Mangifera indica</i> L. (Anacardaceae)
		P20	<i>Carica papaya</i> L. (Caricaceae)
		P21	<i>Garcinia mangostana</i> L. (Clusiaceae)
		P22	<i>Lansium domesticum</i> L. (Meliaceae)
		P23	<i>Lansium domesticum</i> Corr. (Meliaceae)
		P24	<i>Dimocarpus longan</i> Lour. (Sapindaceae)
		P25	<i>Azadirachta indica</i> A. Juss. (Meliaceae)
		P26	<i>Parkia speciosa</i> Hassk. (Fabaceae)
		P27	<i>Syzygium cumini</i> L. (Myrtaceae)
		P28	<i>Syzygium samarangense</i> (Myrtaceae)

S2 The proportion of each landscape structure in different radius scales.

sites	Scale	Lowland evergreen forest	Lower montane evergreen forest	Lowland mosaic	Mangrove	Montane mosaic	Montane open	Large scale plantation	urban
KH-F	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000
KNK-F	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KP-F	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KBT-F	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TB-F	50	0.0000	0.0000	73.1051	0.0000	26.8949	0.0000	0.0000	0.0000
KKW-F	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KL-F	50	0.0000	0.0000	71.5493	0.0000	28.4507	0.0000	0.0000	0.0000
KNH-F	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TNC-F	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KNK-N	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KKW-N	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KNH-N	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KH-N	50	0.0000	0.0000	86.4608	0.0000	13.5392	0.0000	0.0000	0.0000
KL-N	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
TNC-N	50	0.0000	0.0000	70.6538	0.0000	0.0000	0.0000	29.3462	0.0000
KBT-N	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
TB-N	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KP-N	50	0.0000	0.0000	37.9705	0.0000	0.0000	0.0000	62.0295	0.0000
LK-F	50	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
LK-N	50	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KH-F	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000
KNK-F	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KP-F	100	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KBT-F	100	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TB-F	100	0.0000	0.0000	64.0223	0.0000	35.9777	0.0000	0.0000	0.0000
KKW-F	100	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KL-F	100	0.0000	0.0000	63.0563	0.0000	36.9437	0.0000	0.0000	0.0000
KNH-F	100	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TNC-F	100	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KNK-N	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KKW-N	100	0.0000	0.0000	99.9430	0.0000	0.0570	0.0000	0.0000	0.0000
KNH-N	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KH-N	100	0.0000	0.0000	72.6604	0.0000	27.3396	0.0000	0.0000	0.0000
KL-N	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
TNC-N	100	0.0000	0.0000	59.7309	0.0000	0.0000	0.0000	40.2691	0.0000
KBT-N	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
TB-N	100	0.0000	0.0000	4.6249	0.0000	0.0000	0.0000	95.3751	0.0000
KP-N	100	0.0000	0.0000	40.8788	0.0000	0.0000	0.0000	59.1212	0.0000

LK-F	100	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
LK-N	100	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KH-F	250	0.0000	0.0000	0.0000	0.0000	0.4580	0.0000	0.0000	99.5420
KNK-F	250	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KP-F	250	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KBT-F	250	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TB-F	250	0.0000	0.0000	66.6311	0.0000	33.3689	0.0000	0.0000	0.0000
KKW-F	250	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KL-F	250	0.0000	0.0000	53.9853	0.0000	42.8992	0.0000	3.1154	0.0000
KNH-F	250	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TNC-F	250	0.0000	0.0000	89.4193	0.0000	10.5807	0.0000	0.0000	0.0000
KNK-N	250	0.0000	0.0000	8.7160	0.0000	0.0000	0.0000	91.2840	0.0000
KKW-N	250	0.0000	0.0000	87.9830	0.0000	9.8141	0.0000	2.2029	0.0000
KNH-N	250	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KH-N	250	0.0000	0.0000	66.8329	0.0000	33.1671	0.0000	0.0000	0.0000
KL-N	250	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
TNC-N	250	0.0000	0.0000	52.0189	0.0000	0.0000	0.0000	47.9811	0.0000
KBT-N	250	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
TB-N	250	0.0000	0.0000	26.0636	0.0000	0.0000	0.0000	73.9364	0.0000
KP-N	250	0.0000	0.0000	34.4462	0.0000	0.0000	0.0000	65.5538	0.0000
LK-F	250	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
LK-N	250	0.0000	0.0000	91.5226	0.0000	8.4774	0.0000	0.0000	0.0000
KH-F	500	0.0000	1.9628	0.0000	0.0000	21.7455	0.0000	0.0000	76.2917
KNK-F	500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KP-F	500	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
KBT-F	500	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TB-F	500	0.0000	0.0000	74.9790	0.0000	21.6166	0.0000	3.4043	0.0000
KKW-F	500	0.0000	0.0000	97.4252	0.0000	2.5748	0.0000	0.0000	0.0000
KL-F	500	0.0000	0.0000	38.9292	0.0000	35.7899	0.0000	25.2809	0.0000
KNH-F	500	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TNC-F	500	0.0000	0.0000	82.5335	0.0000	17.4665	0.0000	0.0000	0.0000
KNK-N	500	0.0000	0.0000	27.5380	0.0000	0.0000	0.0000	72.4620	0.0000
KKW-N	500	0.0000	0.0000	58.4671	0.0000	23.5100	0.0000	18.0229	0.0000
KNH-N	500	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	100.0000	0.0000
KH-N	500	0.0000	0.0000	66.6475	0.0000	33.3525	0.0000	0.0000	0.0000
KL-N	500	0.0000	0.0000	5.2352	0.0000	0.0000	0.0000	94.7648	0.0000
TNC-N	500	0.0000	0.0000	37.1699	0.0000	0.0000	0.0000	62.8301	0.0000
KBT-N	500	8.7012	0.0000	0.0000	0.0000	0.0000	0.0000	91.2988	0.0000
TB-N	500	0.0000	0.0000	36.8228	0.0000	0.0000	0.0000	63.1772	0.0000
KP-N	500	0.0000	0.0000	30.4915	0.0000	0.0000	0.0000	69.5085	0.0000
LK-F	500	0.0000	0.0000	0.0639	0.0000	0.0000	0.0000	99.9361	0.0000
LK-N	500	0.0000	0.0000	86.9439	0.0000	13.0561	0.0000	0.0000	0.0000
KH-F	1000	0.0000	6.4293	0.0000	0.0000	48.9985	0.0000	0.0000	44.5721
KNK-F	1000	0.0000	0.0000	4.0472	0.0000	0.0000	0.0000	95.9528	0.0000

KP-F	1000	0.0000	0.0000	97.9965	0.0000	0.0000	0.0000	2.0035	0.0000
KBT-F	1000	0.0000	0.0000	90.9644	0.0000	3.6181	0.0000	5.4174	0.0000
TB-F	1000	0.0000	0.0000	78.9287	0.0000	12.5236	0.0000	8.5477	0.0000
KKW-F	1000	0.0000	0.0000	89.7399	0.0000	10.2601	0.0000	0.0000	0.0000
KL-F	1000	0.0000	0.0000	46.8716	0.0000	22.6639	0.0000	30.4645	0.0000
KNH-F	1000	0.0000	0.0000	100.0000	0.0000	0.0000	0.0000	0.0000	0.0000
TNC-F	1000	0.0000	0.0000	88.2908	0.0000	10.8059	0.0000	0.9033	0.0000
KNK-N	1000	0.0000	0.0000	23.4442	0.0000	0.0000	0.0000	76.5558	0.0000
KKW-N	1000	0.6626	0.0000	36.6884	0.0000	33.4429	0.0000	29.2061	0.0000
KNH-N	1000	0.0000	0.0000	4.1197	0.0000	0.0000	0.0000	95.8803	0.0000
KH-N	1000	0.6896	0.0000	50.4147	0.0000	38.4377	0.0000	8.9876	0.0000
KL-N	1000	0.0000	0.0000	7.7736	0.0000	0.0000	0.0000	92.2264	0.0000
TNC-N	1000	0.0000	0.0000	25.9364	0.0000	0.0000	0.0000	74.0636	0.0000
KBT-N	1000	27.5458	0.0000	4.2860	0.0000	0.0000	0.0000	68.1682	0.0000
TB-N	1000	7.2354	0.0000	45.2314	0.0000	0.0000	0.0000	47.5332	0.0000
KP-N	1000	0.0000	0.0000	29.1379	0.0000	0.0000	0.0000	70.8621	0.0000
LK-F	1000	0.0000	0.0000	11.6725	0.0000	0.0000	0.0000	88.3275	0.0000
LK-N	1000	0.0000	0.0000	82.4208	0.0000	14.5124	0.0000	3.0668	0.0000
KH-F	2000	0.0000	11.8541	0.0000	0.0000	53.0346	0.0000	6.4770	28.6343
KNK-F	2000	0.0000	0.0000	25.5287	0.0000	0.0000	0.0000	74.4713	0.0000
KP-F	2000	0.0000	0.0000	90.1724	0.0000	0.0000	0.0000	9.8276	0.0000
KBT-F	2000	0.0000	0.0000	80.9796	0.0000	4.3589	0.0000	14.6616	0.0000
TB-F	2000	0.0000	0.0000	73.4262	0.0000	11.3897	0.0000	15.1841	0.0000
KKW-F	2000	0.0000	0.0000	73.0806	0.0000	26.9194	0.0000	0.0000	0.0000
KL-F	2000	0.0000	0.0000	59.4305	0.0000	17.2986	0.0000	22.1949	0.0000
KNH-F	2000	0.0000	0.0000	98.2076	0.0000	0.5380	0.0000	1.2544	0.0000
TNC-F	2000	0.0000	0.0000	79.7342	0.0000	18.4270	0.0000	1.8389	0.0000
KNK-N	2000	5.5464	0.0000	10.6392	0.0000	0.0000	0.0000	83.8144	0.0000
KKW-N	2000	7.2515	0.0000	48.3846	0.0000	21.8158	0.0000	22.5481	0.0000
KNH-N	2000	0.0000	0.0000	2.5677	0.0000	0.0000	0.0000	97.4323	0.0000
KH-N	2000	4.5495	0.0000	28.8831	0.0000	31.7216	0.0000	28.8246	0.0000
KL-N	2000	4.0322	0.0000	14.1029	0.0000	2.0392	0.0000	79.2876	0.0000
TNC-N	2000	12.8042	0.0000	26.0030	0.0000	1.7030	0.0000	59.4898	0.0000
KBT-N	2000	40.1923	0.0000	5.3707	0.0000	0.0000	0.0000	54.4370	0.0000
TB-N	2000	17.9807	0.0000	46.1290	0.0000	3.3742	0.0000	32.5161	0.0000
KP-N	2000	0.2069	0.0000	19.9993	0.0000	0.0000	0.0000	79.7938	0.0000
LK-F	2000	0.0000	0.0000	36.5532	0.0000	0.0000	0.0000	63.4468	0.0000
LK-N	2000	0.0000	0.0000	70.1554	0.0000	9.6620	0.0000	20.1826	0.0000
KH-F	4000	0.0000	15.0727	0.0000	0.0000	65.7901	0.0000	16.1427	2.9944
KNK-F	4000	0.4751	0.0000	39.7544	0.0000	1.1888	0.0000	58.5670	0.0148
KP-F	4000	0.0000	0.0000	85.2233	0.0000	0.6797	0.0000	13.9706	0.1264
KBT-F	4000	0.0000	0.0000	65.8068	0.0000	10.1715	0.0000	23.0979	0.9238
TB-F	4000	0.0000	0.0000	58.7088	0.3795	19.0688	0.0000	21.1461	0.6968
KKW-F	4000	1.2293	0.0000	70.1166	0.0000	24.5809	0.0000	3.5758	0.4973

KL-F	4000	0.4008	0.0000	55.2508	0.0000	10.5958	0.0000	33.0809	0.0000
KNH-F	4000	0.0000	0.0000	84.2833	0.0000	2.0133	0.0000	13.6756	0.0278
TNC-F	4000	0.0000	0.0000	77.7931	0.0000	20.5239	0.0000	1.6683	0.0148
KNK-N	4000	19.0570	0.0000	8.5814	0.0000	0.0000	0.0000	71.6321	0.7296
KKW-N	4000	3.6915	0.0000	59.5381	0.0000	19.1124	0.0000	17.6580	0.0000
KNH-N	4000	1.2468	0.0000	5.5328	0.0000	0.0000	0.0000	92.0041	1.2164
KH-N	4000	2.8825	0.0000	31.8712	0.0000	26.9879	0.0000	32.0121	0.6207
KL-N	4000	8.4028	1.0042	22.6648	0.0000	6.1153	0.0000	61.2754	0.0000
TNC-N	4000	34.5497	0.0000	20.6871	0.0000	0.3169	0.0000	43.4610	0.9853
KBT-N	4000	47.5411	0.8036	6.5094	0.0000	0.0000	0.0000	44.6138	0.5323
TB-N	4000	25.2736	0.0000	38.8311	0.0000	6.0038	0.0000	29.4303	0.4612
KP-N	4000	10.3140	0.0000	15.7169	0.0000	0.0000	0.0000	73.6953	0.2739
LK-F	4000	0.0000	0.0000	55.5340	0.0000	1.5918	0.0000	42.7838	0.0903
LK-N	4000	2.0421	0.0000	53.7979	0.0000	4.7584	0.0000	39.3443	0.0572
KH-F	6000	0.0000	19.0519	0.0000	0.0000	57.1314	0.0000	20.7023	3.1144
KNK-F	6000	1.2120	0.0000	35.8292	0.0000	0.9626	0.0000	61.8614	0.1348
KP-F	6000	0.0670	0.0000	77.6549	0.0000	0.9662	0.0000	20.9363	0.2464
KBT-F	6000	0.9964	0.0000	59.2047	0.0000	10.8502	0.0000	27.9049	1.0438
TB-F	6000	0.0000	0.0000	48.5070	8.9882	23.0922	0.0000	18.2747	0.8168
KKW-F	6000	1.1570	0.0000	71.6445	0.0000	18.9332	0.0000	7.6480	0.6173
KL-F	6000	0.6680	0.0000	52.7245	0.0000	9.0292	0.0000	36.7838	0.1200
KNH-F	6000	0.5271	0.0000	72.0605	0.0000	4.4499	0.0000	22.8146	0.1478
TNC-F	6000	0.0000	0.0000	76.3996	0.0000	21.4957	0.0000	1.9699	0.1348
KNK-N	6000	26.9748	0.0000	12.8260	0.0000	0.0000	0.0000	59.3497	0.8496
KKW-N	6000	2.0729	0.0000	64.7149	0.0000	16.8520	0.0000	16.0903	0.1200
KNH-N	6000	1.5243	0.0000	9.9600	0.0000	0.0000	0.0000	87.1794	1.3364
KH-N	6000	1.7220	0.0000	33.9216	0.0000	26.1788	0.0000	32.2564	0.7407
KL-N	6000	11.4243	2.5538	26.3298	0.0000	4.8699	0.0000	54.3524	0.1200
TNC-N	6000	42.0745	0.1499	16.8159	0.0000	0.0000	0.0000	39.8544	1.1053
KBT-N	6000	44.3191	2.3703	13.1648	0.0000	0.0000	0.0000	39.4935	0.6523
TB-N	6000	31.1034	0.0000	31.0801	0.0000	12.4137	0.0000	24.7216	0.5812
KP-N	6000	18.9065	0.0000	16.3170	0.0000	0.0000	0.0000	63.7945	0.3939
LK-F	6000	0.0457	0.0000	63.6055	0.0000	1.6279	0.0000	34.5105	0.2103
LK-N	6000	4.1410	0.0000	49.5371	0.0000	3.4559	0.0000	42.6888	0.1772
KH-F	8000	0.0000	25.6689	0.0000	0.0000	41.2587	0.0000	18.9630	0.0708
KNK-F	8000	3.4383	0.0000	31.2898	0.0000	0.0000	0.0000	46.5974	0.0000
KP-F	8000	0.8321	0.0000	70.3840	0.0000	0.9990	0.0000	26.7839	0.3917
KBT-F	8000	5.2607	0.0708	56.0498	0.0000	10.5376	0.0000	27.6278	0.0000
TB-F	8000	0.0000	0.0000	42.6568	17.9954	19.9389	0.0000	15.0543	0.7535
KKW-F	8000	1.0357	0.0000	70.8872	0.0000	13.1809	0.0000	10.5578	0.0709
KL-F	8000	1.9449	0.1135	50.1426	0.0000	8.1695	0.0000	39.0984	0.5312
KNH-F	8000	0.8738	0.0000	64.9177	0.0000	5.4411	0.0000	28.7674	0.0000
TNC-F	8000	0.0000	0.0000	77.5907	0.0000	20.3633	0.0000	1.9067	0.0000
KNK-N	8000	30.5110	0.0000	15.7844	0.0000	0.0000	0.0000	53.7046	0.0000

KKW-N	8000	1.3098	0.0000	68.3492	0.0000	15.3228	0.0000	14.5454	0.1417
KNH-N	8000	2.0447	0.0000	12.7122	0.0000	0.0000	0.0000	85.2331	0.0000
KH-N	8000	1.4748	0.0000	35.1111	0.0000	26.8896	0.0000	31.7624	4.0776
KL-N	8000	13.9507	2.5290	28.2822	0.0000	4.1252	0.0000	50.7251	0.3778
TNC-N	8000	45.5777	1.1514	15.2302	0.0000	0.6775	0.0000	37.3631	0.0000
KBT-N	8000	40.4030	3.3589	18.1618	0.0000	0.7508	0.0000	37.3155	0.0000
TB-N	8000	32.5255	0.0000	27.4126	1.9624	15.7636	0.0000	22.0816	0.0945
KP-N	8000	23.0731	0.0000	18.1588	0.0000	0.6608	0.0000	57.4516	0.6557
LK-F	8000	0.7389	0.0000	64.7077	0.0000	0.0000	0.0000	29.3629	0.0000
LK-N	8000	6.4864	0.0000	47.3111	0.0000	2.3652	0.0000	43.4775	0.0000
KH-F	10000	0.0000	30.3276	0.0000	0.0000	42.1833	0.0000	16.8407	0.0777
KNK-F	10000	5.6493	0.0000	29.7659	0.0000	0.8124	0.0000	63.7624	0.0000
KP-F	10000	2.8268	0.0000	64.2496	0.0000	2.1603	0.0000	30.2315	0.4218
KBT-F	10000	8.8773	0.2769	54.4423	0.0000	9.4733	0.0000	26.5913	0.0000
TB-F	10000	0.6735	0.0000	38.5282	24.9714	18.4938	0.0000	13.4772	0.9985
KKW-F	10000	1.7741	0.0090	68.4779	0.0000	16.9717	0.0000	12.6345	0.1228
KL-F	10000	3.3546	0.6476	47.2457	0.0000	7.4473	0.0000	40.8965	0.4082
KNH-F	10000	1.2130	0.0000	60.9480	0.0000	4.9518	0.0000	32.8872	0.0000
TNC-F	10000	0.6729	0.0000	76.5593	0.0000	19.5069	0.0000	2.6628	0.0000
KNK-N	10000	32.0005	0.0000	18.2177	0.0000	0.0737	0.0000	49.6980	0.0000
KKW-N	10000	1.3216	0.0000	68.2120	0.0000	16.1700	0.0000	14.1699	0.1164
KNH-N	10000	2.2692	0.0000	15.8201	0.0000	0.0393	0.0000	81.8714	0.0000
KH-N	10000	1.3250	0.0000	37.1018	0.0000	26.7152	0.0000	31.6300	3.2280
KL-N	10000	16.2410	2.1682	28.9099	0.0000	3.8288	0.0000	48.5283	0.3237
TNC-N	10000	48.6685	1.6028	14.7154	0.0000	0.7629	0.0000	34.2503	0.0000
KBT-N	10000	36.1268	3.9842	21.4414	0.0000	1.8068	0.0000	36.5693	0.0000
TB-N	10000	32.6592	0.0000	26.7615	3.6782	15.4264	0.0000	20.7709	0.1165
KP-N	10000	25.4942	0.0000	20.3157	0.0000	0.6846	0.0000	52.9390	0.5665
LK-F	10000	2.0875	0.0000	61.6129	0.0000	3.5069	0.0000	32.7927	0.0000
LK-N	10000	9.4146	0.2460	45.5657	0.0000	2.2733	0.0000	42.5004	0.0000
KH-F	15000	0.2575	33.9422	0.0000	0.0000	41.0489	0.0000	17.5185	0.5517
KNK-F	15000	9.0442	0.0000	28.3138	0.0000	1.5201	0.0000	61.1219	0.0000
KP-F	15000	8.8520	0.0064	57.6407	0.0000	3.5322	0.0000	29.5685	0.4002
KBT-F	15000	13.0374	1.1617	49.9144	0.0000	8.3607	0.0000	26.3212	0.0000
TB-F	15000	7.7843	0.0000	32.1979	26.8720	15.8111	0.0000	13.6593	1.6854
KKW-F	15000	5.9041	0.5299	62.0401	0.0000	18.6863	0.0000	12.4174	0.3052
KL-F	15000	7.0919	0.9257	41.5479	0.0000	8.6319	0.0000	40.3278	0.2601
KNH-F	15000	2.0178	0.0000	56.2811	0.0000	2.2873	0.0000	37.3598	0.0541
TNC-F	15000	5.5932	0.0273	70.5205	0.0000	16.2869	0.0000	7.4453	0.0000
KNK-N	15000	29.8818	0.0000	17.9735	0.0000	0.3718	0.0000	51.5148	0.2580
KKW-N	15000	5.0471	0.2595	63.2939	0.0000	18.8669	0.0000	12.0822	0.3017
KNH-N	15000	3.7673	0.1258	24.2640	0.0000	2.2032	0.0000	69.6368	0.0029
KH-N	15000	1.1833	0.0000	39.1487	0.0000	27.2001	0.0000	30.1126	2.2356
KL-N	15000	15.2525	2.2332	29.2335	0.0000	4.6207	0.0000	48.4419	0.2182

TNC-N	15000	46.6388	1.3661	17.1431	0.7560	0.6053	0.0000	33.4908	0.0000
KBT-N	15000	29.0421	5.0495	27.1097	0.0000	2.5377	0.0000	36.1806	0.0000
TB-N	15000	31.8743	0.0000	26.4827	7.5705	12.6426	0.0000	20.3784	0.3415
KP-N	15000	24.9522	0.0182	24.8104	0.0000	0.8266	0.0000	48.9958	0.3968
LK-F	15000	6.8243	0.3655	50.7257	0.0000	5.2642	0.0000	36.7173	0.0000
LK-N	15000	12.8796	0.8045	40.6589	0.0000	2.8112	0.0000	42.8457	0.0000
KH-F	20000	0.4557	38.0552	0.0000	0.0000	37.1826	0.0000	19.2462	0.6669
KNK-F	20000	11.2398	0.0000	26.4283	0.0000	2.0019	0.0000	60.0841	0.2459
KP-F	20000	11.6987	0.0135	52.4448	0.0000	4.4877	0.0000	30.8802	0.4751
KBT-F	20000	14.2878	2.2856	46.9422	0.1339	7.7935	0.0000	27.3134	0.0000
TB-F	20000	13.4558	0.0000	29.2473	25.3808	13.4216	0.0000	15.2114	1.8745
KKW-F	20000	10.4127	0.5809	55.6012	0.0000	20.6544	0.0000	11.7421	0.3438
KL-F	20000	7.9125	1.3056	37.2793	0.0000	12.7869	0.0000	40.5481	0.1676
KNH-F	20000	3.0102	0.0000	54.1759	0.0000	3.9434	0.0000	38.6084	0.2621
TNC-F	20000	11.4862	0.2626	64.3207	0.0000	14.2565	0.0000	9.6638	0.0102
KNK-N	20000	24.9500	0.0000	19.6423	0.0820	1.1656	0.0000	53.7488	0.4114
KKW-N	20000	8.7156	0.4380	56.9530	0.0000	21.7563	0.0000	11.0715	0.3418
KNH-N	20000	5.1268	0.3304	32.3512	0.0000	3.5685	0.0000	58.4966	0.1266
KH-N	20000	1.1027	0.0000	39.4221	0.0000	28.0011	0.0000	29.3782	1.5769
KL-N	20000	12.9651	2.4316	29.2445	0.0000	7.3228	0.0000	47.6031	0.1455
TNC-N	20000	40.6611	1.0217	22.6263	0.9741	1.2474	0.0000	33.4693	0.0000
KBT-N	20000	23.6995	5.0870	32.0077	0.0000	3.3314	0.0135	35.3988	0.0000
TB-N	20000	28.7413	0.0000	26.2257	10.6751	11.9737	0.0000	20.6989	1.0791
KP-N	20000	22.5320	0.1981	30.5507	0.0000	2.0468	0.0000	44.2161	0.4564
LK-F	20000	11.2840	1.6957	41.1811	0.0071	5.8406	0.0051	39.8584	0.0150
LK-N	20000	15.8994	2.1502	34.2791	0.0000	3.8114	0.0000	43.7916	0.0134
KH-F	30000	0.4820	43.5197	0.0000	0.0000	36.2407	0.0000	18.8050	0.9490
KNK-F	30000	12.2151	0.0000	29.2942	0.1789	3.0056	0.0000	54.1858	0.4159
KP-F	30000	11.2634	0.5252	48.6180	0.0000	8.0249	0.0000	30.9896	0.3990
TB-F	30000	15.7487	0.0000	27.5289	20.1466	15.9605	0.0000	18.5522	2.0432
KKW-F	30000	12.3213	0.4340	51.4101	0.0000	15.8993	0.0000	14.2707	0.4541
KL-F	30000	7.0273	1.8372	34.1935	0.0000	17.2944	0.0000	39.1701	0.0976
KNH-F	30000	5.7009	0.1550	52.2757	0.0000	0.0000	0.0000	31.0045	0.2731
TNC-F	30000	15.9802	0.3569	54.9169	0.2819	14.6891	0.0000	12.9243	0.8208
KNK-N	30000	20.8029	0.0000	24.5376	0.2454	3.5878	0.0000	50.1981	0.4983
KKW-N	30000	11.2857	0.3656	52.1633	0.0000	21.9380	0.0000	13.3996	0.4888
KNH-N	30000	6.5488	0.9000	39.5118	0.0000	2.5010	0.0000	47.4717	0.1893
KH-N	30000	0.8902	0.0000	39.9888	0.0000	28.8591	0.0000	27.8506	1.4368
KL-N	30000	9.6052	2.6727	30.9718	0.0000	11.8250	0.0000	44.0494	0.0886
TNC-N	30000	32.6292	0.6735	31.2135	0.8122	4.1292	0.0000	29.8402	0.0985
KBT-N	30000	14.2629	2.6059	47.4546	0.8774	7.2312	0.0066	26.9447	0.0460
KBT-N	30000	19.3569	4.2655	39.2754	0.6046	1.7171	0.0131	31.0986	0.0411
TB-N	30000	24.2687	0.0968	27.5433	10.6941	13.9011	0.0000	21.4974	1.3504
KP-N	30000	17.0896	1.1119	39.4333	0.0000	4.4867	0.0066	36.7434	0.3688

LK-F	30000	14.1946	3.6784	31.5221	0.1409	4.7748	0.0138	43.3348	0.7834
LK-N	30000	17.4898	4.6392	27.0265	0.1324	3.3044	0.0107	45.6904	0.3763

S3 Summary of model selection for each dependent variable. DF, mean distance to the forest edge; LM, mean low mosaic; MM, mean montane mosaic; PT, mean plantation; Ur, mean urban.

Network metric	Radius (m)	Model	ΔAIC	AIC (higher-lowest)
Robustness	1000	$y = \beta_0 + \beta_1 DF + \beta_2 LM + \beta_3 PT$	0	-46.939
		$y = \beta_0 + \beta_1 DF + \beta_2 LM + \beta_3 PT + \beta_4 DF.PT + \beta_5 DF.LM + \beta_6 LM.PT$	64.078	17.139
		$y = \beta_0 + \beta_1 DF + \beta_2 LM + \beta_3 PT + \beta_4 DF.PT$	12.477	-34.463
		$y = \beta_0 + \beta_1 DF + \beta_2 LM + \beta_3 PT + \beta_4 DF.LM$	12.389	-34.549
Evenness	4000	$y = \beta_0 + \beta_1 DF + \beta_2 MM + \beta_3 UR + \beta_4 DF.UR$	0	-39.476
		$y = \beta_0 + \beta_1 DF + \beta_2 MM + \beta_3 UR + \beta_4 DF.MM$	4.209	-35.266
		$y = \beta_0 + \beta_1 DF + \beta_2 LM + \beta_3 MM + \beta_4 UR$	11.824	-27.651
		$y = \beta_0 + \beta_1 DF + \beta_3 MM + \beta_4 UR + \beta_5 DF.MM + \beta_6 DF.UR + \beta_7 MM.UR$	19.385	-20.091
		$y = \beta_0 + \beta_1 DF + \beta_2 MM + \beta_3 UR + \beta_4 MM.UR$	6.929	-32.547

S4 The species code number and morphotype species of insect pollinators

Code numbers	Families	Genera	Species	Author name
sp.1	Order Blattodea			
	Blattellidae	unidentified	sp.	
	Order Coleoptera			
sp.2	Brentidae	<i>Eubactrus</i>	sp.	
sp.3	Bruchidae	unidentified	sp.1	
sp.4		unidentified	sp.2	
sp.5	Cerambycidae	<i>Chlorophorus</i>	<i>annularis</i>	Fabricius
sp.6		<i>Polyzonus</i>	<i>obtusus</i>	Bates
sp.7		<i>Polyzonus</i>	sp.	
sp.8	Chrysomelidae	<i>Aulacophora</i>	sp.	
sp.9		<i>Chrysochus</i>	sp.	
sp.10		<i>Donacia</i>	<i>aenaria</i>	Baly
sp.11		<i>Galerupipla</i>	sp.	
sp.12		<i>Luperomorpha</i>	sp.	
sp.13	Cleridae	unidentified	sp.	
sp.14	Curculionidae	<i>Ectatorhinus</i>	sp.	
sp.15		<i>Episomus</i>	sp.	
sp.16	Elateridae	<i>Alaus</i>	sp.	
sp.17		<i>Diploconus</i>	sp.1	
sp.18		<i>Diploconus</i>	sp.2	
sp.19	Lycidae	<i>Lycostomus</i>	sp.1	
sp.20		<i>Lycostomus</i>	sp.2	
sp.21		<i>Lycostomus</i>	sp.3	
sp.22		<i>Lycostomus</i>	sp.4	
sp.23	Cantharidae	unidentified	sp.	
sp.24	Nitidulidae	Unidentified	sp.1	
sp.25		Unidentified	sp.2	
sp.26	Scarabaeidae	<i>Gametis</i>	<i>histrion</i>	Olivier
sp.27		<i>Glycyphana</i>	<i>nicobarica</i>	Janson
sp.28		<i>Glycyphana</i>	<i>horsfieldi</i>	Hope
sp.29		<i>Glycyphana</i>	<i>quadricolor</i>	Wiedemann
			<i>quadricolor</i>	

sp.30		<i>Ixorida</i>	<i>mouhotii</i>	Wallace
sp.31		unidentified	sp.	
sp.32	Staphylinidae	unidentified	sp.	
	Order Diptera			
sp.33	Asilidae	<i>Proctacantella</i>	sp.	
sp.34		<i>Promachus</i>	sp.	
sp.35	Bombycidae	<i>Systropus</i>	sp.1	
sp.36		<i>Systropus</i>	sp.2	
sp.37		<i>Systropus</i>	sp.3	
sp.38	Calliphoridae	<i>Chrysomyia</i>	<i>megacephala</i>	Fabricius
sp.39		<i>Chrysomyia</i>	sp.1	
sp.40		<i>Chrysomyia</i>	sp.2	
sp.41		<i>Hypopygropsis</i>	sp.	
sp.42		unidentified	sp.	
sp.43	Dolichopodidae	unidentified	sp.	
sp.44	Drosophilidae	<i>Drosophila</i>	sp.	
sp.45		unidentified	sp.	
sp.46	Empididae	<i>Hilara</i>	sp.	
sp.47	Muscidae	unidentified	sp.1	
sp.48		unidentified	sp.2	
sp.49		unidentified	sp.3	
sp.50		unidentified	sp.4	
sp.51		unidentified	sp.5	
sp.52		unidentified	sp.6	
sp.53		unidentified	sp.7	
sp.54	Sarcophagidae	<i>Parasarcophaga</i>	sp.	
sp.55	Stratiomyidae	<i>Hermetia</i>	sp.	
sp.56		<i>Ptecticus</i>	sp.	
sp.57		<i>Stratiomys</i>	sp.	
sp.58		Unidentified	sp.	
sp.59	Syrphidae	<i>Eristalis</i>	<i>arvorum</i>	(Fabricius)
sp.60		<i>Eristalis</i>	<i>obscuritarsis</i>	Meijere
sp.61		<i>Helophilus</i>	<i>bengaliensis</i>	Wiedemann
sp.62		<i>Helophilus</i>	sp.1	
sp.63		<i>Helophilus</i>	sp.2	
sp.64		<i>Megapis</i>	sp.	
sp.65		<i>Physocephala</i>	sp.	
sp.66		<i>Rhingia</i>	sp.1	
sp.67		<i>Rhingia</i>	sp.2	
sp.68		<i>Rhingia</i>	sp.3	
sp.69		<i>Rhingia</i>	sp.4	
sp.70		<i>Syrphus</i>	sp.1	
sp.71		<i>Syrphus</i>	sp.2	

sp.72		unidentified	sp.	
sp.73	Tabanidae	<i>Chrysops</i>	<i>dispar</i>	(Fabricius)
sp.74		<i>Chrysops</i>	<i>fasciata</i>	Wiedemann
sp.75	Tachinidae	<i>Drino</i>	sp.1	
sp.76		<i>Drino</i>	sp.2	
sp.77		<i>Drino</i>	sp.3	
sp.78	Tephritidae	<i>unidentified</i>	sp.	
sp.79	Therevidae	<i>unidentified</i>	sp.	
sp.80	Tipulidae	<i>Tipula</i>	sp.	
	Order Hemiptera			
sp.81	Coreidae	<i>Clavigralla</i>	sp.	
sp.82		<i>Riptortus</i>	<i>linearis</i>	Fabricius
sp.83		<i>Serinetha</i>	<i>abdominalis</i>	Fabricius
sp.84		unidentified	sp.1	
sp.85		unidentified	sp.2	
sp.86		unidentified	sp.3	
sp.87	Lygaeidae	<i>Geocoris</i>	sp.	
sp.88		<i>Graptostethus</i>	<i>servus</i>	Fabricius
sp.89		unidentified	sp.1	
sp.90		unidentified	sp.2	
sp.91	Miridae	unidentified	sp.	
sp.92	Pentatomidae	<i>Eocanthecona</i>	<i>furcellata</i>	(Wolff)
sp.93		<i>Erothesima</i>	<i>fullo</i>	Thunberg
sp.94		<i>Eusarcocoris</i>	<i>guttiger</i>	Thunberg
sp.95	Reduviidae	<i>Chitapa</i>	sp.	
sp.96		<i>Ectomocoris</i>	sp.	
sp.97	Reduviidae	<i>Rhynocoris</i>	sp.1	
sp.98		<i>Rhynocoris</i>	sp.2	
sp.99		<i>Sycanus</i>	<i>collaris</i>	Fabricius
sp.100		unidentified	sp.	
sp.101	Scutelleridae	<i>Callidea</i>	sp.	
sp.102		<i>Chrysocoris</i>	<i>grandis</i>	Thunberg
sp.103		<i>Chrysocoris</i>	<i>stolii</i>	Wolff
	Order Hymenoptera			
sp.104	Apidae	<i>Amegilla</i>	sp.	
sp.105		<i>Apis</i>	<i>andreniformis</i>	Smith
sp.106		<i>Apis</i>	<i>cerana indica</i>	Fabricius
sp.107		<i>Apis</i>	<i>dorsata</i>	Fabricius
sp.108		<i>Apis</i>	<i>florea</i>	Fabricius
sp.109		<i>Apis</i>	<i>mellifera</i>	Linnaeus
			<i>ligustica</i>	
sp.110		<i>Ceratina</i>	sp.1	
sp.111		<i>Ceratina</i>	sp.2	

sp.112		<i>Ceratina</i>	sp.3	
sp.113		<i>Pithitis</i>	<i>smaragdula</i>	Fabricius
sp.114		<i>Podalirius</i>	<i>crocea</i>	Bingham
sp.115		<i>Thyreus</i>	sp.	
sp.116		<i>Lisotrigona</i>	<i>scintillans</i>	
sp.117		<i>Heterotrigona</i>	<i>erythrogastra</i>	
sp.118		<i>Heterotrigona</i>	<i>itama</i>	
sp.119		<i>Geniotrigona</i>	<i>thoracica</i>	
sp.120		<i>Lophotrigona</i>	<i>canifrons</i>	
sp.121		<i>Tetragonilla</i>	<i>collina</i>	Smith
sp.122		<i>Tetragonula</i>	<i>laeviceps</i>	Smith
sp.123		<i>Tetrigona</i>	<i>melanoleuca</i>	Cockerell
sp.124		<i>Trigona</i>	<i>pagdeni</i>	Schwarz
sp.125		<i>Lepidotrigona</i>	<i>ventralis</i>	Smith
sp.126		<i>Trigona</i>	sp.1	
sp.127		<i>Trigona</i>	sp.2	
sp.128		<i>Trigona</i>	sp.3	
sp.129		<i>Trigona</i>	sp.4	
sp.130		<i>Xylocopa</i>	<i>aestuans</i>	(Linnaeus)
sp.131		<i>Xylocopa</i>	<i>collaris</i>	Cockerell
sp.132		<i>Xylocopa</i>	<i>latipes</i>	(Drury)
sp.133	Chrysididae	<i>Stilbum</i>	<i>cyanarum</i>	(Förster)
sp.134		<i>Stilbum</i>	sp.	
sp.135	Evaniidae	<i>Evania</i>	sp.	
sp.136	Formicidae	<i>Anoplolepis</i>	<i>gracilipes</i>	(Smith)
sp.137		<i>Camponotus</i>	sp.1	
sp.138		<i>Camponotus</i>	sp.2	
sp.139		<i>Camponotus</i>	sp.3	
sp.140		<i>Camponotus</i>	sp.4	
sp.141		<i>Iridomyrmex</i>	sp.	
sp.142		<i>Meranoplus</i>	sp.	
sp.143		<i>Monomorium</i>	sp.1	
sp.144		<i>Monomorium</i>	sp.2	
sp.145		<i>Ochetellus</i>	sp.1	
sp.146		<i>Ochetellus</i>	sp.2	
sp.147		<i>Oecophylla</i>	<i>smaragdina</i>	Fabricius
sp.148		<i>Paratrechina</i>	sp.1	
sp.149		<i>Paratrechina</i>	sp.2	
sp.150		<i>Paratrechina</i>	sp.3	
sp.151		<i>Solenopsis</i>	<i>geminata</i>	(Fabricius)
sp.152	Formicidae	<i>Tetraponura</i>	<i>rufonigra</i>	(Jerdon)
sp.153		unidentified	sp.	
sp.154	Halictidae	<i>Halictus</i>	sp.1	

sp.155		<i>Halictus</i>	sp.2	
sp.156		<i>Halictus</i>	sp.3	
sp.157		<i>Lasioglossum</i>	sp.1	
sp.158		<i>Lasioglossum</i>	sp.2	
sp.159		<i>Lasioglossum</i>	sp.3	
sp.160		<i>Lasioglossum</i>	sp.4	
sp.161		<i>Nomia</i>	<i>albofasciata</i>	Smith
sp.162		<i>Nomia</i>	sp.1	
sp.163		<i>Nomia</i>	sp.2	
sp.164		<i>Nomia</i>	sp.3	
sp.165		<i>Nomia</i>	sp.4	
sp.166		<i>Nomia</i>	sp.5	
sp.167		unidentified	sp.	
sp.168	Megachilidae	<i>Coelioxys</i>	sp.	
sp.169		<i>Euaspis</i>	sp.1	
sp.170		<i>Euaspis</i>	sp.2	
sp.171		<i>Lithurge</i>	sp.	
sp.172		<i>Megachile</i>	<i>hera</i>	Bingham
sp.173		<i>Megachile</i>	<i>disjuncta</i>	(Fabricius)
sp.174		<i>Megachile</i>	<i>ampulata</i>	Smith
sp.175		<i>Megachile</i>	sp.1	
sp.176		<i>Megachile</i>	sp.2	
sp.177		<i>Megachile</i>	sp.3	
sp.178	Megachilidae	<i>Megachile</i>	sp.4	
sp.179		<i>Megachile</i>	sp.5	
sp.180		<i>Megachile</i>	sp.6	
sp.181		<i>Megachile</i>	sp.7	
sp.182		<i>Megachile</i>	sp.8	
sp.183		<i>Megachile</i>	sp.9	
sp.184		<i>Megachile</i>	sp.10	
sp.185		<i>Megachile</i>	sp.11	
sp.186		<i>Megachile</i>	sp.12	
sp.187		<i>Megachile</i>	sp.13	
sp.188		<i>Megachile</i>	sp.14	
sp.189		<i>Megachile</i>	sp.15	
sp.190		unidentified	sp.	
sp.191	Mutillidae	<i>Trogaspidia</i>	sp.	
sp.192	Pompilidae	<i>Pompilus</i>	sp.1	
sp.193		<i>Pompilus</i>	sp.2	
sp.194	Scoliidae	<i>Camsomeris</i>	<i>collaris 4-fasciata</i>	Fabricius
sp.195		<i>Camsomeris</i>	<i>phalerata</i>	Saussure
sp.196		<i>Liacos</i>	sp.	

sp.197		<i>Megascolia</i>	<i>azurea</i>	Fabricius
			<i>rubiginosa</i>	
sp.198		<i>Scolia</i>	<i>quadripustulata</i>	Saussure
			<i>humeralis</i>	
sp.199		<i>Scolia</i>	sp.1	
sp.200		<i>Scolia</i>	sp.2	
sp.201	Scoliidae	<i>Scolia</i>	sp.3	
sp.202		<i>Scolia</i>	sp.4	
sp.203		unidentified	sp.1	
sp.204		unidentified	sp.2	
sp.205		unidentified	sp.3	
sp.206		unidentified	sp.4	
sp.207		unidentified	sp.5	
sp.208	Sphecidae	<i>Chalybion</i>	<i>benjalense</i>	(Dahlbom)
sp.209		<i>Chlorion</i>	<i>lobatum</i>	(Fabricius)
sp.210		<i>Chlorion</i>	sp.1	
sp.211		<i>Chlorion</i>	sp.2	
sp.212		<i>Episylon</i>	sp.	
sp.213		<i>Liris</i>	sp.	
sp.214		<i>Sceliphron</i>	<i>javanum</i>	(Lepeletier)
sp.215		<i>Sphex</i>	<i>argentatus</i>	Fabricius
sp.216		<i>Sphex</i>	<i>sericeus</i>	Lepeletier
			<i>lineolus</i>	
sp.217		<i>Sphex</i>	<i>viduatus</i>	Christ
sp.218		<i>Sphex</i>	sp.1	
sp.219		<i>Sphex</i>	sp.2	
sp.220	Vespidae	<i>Apodynerus</i>	sp.	
sp.221		<i>Auterhynchium</i>	sp.	
sp.222		<i>Delta</i>	<i>esuriens</i>	Fabricius
sp.223		<i>Delta</i>	sp.1	
sp.224		<i>Delta</i>	sp.2	
sp.225		<i>Delta</i>	sp.3	
sp.226	Vespidae	<i>Delta</i>	sp.4	
sp.227		<i>Delta</i>	sp.5	
sp.228		<i>Eumenes</i>	<i>conica</i>	Fabricius
sp.229		<i>Eumenes</i>	sp.1	
sp.230		<i>Eumenes</i>	sp.2	
sp.231		<i>Eumenes</i>	sp.3	
sp.232		<i>Phimenes</i>	sp.1	
sp.233		<i>Phimenes</i>	sp.2	
sp.234		<i>Polistes</i>	<i>stigma</i>	(Fabricius)
sp.235		<i>Polistes</i>	sp.1	
sp.236		<i>Polistes</i>	sp.2	

sp.237		<i>Polistes</i>	sp.3	
sp.238		<i>Polistes</i>	sp.4	
sp.239		<i>Polistes</i>	sp.5	
sp.240		<i>Rhynchium</i>	<i>haemorrhoidala</i>	(Fabricius)
sp.241		<i>Rhynchium</i>	<i>quincecinctum</i>	(Fabricius)
sp.242		<i>Vespa</i>	<i>affinis</i>	(Linnaeus)
sp.243		<i>Vespa</i>	sp.1	
sp.244		<i>Vespa</i>	sp.2	
sp.245		<i>Vespa</i>	sp.3	
sp.246		<i>Vespa</i>	sp.4	
sp.247		<i>Vespa</i>	sp.5	
sp.248		<i>Vespa</i>	sp.6	
Order Lepidoptera				
sp.249	Acraeidae	<i>Acraea</i>	<i>violae</i>	Fabricius
sp.250	Arctiidae	<i>Amata</i>	<i>sperbius</i>	Fabricius
sp.251		<i>Amata</i>	sp.	
sp.252		<i>Argina</i>	sp.	
sp.253		<i>Euchromia</i>	<i>elegantissima</i>	Wallgram
sp.254		unidentified	sp.1	
sp.255		unidentified	sp.2	
sp.256	Danaidae	<i>Danaus</i>	<i>chrysippus</i>	(Linnaeus)
			<i>chrysippus</i>	
sp.257		<i>Danaus</i>	<i>genutia genutia</i>	(Cramer)
sp.258		<i>Euploea</i>	<i>aglae limborgii</i>	Moore
sp.259		<i>Euploea</i>	<i>core godartii</i>	(Lucas)
			<i>klugii</i>	Felder
sp.260		<i>Euploea</i>	<i>erichsonii</i>	
sp.261		<i>Euploea</i>	sp.	
sp.262		<i>Ideopsis</i>	sp.	
sp.263	Gelechiidae	unidentified	sp.	
sp.264	Geometridae	unidentified	sp.	
sp.265	Hesperiidae	<i>Caltoris</i>	<i>bromus</i>	Leech
			<i>bromus</i>	
sp.266		<i>Spialia</i>	<i>galba</i>	(Fabricius)
sp.267		<i>Telicota</i>	<i>linna</i>	Evans
sp.268		unidentified	sp.1	
sp.269		unidentified	sp.2	
sp.270		unidentified	sp.3	
sp.271		unidentified	sp.4	
sp.272	Lycaenidae	<i>Amblypodia</i>	<i>anita anita</i>	Hewitson
sp.273		<i>Cyclosia</i>	<i>panthona</i>	Cramer
sp.274	Lycaenidae	<i>Everes</i>	<i>lacturnus rileyi</i>	Godfrey
sp.275		<i>Loxura</i>	<i>atymnus</i>	Fruhstofer

sp.276		<i>Rapala</i>	<i>continentalis</i> <i>pheretima</i>	(Hewitson)
sp.277		<i>Spindasis</i>	<i>petosiris</i> <i>syama terana</i>	(Fruhstorfer)
sp.278		<i>Surendra</i>	<i>quercetorum</i> <i>quercetorum</i>	(Moore)
sp.279		<i>Zizina</i>	<i>otis sangra</i>	(Moore)
sp.280		unidentified	sp.	
sp.281	Noctuidae	unidentified	sp.	
sp.282	Nymphalidae	<i>Cethosia</i>	<i>cyane euanthus</i>	Fruhstorfer
sp.283		<i>Cirrochoa</i>	<i>tyche mithila</i>	Moore
sp.284		<i>Junonia</i>	sp.	
sp.285		<i>Neptis</i>	<i>hylas kamarupa</i>	Moore
sp.286		<i>Tanaecia</i>	sp. <i>agamemnon</i>	
sp.287		unidentified	sp.	
sp.288	Papilionidae	<i>Chilasa</i>	<i>clytia clytia</i>	(Evans)
sp.289		<i>Graphium</i>	<i>agamemnon</i> <i>agamemnon</i>	Linnaeus
sp.290		<i>Graphium</i>	<i>doson axion</i>	(Felder)
sp.291		<i>Lamproptera</i>	<i>meges virescens</i>	(Butler)
sp.292	Papilionidae	<i>Pachliopta</i>	<i>aristolochiae</i> <i>goniopeltis</i>	(Rothschild)
sp.293		<i>Papilio</i>	<i>demoleus</i> <i>malayanus</i>	Wallace
sp.294		<i>Papilio</i>	<i>memnon agenor</i>	Linnaeus
sp.295		<i>Papilio</i>	<i>polytes romulus</i>	Cramer
sp.296		<i>Pathysa</i>	<i>antiphates</i> <i>pompilius</i>	(Fabricius)
sp.297		<i>Troides</i>	<i>aeacus aeacus</i>	Felder
sp.298	Pieridae	<i>Appias</i>	<i>albina darada</i>	
sp.299		<i>Appias</i> <i>Catopsilia</i>	<i>olferna olferna</i> <i>pomona</i>	
sp.300			<i>pomona</i>	
sp.301		<i>Eurema</i>	sp.	
sp.302		<i>Ixias</i>	<i>pyrene</i> <i>yunnanensis</i>	(Druce)
sp.303		<i>Leptosia</i>	<i>nina nina</i>	(Fabricius)
sp.304	Pyrilidae	unidentified	sp.1	
sp.305		unidentified	sp.2	
sp.306	Satyridae	<i>Mycalesis</i>	sp.	
sp.307		<i>Ypthima</i>	sp.	
sp.308		<i>Melitta</i>	sp.3	

sp.309	Sphingidae	<i>Cephonodes</i>	<i>hylas hylas</i>	(Linnaeus)
sp.310	Tortricidae	unidentified	sp.	
	Order Mantodea			
sp.311	Mantidae	<i>Mantis</i>	<i>religiosa</i>	Linnaeus
sp.312		unidentified	sp.	
	Order Orthoptera			
sp.313	Acrididae	unidentified	sp.	
sp.314	Tettrigoniidae	unidentified	sp.1	
sp.315		unidentified	sp.2	
sp.316		unidentified	sp.3	

S6 Results from the structural equation model showing regression, covariance, and variance to predict the relationships between environmental variables (land use and forest proximity) and pollinator community composition (richness and abundance) prevalence on pollination network structure (robustness and interaction evenness).

	Variables	Estimate	SE	Z-value	P-value	Standardized
Regression:						
Richness	Distance to forest edge	-71.708	4.85	-14.785	0.0001 **	-1.260
	Urban	-10.954	4.795	-2.284	0.022*	-0.149
	Low.mosaic (1 km)	0.531	0.067	7.915	<0.001***	0.665
Abundance	Distance to forest edge	-16.418	1.695	-9.684	<0.001***	-1.171
	Urban	-3.235	1.688	-1.917	0.055	0.179
	Low.mosaic (1 km)	0.197	0.024	8.260	<0.001***	0.986
Evenness	Distance to forest edge	-0.034	0.013	-2.621	0.009*	-0.447
	Urban	0.042	0.017	2.566	0.010*	0.437
Robustness	Distance to forest edge	-0.002	0.015	-0.154	0.878	-0.030
	Low.mosaic (1 km)	0.001	0.001	2.404	0.016*	0.420
	Abundance	0.004	0.001	4.923	<0.001***	0.756
Covariance:						
Richness	Abundance	16.615	6.169	2.693	0.007*	0.760
	Evenness	-0.050	0.034	-1.484	0.138	-0.235
	Robustness	-0.019	0.014	-1.342	0.180	-0.210
Evenness	Robustness	-0.001	0.001	-2.265	0.791	-0.061
Variance:						
	Richness	63.248	19.753	3.202	0.001**	0.080
	Abundance	7.547	2.448	3.082	0.002*	0.157
	Evenness	0.001	0.001	3.082	0.002*	0.527
	Robustness	0.001	0.001	3.082	0.002*	0.084