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Diversity of bats in three selected forest types in Peninsular Malaysia

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Abstract: Bats, occupying a variety of habitats, play important roles in the tropical forest. Through this study, comparisons on bat species richness and evenness in primary forest, secondary forest, and urban forest were made. Sampling was conducted between 18:30 PM and 06:30 AM using 10 mist-nets and four harp traps for three consecutive nights at the primary and secondary forest of Ulu Gombak Forest Reserve and urban forest in the Universiti Malaya Botanical Garden. This study progressed from February 2012 until April 2014. A total number of 1226 individuals representing 46 species were managed to be captured throughout the period of this study. From this, a total of 396 individuals of bats from 33 species were recorded in primary forest, 608 individuals of bats from 31 species were recorded in secondary forest and 222 individuals of bats from 11 species were recorded in the urban forest. The primary forest (Shannon–Wiener, $H' = 2.516$) has a higher diversity of bats compared to the secondary forest (Shannon–Wiener, $H' = 2.476$) and the urban forest (Shannon–Wiener, $H' = 1.527$). However, the urban forest has a higher evenness index calculated ($E = 0.4184$) compared to the primary forest ($E = 0.3994$) and the secondary forest ($E = 0.3718$). Species richness in the secondary forest is the highest ($Dmn = 1.616$) followed by the primary forest ($Dmn = 1.257$) and the urban forest ($Dmn = 0.7383$). This study showed that the primary forest is more diversified compared to other habitats although more individuals were recorded in the secondary forest.

Key words: Primary forest, secondary forest, urban forest, bats

1. Introduction

Anthropogenic disturbance can cause species loss and extinction of many bat taxa (Kingston, 2010). The tropical forest landscape had changed dramatically due to human activities (Fukuda et al., 2009), with the existing forest becoming fragmented causing habitat loss and decreasing in food resources for bats (Azlan, 2000). Bats occupy a variety of habitats including primary forest, secondary forest, mangrove, cultivated areas, orchards, gardens, and urban areas (Boon and Corlett, 1989; Tan et al., 1998; Francis, 2008). They are important indicators of the state of ecological communities and bat survey is often used for conservation planning (Francis et al., 2010).

In Southeast Asia, the bat communities have been greatly underestimated (Kingston et al., 2003a). Malaysia is a critical country for international bat conservation with the total count of 133 species throughout the country (Kingston, 2012), and 110 bat species recorded in Peninsular Malaysia (Lim et al., 2017). Of the total number of species documented in the country, 10 species are listed as vulnerable and one species, *Hipposideros coxi* (Shelford, 1901), is listed as endangered in the IUCN Red List

(IUCN, 2016). Among major threats to bats are habitat loss and hunting (Mickelburgh et al., 2002), but new threats have emerged over the years such as diseases of bats and climate changes (Welbergen et al., 2008; O'Shea et al., 2016; Frick et al., 2019). Habitat fragmentation resulting from anthropogenic activities are somewhat less severe for bats than for other animal groups (Gibson et al., 2011), nonetheless affecting bats assemblage structure (Meyer, 2016).

Bat species play an important role in our ecosystem. At least 31 Malaysian plant species rely on Old World fruit bats (Megachiroptera) to pollinate them including durian, petai, mango, banana, guava, jackfruit, and papaya (Kingston et al., 2006). According to Struebig et al. (2010), Old World fruit bats exhibit dispersal capabilities and generalist feeding habits. *Eonycteris spleae* (Dobson, 1871), a long-tongued fruit bat that is widely distributed in Southeast Asia remains an important pollinator of commercial food crops such as durian (Lim, 2018). Acharya et al. (2015) recorded that this species travelled a long distance to foraging areas with durian, moving one-way between flowering patches of durian. Members

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of the suborder Microchiroptera play an important role as biological control agents on insect populations in forests and agriculture (Zubaid et al., 2004). Every night, insectivorous bats eat at least half of their body weights, which is equivalent to 600 mosquito-sized insects in an hour, and large colonies can consume over 2000 t of insects per year (Kingston et al., 2006; Kolkert et al., 2019).

Lowland forest is valuable to the logging industry because it is rich in dipterocarp species and recently logged areas require long periods of time to recover (Sodhi et al., 2004). Didham et al. (1996) stated that the effects of habitat disruption may reduce diversity of bats because of changes as edge effects alter the forest microclimate and population of the insects. Edge effects lower humidity and increase light, temperature, wind disturbance, and desiccation. These physical alterations lead to a decrease in insect populations due to reductions in plant reproductive success (Didham et al., 1996). Narrow-space foragers and open-space bats responded differently to forest edges, where open-space bats had higher counts at edges (Estrada et al., 2010). Meyer and Kalko (2008), in their study of gleaning bats, stated that species compositions did not change significantly between interior and forest edge; however, edge sensitivity has been identified as the species' most known trait of vulnerability to fragmentation.

Fragmented forest may influence habitat use by foraging bats due to effects in flight, prey, and roost abundance. According to Kingston et al. (2003b), insectivorous bats used different foraging strategies depending on whether they were in highly cluttered space, small clearings like over small streams, and open spaces above the forest. Bats did not prefer highly cluttered vegetation because it affected the efficiency of flight. Some species may roost in highly cluttered areas but feed in less cluttered vegetation. Some bats avoid open areas to avoid predators or high winds, which may interfere with flight or prey capture as reported by Patriquin and Barclay (2003).

Russo et al. (2010) stated that diversity of bats in an area is dependent on the foraging area, availability of roosting, and food resources. Bats can access resources that are widely scattered in the environment because they are able to commute between forest patches and utilize matrix habitat for several kilometers in one night. However, some insectivorous bat species have a limited foraging range due to energetically expensive flight that is not suitable for long distance (Struebig et al., 2008). Forest bats are strictly dependent on the forest structure for foraging and roosting but some bats that can be found in other types of vegetation are influenced by the size of wing, type of maneuverability, roosting sites, and also foraging type (Patriquin and Barclay, 2003). Therefore, the aim of this study was to compare diversity, species richness, and evenness of bat species between three the primary forest, secondary forest, and urban forest.

2. Materials and methods

2.1. Study sites

The study was carried out at two sites in Ulu Gombak Forest Reserve in Selangor representing the primary and secondary forest, and Universiti Malaya Rimba Ilmu Botanical Garden in Kuala Lumpur representing urban forest (Figure 1). These study sites were selected as they differed in forest structure. The primary forest (3°19.191'N, 101°44.512'E) is an intact forest of Ulu Gombak Forest Reserve. It is located alongside the east-coast highway. A variety of tree species that form the canopy and emergent layers can be seen. The variations in canopy height are much larger than in the regenerating forest which intermittently occurred via gap formation. Many towering trees of the family Dipterocarpaceae (*Shorea* spp. and *Dipterocarpus* spp.) and *Ficus* sp. are present in this area. Bamboo and small shrubs are also present in some areas within this study site. The secondary or logged forest (3°20.033'N, 101°46.347'E) is a regenerated forest that has been logged approximately 30 years ago. Tree height in the forest varies and there are many bamboo trees as a result of disturbance. Other vegetation types in this area are rattan, pandan, small palm trees, *Macaranga* spp., and aggregation of medium sized trees. Canopy heights in this area are much lower than in the primary forest due to the fact that the trees grow immediately after logging and the canopy gap is uniform. The forest floor is dense with shrub vegetation covering the ground while some patch area is an open area with no tree. The urban forest (3°8'N, 101°40'E) is a botanical garden located in the Universiti Malaya campus. The garden was established in 1974 and planted with a diversity of plants in the need to conserve and study flora in Malaysia (Wong, 1997). The collections were labelled to provide names and information of plants to visitors. Wong (1997) mentioned medicinal plants species such as *Orthosiphon aristatus* (Blume) Miq. and *Catharanthus roseus* (L.) G. Don that can be found in the vicinity. The Palms, the Citrus, and the Citroid Collection are the main collections of the botanical garden. Various other plant species including ferns, bamboos, fruiting-tree, and timber are also planted. Most species of plants in the garden are indigenous to the region but there are also plants from other continents in the collection.

2.2. Sampling methods

Samplings were conducted every month at the three selected sites alternately between February 2012 and April 2014 (Table 1) using mist-nets and four-bank harp traps. Mist-net was made up of nylon and has a dimension of 2.5 m high, 12 m long, and 38 mm mesh size. Poles and ropes were used to erect the nets. Four-bank harp trap is made up of an aluminum rectangular frame with four-bank vertical nylon lines and a canvas bag attached to it for holding trapped bats (Francis, 1989). Harp traps were

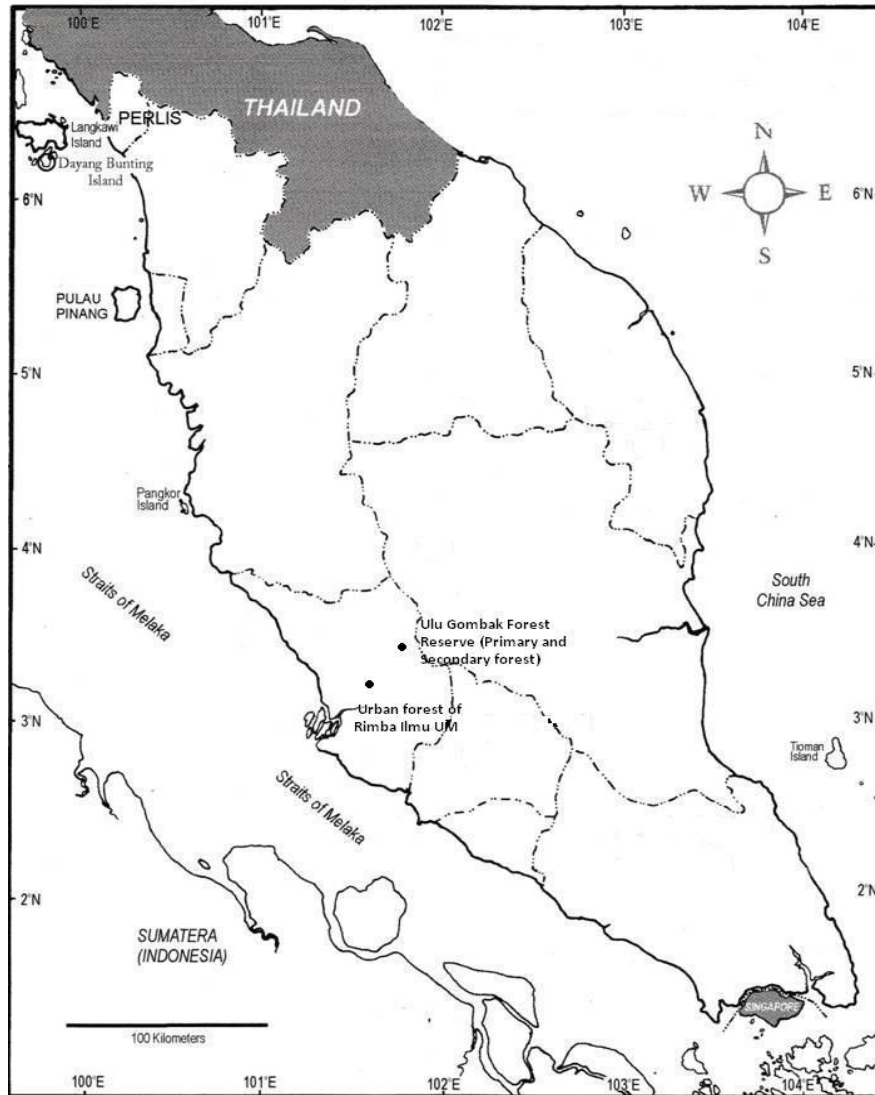


Figure 1. Map showing three sampling localities: the primary forest, secondary forest of Ulu Gombak Forest Reserve, Selangor, and urban forest at Universiti Malaya Rimba Ilmu Botanical Garden, Kuala Lumpur.

Table 1. Frequency of visits for each selected site.

Forest type	Dates of visit
Primary forest	8–11 Feb 2012; 16–19 May 2012; 4–7 Sept 2012; 7–10 Jan 2013; 23–26 Apr 2013; 19–22 Aug 2013; 10–13 Nov 2013; 10–13 Feb 2014
Secondary forest	4–7 Mar 2012; 22–25 June 2012; 2–5 Oct 2012; 5–8 Feb 2013; 15–18 May 2013; 2–5 Sept 2013; 12–15 Dec 2013; 20–23 Mar 2014
Urban forest	12–15 Apr 2012; 11–14 July 2012; 4–7 Nov 2012; 12–15 Mar 2013; 3–6 June 2013; 20–23 Oct 2013; 4–7 Jan 2014, 5–8 Apr 2014

set up in corridors in between trees. Mist-nets and harp traps that were placed at ground level were selectively installed at areas that were potentially used as flyways, well-established trails, or in small clearing areas, near roosting sites, and near rivers or any water sources within the selected sites. For each visit, 10 mist-nets and four four-bank harp traps were set up for a period of three nights. These mist-nets and harp traps were left open overnight and the nets were closed during the day. Mist-nets and harp traps were opened at 18:30 PM and checked at 19:30 PM, 20:30 PM, 21:30 PM, 22:30 PM and 23:30 PM and the final check at 06:30 AM. More frequent visits were

done in the event where the capture rate was high. Regular monitoring is not needed if the capture rate is low since it can increase disturbance and may affect the capture rate (Barlow, 1999).

2.3. Bat species identification

All trapped bats were extracted from nets and traps and were temporarily kept inside cloth bags. Individuals captured were marked by wing punctuation to avoid double counting during the visit. Bats were then identified up to species level using the information from field guides following Francis (2008) and Kingston et al. (2006). The standard morphological measurements were recorded and the pictures of bats were taken for correct identification and future reference. Vernier caliper (measured in millimeters), steel ruler and spring scales (measure weight ranges up to 100 g) were used in measuring the external morphological characters. Morphological characters that were measured are ear length (E), forearm length (FA), tibia length (TB), tail length (l), weight (g), and sex (male/female). The sex of the bats can be easily identified by the presence of nipples for female and prominent penis for males. All the morphological measurements were recorded in a data sheet and all bats were released at the site of where they were captured after processing.

2.4. Data analysis

Analyses were done to determine the species richness, evenness, abundance, and significant differences between the three sites. Shannon–Wiener (H) was used to determine species diversity while evenness (E) in the community was calculated using Shannon–Wiener equitability. Species richness (R) was calculated using Menhinick's Richness index. In order to determine the ratio of species number to individuals captured and species dominance, relative abundance index was calculated. An ANOVA test was used to compare the mean of bats captured in the three habitat types. If the P-value is below 0.05, there is a statistically significant difference between the three sites while if the P-value is more than 0.05 it shows no significant difference. Then, the species accumulation curve was plotted for the three forest types to illustrate the completeness of sampling efficiency. The first-order Jackknife method was used to estimate projected species richness at increasing levels of sampling effort. The number of species is estimated using Chao, ACE, and Jackknife. Jackknife estimate is based on the number of unique species presented in each observation (Smith and Pontius, 2006). The analysis can give an estimate of species richness that estimates the number of species obtained if the sampling is continued. If the curve is flat, it shows that the sampling has reached asymptotes and can be stopped. The statistical analyses were analyzed using PAST software and the species accumulation curve was plotted using the Estimate S Version 9.1.0.

3. Results

3.1. Species accounts

The samplings have resulted in the capture of 1226 individuals representing 46 species. A total of 396 individuals of bats from 33 species were recorded in the primary forest, 608 individuals of bats from 31 species were recorded in the secondary forest, and 222 individuals of bats from 11 species were recorded in the urban park (see Appendix A). From the seven families recorded in the three habitat types, the family Vespertilionidae recorded the highest number of species in the secondary forest with 13 species (95 individuals). The family Vespertilionidae has also recorded the highest number of species in the primary forest with nine species composed of 49 individuals (Figure 2). The family Pteropodidae has the highest number of individuals in the secondary forest with 305 individuals from eight species. *Cynopterus brachyotis* (Müller, 1838) comprises the highest number of bats captured from the family Pteropodidae in all three habitat types. The family Hipposideridae dominated the number with seven species (182 individuals) in the primary forest. For the family Rhinolophidae, six species were recorded at primary and secondary forests respectively, with 35 individuals found in the primary forest and 37 individuals recorded in the secondary forest. The family Nycteridae with only one species presented in the region recorded only four individuals in the primary forest (Figure 3). The family Emballonuridae has a low number of species captured with only two species at the primary forest while the family Megadermatidae recorded both species in the family at the primary forest.

3.2. Relative abundance

Seven families of bats were recorded in this study. Of all the families, the family Pteropodidae has recorded a high relative abundance in all the three habitat types. The family Pteropodidae accounted for 29.86% in the primary forest, 50.23% in the secondary forest, and 78% in the urban forest. In the primary forest, the family Hipposideridae was the highest with 46.47% of total capture. *Hipposideros cervinus* (Gould, 1854) represents the most captured species from the family Hipposideridae. The secondary forest and the urban forest have also recorded a high capture of the family Hipposideridae compared to the other families. The family Rhinolophidae was only captured in the primary and the secondary forest with 8.94% and 5.92% of total capture respectively. The family Emballonuridae (1.53%) and the family Megadermatidae (1.79%) were only present in the primary forest. The family Nycteridae was only present in the primary forest with 1.02% and the secondary forest with 0.16% of total capture (Figure 4). *C. brachyotis* shows the highest species relative abundance in the two habitat types; the secondary forest and the urban forest, whereas *H. cervinus* was the most dominant species in the

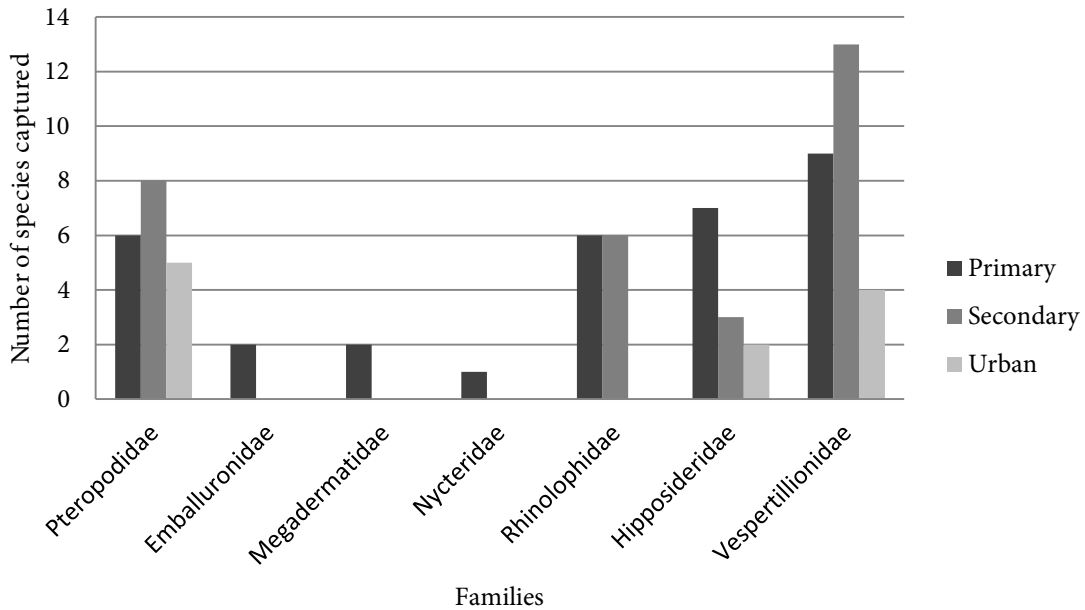


Figure 2. Number of species captured according to families in the three habitat types.

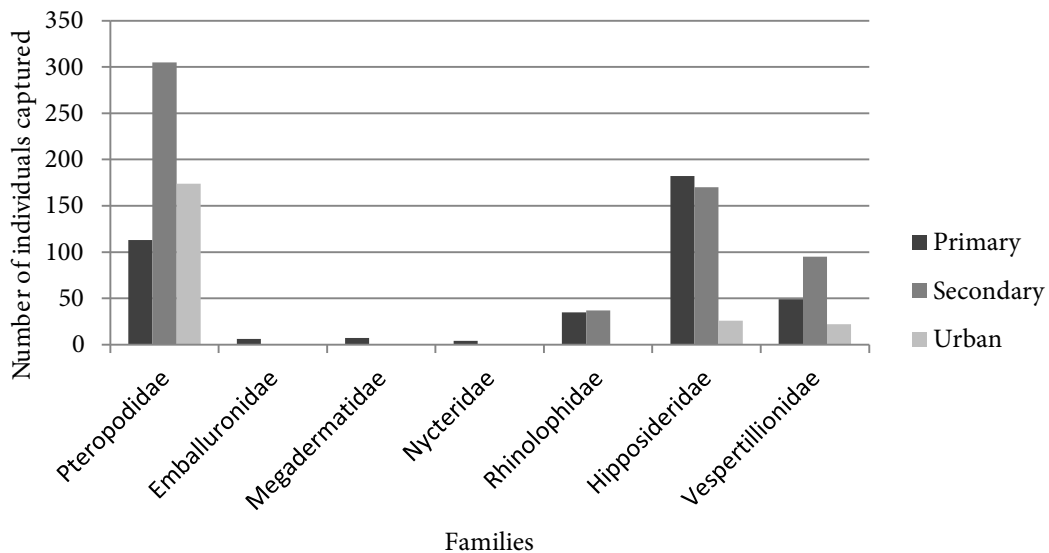


Figure 3. Number of individuals captured according to families in the three habitat types.

primary forest. In the primary forest, *H. cervinus* and *C. brachyotis* were the two species that showed the highest relative abundance with 32.4% and 21.94% of total capture respectively. *C. brachyotis* (27.14%) and *H. cervinus* (16.61%) were also dominant in the secondary forest. Although more than 100 individuals of *H. cervinus* were captured respectively in the primary and the secondary forest, only 17 individuals of *H. cervinus* were captured in the urban forest. In the urban forest, *C. brachyotis* being

the most abundant species represented 59.91% of total capture followed by *C. horsfieldi* (Gray, 1843) with 9.46% of total capture. *H. larvatus* (Horsfield, 1823), *H. diadema* (Geoffroy, 1813), *H. galleritus* (Cantor, 1846), and *H. doriae* (Peters, 1871) were only found in the primary forest. *Macroglossus sobrinus* (Andersen, 1911) and *M. Minimus* (Geoffroy, 1810) were only found in the secondary forest and the urban forest. *Scotophilus kuhlii* (Leach, 1821) was only found in the urban forest. There were several species

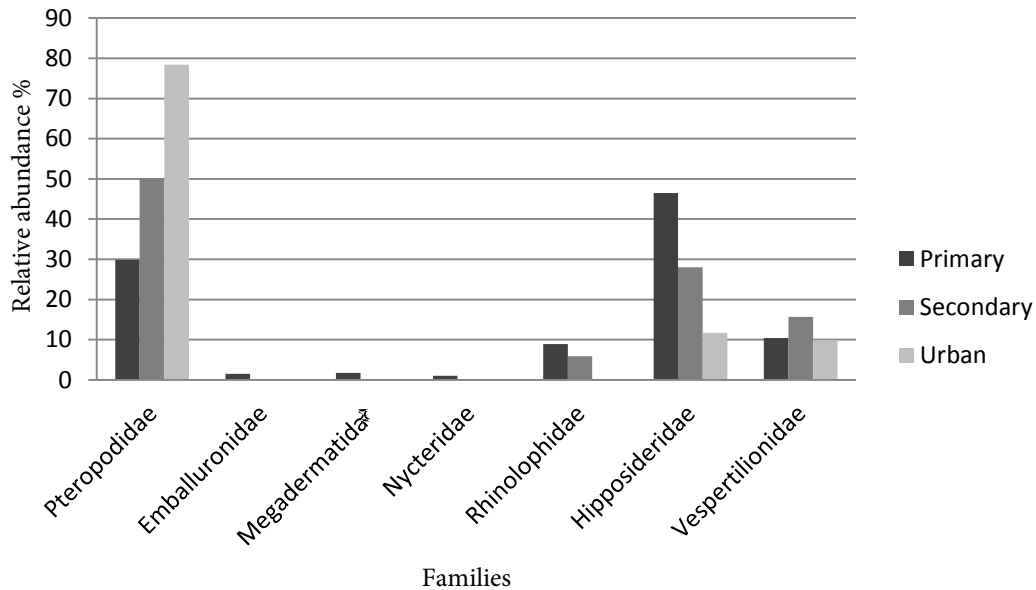


Figure 4. Relative abundance (%) of families in the three habitat types.

that were represented by only one individual in one habitat type but were represented by more than one individual in another habitat type. For example, only one individual of *Chironax melanocephalus* (Temminck, 1825) was recorded in the primary forest but 19 individuals were recorded in the secondary forest (Table 2).

3.3. Species richness and evenness

The species diversity index calculated shows that the primary forest (Shannon–Wiener, $H' = 2.516$) has a higher diversity of bats compared to the secondary forest (Shannon–Wiener, $H' = 2.476$) and urban forest (Shannon–Wiener, $H' = 1.527$). However, the urban forest has a higher evenness index calculated ($E = 0.4184$) compared to the primary forest ($E = 0.3994$) and the secondary forest ($E = 0.3718$). Species richness in the secondary forest is the highest ($Dmn = 1.616$) followed by the primary forest ($Dmn = 1.257$) and urban forest ($Dmn = 0.7383$) (Table 3). The ANOVA test showed that there was a significant difference in the diversity of bats captured in all three habitat types ($F = 1.385$, $p = 0.02539$). The species accumulation curve showed that there was an increase of species captured in each habitat (Figure 5). The result is very close to CHAO estimator where it estimates 33 species for the primary forest, 34 species for the secondary forest, and 11 species for the urban forest. Jackknife estimator estimated that there are probably 40 species in the primary forest, 38 species in the secondary forest and 12 species in the urban forest.

3.4. Capture rate

The total trapping effort using mist nets were 2880 h and for harp traps were 1152 h. The capture rate using mist-nets was 0.04 in the primary forest, 0.10 in the secondary forest, and 0.06 in the urban forest. Harp traps recorded the capture rates of 0.25 in the primary forest, 0.27 in the secondary forest, and 0.04 in the urban forest. The capture rates for harp traps were greater in which they recorded 650 individuals as compared to the capture rates for mist-nets which comprised 576 individuals.

4. Discussion

4.1. Species accounts

There are 110 bat species recorded in Peninsular Malaysia (Lim et al., 2017). In this study, 46 bat species from seven families, i.e. Pteropodidae, Emballonuridae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, and Vespertilionidae were recorded within the three habitat types. Comprehensive sampling time, intensive trapping and sampling design (Trevelin et al., 2017), equipment, i.e. radiotelemetry, and manpower strongly influence the number of bat species captured (Kingston et al., 2006). The family Vespertilionidae demonstrates the highest number of species captured in the primary forest. This family is the largest, most diverse, and most widespread family of bats occurring in every continent except the Antarctica (Francis, 2019).

The highest number of species at the secondary forest is contributed by the family Pteropodidae. They are important seed dispersers and pollinating agents for some

Table 2. Relative abundance of bat species captured in the three habitat types.

Family	Species	Relative abundance (%)		
		Primary	Secondary	Urban
Pteropodidae	<i>Balionycteris maculata</i>	4 (1.02)	52 (8.62)	
	<i>Cynopterus brachyotis</i>	86 (21.94)	165 (27.14)	133 (59.91)
	<i>Cynopterus horsfieldi</i>	11 (2.81)	42 (6.91)	21 (9.46)
	<i>Chironax melanocephalus</i>	1 (0.26)	19 (3.13)	
	<i>Eonycteris spleae</i>		2 (0.33)	7 (3.15)
	<i>Macroglossus minimus</i>		1 (0.16)	5 (2.25)
	<i>Macroglossus sobrinus</i>		3 (0.49)	8 (3.60)
	<i>Megaerops ecaudatus</i>	6 (1.53)	21 (3.45)	
	<i>Penthetor lucasi</i>	5 (1.28)		
Emballonuridae	<i>Emballonura monticola</i>	2 (0.51)		
	<i>Taphozus longimanus</i>	4 (1.02)		
Megadermatidae	<i>Megaderma lyra</i>	3 (0.77)		
	<i>Megaderma spasma</i>	4 (1.02)		
Nycteridae	<i>Nycteris tragata</i>	4 (1.02)	1 (0.16)	
Rhinolophidae	<i>Rhinolophus acuminatus</i>	6 (1.53)		
	<i>Rhinolophus affinis</i>	1 (0.26)	6 (0.99)	
	<i>Rhinolophus lepidus</i>		1 (0.16)	
	<i>Rhinolophus luctus</i>	4 (1.02)	1 (0.16)	
	<i>Rhinolophus sedulus</i>	4 (1.02)	12 (1.97)	
	<i>Rhinolophus stheno</i>	5 (1.28)	4 (0.66)	
	<i>Rhinolophus trifoliatus</i>	15 (3.83)	13 (2.14)	
Hipposideridae	<i>Hipposideros bicolor</i>	28 (7.14)	52 (8.62)	9 (4.05)
	<i>Hipposideros cervinus</i>	127 (32.40)	101 (16.61)	17 (7.66)
	<i>Hipposideros cineraceus</i>	9 (2.30)	17 (2.80)	
	<i>Hipposideros diadema</i>	9 (2.30)		
	<i>Hipposideros doriae</i>	2 (0.51)		
	<i>Hipposideros galleritus</i>	3 (0.80)		
Vespertilionidae	<i>Hipposideros larvatus</i>	4 (1.02)		
	<i>Glischropus tylopus</i>	2 (0.51)		
	<i>Kerivoula hardwickii</i>		3 (0.49)	
	<i>Kerivoula intermedia</i>	9 (2.30)	2 (0.33)	
	<i>Kerivoula minuta</i>		2 (0.33)	
	<i>Kerivoula papillosa</i>	6 (1.53)	20 (3.29)	
	<i>Kerivoula pellucida</i>	11 (2.81)	8 (1.32)	
	<i>Murina aenea</i>	7 (1.79)		
	<i>Murina suilla</i>	2 (0.51)	6 (0.99)	
	<i>Murina cyclotis</i>		3 (0.49)	
	<i>Myotis ater</i>			3 (1.35)
	<i>Myotis muricola</i>		6 (0.99)	4 (1.80)
	<i>Myotis ridleyi</i>	7 (1.79)	33 (5.43)	
	<i>Myotis rosseti</i>		1 (0.16)	
	<i>Pipistrellus tenuis</i>		1 (0.16)	
	<i>Philetor brachypterus</i>	3 (0.77)		
	<i>Scotophilus kuhlii</i>			10 (4.50)
<i>Tylonycteris pachypus</i>	2 (0.51)	5 (0.82)	5 (2.25)	
<i>Tylonycteris robustula</i>		5 (0.82)		
Total records		396 (100)	608 (100)	222 (100)
Number of species		33	31	11
Number of families		7	5	4

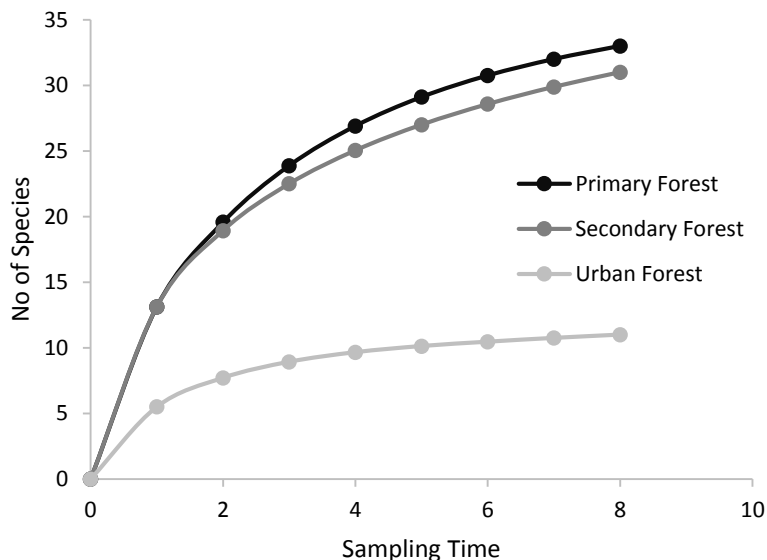


Figure 5. Species accumulation curves indicating the cumulative number of species encountered relative to sampling time.

Table 3. Diversity, richness, and evenness for the three types of habitat.

	Primary forest	Secondary forest	Urban forest
Number of species, S	33	31	11
Number of individuals, N	396	608	222
Menhinicks's index	1.257	1.616	0.7383
Shannon's diversity index H	2.516	2.476	1.527
Shannon's equitability EH	0.3994	0.3718	0.4184

plant species and therefore play an important role in forest regeneration (Cosson et al., 1999; Hodgkison et al., 2006), maintaining forest diversity (Bonaccorso and Gush, 1987), and maintaining economically important fruit crops in the region (Acharya et al., 2015; Aziz, et al., 2017). *C. brachyotis* is the biggest contributor of species captured for the family Pteropodidae. Members of *C. brachyotis* can be found in many habitats including primary forest, secondary forest, agricultural landscape, orchard, mangrove, hill, and disturbed habitats (Ketol et al., 2009; Struebig et al., 2010; Karuppudurai et al., 2018).

The family Hipposideridae is a diverse group of insectivorous bats (Murray et al., 2018). The high number of species from the family Hipposideridae in the primary

forest marks that the habitat has an abundance of insects. Insectivorous bats that live in a large colony consume about 2000 t of insects a year (Kingston et al., 2003b; Tingga et al., 2012) and taken in about 30% to 100% of their body weight in prey each night (Kunz et al., 2011; Kolkert et al., 2019).

The families Nycteridae and Megadermatidae which comprise a single and double species respectively were only captured in the primary forest. *Megaderma spasma* (Linnaeus, 1758) is a species whose members inhabit forests while *M. lyra* (Geoffroy, 1810) members prefer abandoned buildings, mines, and tunnels as habitat (Csorba et al., 2008). In this study, *M. lyra* members were captured in the primary forest conceivably because the forest was situated close to a mining area. Only a small number of *M. spasma* individuals were recorded exhibiting a small colony size presented in the habitat. Members of this species live in a very small colony consisting of two individuals but can reach up to 30 individuals depending on the size of the area (Kingston et al., 2006; Csorba et al., 2008; Balete, 2010).

4.2. Relative abundance

The diversity of the family Hipposideridae was the highest in the primary forest. Zubaid (1988) and Azlan et al. (2000) reported that insectivorous bats are more specialized in their feeding behavior and thus more seriously affected by habitat change. Insect diversity is strongly related to plant diversity (Murdoch et al., 1972; Azlan et al., 2000). Forest fragmentation not only influences the abundance

and diversity of insects but also modifies higher-order interactions between insects and other organisms, both directly and indirectly (Didham et al., 1996). Insectivorous bats can be opportunistic predators where they forage in areas with abundant prey sources and select particular insects' family within many taxa available (McCracken et al., 2012; Heim et al., 2017).

Pteropodidae bats are known as important and effective plant pollinators (Acharya et al., 2015; Stewart and Dudash, 2017). In the secondary forest, the family Pteropodidae was recorded as the most captured. They are regarded as keystone species for forest regeneration, visiting at least 141 plant species including a number of commercially important plants (*Durio*, *Ceiba*, and *Parkia*) for nectar or pollen (Marshall, 1985; Fujita and Tuttle, 1991). In more recent studies (Sritongchuay et al., 2016; Stewart and Dudash, 2017), bats were recorded visiting *Ceiba pentandra*, *Durio zibethinus*, *Musa acuminata*, *Oroxylum indicum*, *Parkia speciosa*, *Parkia timoriana*. The existence of roost sites provided by *Macaranga* sp., palma (*Orania sylvicola*), and rattan (*Calamus* sp.) used by fruit bats in a small colony increases the success of capturing Pteropodidae bats (Campbell et al., 2006). Fruit bats such as *Cynopterus brachyotis* are among the species that are the most tolerant of human disturbance (Evelyn and Stiles, 2003) and are less sensitive to landscape changes as frugivorous bats are able to explore wide range of resources (Sritongchuay and Brumrungsri, 2019). Their ability to enter a wide variety of areas contributes to their ecological roles as seed dispersers (Fukuda et al., 2009). On the other hand, *Balionycteris maculata* (Thomas, 1893) was abundant in the secondary forest. They are primarily a forest species, found from lowland to hill and occasionally montane forest (Tingga et al., 2012). This species roost in the cavities in the root masses of epiphytic plant species, active arboreal nest of the ants, abandoned arboreal termites nest, and the hollow base of a large detached branch (Hodgkison et al., 2004b). The secondary forest provides a suitable habitat for this species because of the presence of logs and branches remnants from logging activities.

The urban forest has a very high capture rate of Pteropodidae bats with *C. horsfieldii* as the most captured species. The urban forest which was planted with many fruit trees may be adequate food resources for most frugivorous bats. Palm vicinity in the urban forest has contributed to roosting sites for bats. Hodgkison et al. (2004a) stated that this species forages at all heights below the canopy, utilizing both synchronously and asynchronously fruiting trees. The wide range of fruit diet explains the presence of this species in the urban forest. Meanwhile, the family Vespertilionidae was also found in the urban forest. *Tylonycteris pachypus* (Temminck, 1840)

members were captured as a result of an abundance of bamboo groves presented at site. These bats roost in small groups in the internodes of live bamboo stem (Payne, 1985) entering and exiting through small vertical slits (Feng et al., 2008). *Scotophilus kuhlii* members roost under house roofs, in palm tree leaves, and in hollow trees and forage for aerial insects in open areas, around towns, and over forests (Payne, 1985). A small building in the vicinity may have been a roosting site for this species. The activity pattern and home range of this species are often random and influenced by food availability, preferences, and breeding behavior (Atikah, 2015).

H. cervinus was captured extensively in the primary and the secondary forests since this species usually roosts in large colonies (Francis, 2019). According to Payne et al. (1985), this species has been noted to feed in the forest understory, increasing the chance of being caught by the understory harp traps. This species usually emerges as a group to prey for insects and the high relative abundance of this species shows that the area receives an abundance of insects. According to Kingston (2006), *H. cervinus* can be found in primary forests, fed under the canopy with *H. bicolor* (Temminck, 1834). This also explains the abundance of *H. bicolor* in both the primary and the secondary forest.

Macroglossus spp. were captured in the secondary forest and the urban forest but none in the primary forest. Nectarivorous bat species are the more important pollinators because of the pollen transfer effectiveness (Stewart and Dudash, 2017). *M. minimus* is an important pollinator of mangroves (*Sonneratia*) and native bananas (*Musa*) (Payne et al., 1985; Bonaccorso and McNAb, 1997). Winkelmann (2003) noted that *M. sobrinus* is abundant in inland forest and is considered a banana specialist.

Philetor brachypterus (Temminck, 1840) was recorded in the primary forest. According to Francis (2019), this species is usually found near intact forest. The presence of this species in primary forest suggested that this species depends on pristine forest and is sensitive to disturbance or landscape changes.

Nycteris tragata (Andersen, 1912) was present at both the primary forest and the secondary forest. This species largely roosts in mature rainforest and hunts insects by passive listening for prey (Francis, 2019) suggesting it has restricted movement. *Murina aenae* (Hill, 1964) was only captured in the primary forest. According to Struebig (2008), many forest-interior insectivorous species are likely to be restricted to the forest, and some of these species (e.g., *Murina aenea*, *M. rozendaali* (Hill & Francis, 1984), *Phoniscus jagorii* (Peters, 1866)) have mostly been recorded in an undisturbed habitat. Fragmentation of the habitat affected insectivorous bat species that roost in tree cavities or foliage, more than cave-roosting species (Struebig et al., 2009; Meyer et al., 2016).

4.3. Species richness and evenness

In this study, the species richness and species diversity of bats were higher in the primary forest than in the secondary forest and the urban forest. Species richness and diversity of bats were always higher in a natural forest (Danielsen and Heegaard, 1995). High species diversity shows the complexity of habitat and a low level of disturbances in the habitat (Molles, 2005). However, this study showed that the evenness of bats in the urban forest was higher compared to the primary and the secondary forests. This was probably because the abundance of each species was more evenly distributed and the difference of abundance between each species was low compared to the primary and secondary forests (Shafie et al., 2011).

High species diversity in the primary forest consisted of insectivorous bats from the families Hipposideridae, Rhinolophidae, and Vespertilionidae. *Murina aenea* which is only captured in the primary forest is categorized as vulnerable (VU) in the IUCN Red List. Bats from the families Vespertilionidae and Emballonuridae forage in open areas and the edge of forest (Denzinger and Schnitzler, 2013). The primary forest has a more open area than the secondary forest which is denser. During sampling, many insectivorous bats were captured around the forest edge. Morris et al. (2010) noted that bat activity patterns were strongly related to forest edge. This is because the forest edge functions similarly to natural forest gaps as it provides more foraging opportunities for bats. Insectivorous bats prefer to forage or commute along the forest edge. Bats that commute along forest edges are more readily able to exploit disturbed habitat. The environmental conditions make forest edge habitats appealing to bats (Hogberg et al., 2002). Since the forest is located along the road, forest edge plays an important role in the foraging of bats.

The high abundance of species such as *H. cervinus*, *H. bicolor*, *C. brachyotis*, *C. horsfieldii*, and *B. maculata* contributes to the species richness in the secondary forest. Hipposideridae was abundant in the study maybe because of the existence of caves in the study area. Caves support food sources, roosting sites, and safety encouraging the breeding of the species (Henderson and Broders, 2008). Large cave systems can greatly influence bat assemblage structure (Lim et al., 2014). Although no caves were found in this study, the abundance of this species indicates the presence of caves in the area. A close distance of food sources and roosting sites causes the species to gather at the same area (Hein et al., 2009). The presence of bats is highly affected by food sources. The drastic increase in food sources can cause the habitat to be the hotspot for bats (Hodgkison et al., 2004b).

The secondary forest shows higher species richness compared to the primary forest and the urban forest. Some species take advantage of the changes of the forest because

the logging effect may increase in feeding opportunity (Clarke et al., 2005). Moreover, changes in forest are not pronounced to all bats. Kerivoulinae recorded five species in the secondary forest which is denser with understory vegetation compared to primary forest. Dense vegetation that was created in a complex environment can impede the flight of some bats species and limit their locomotion (Kalko et al., 1996). However, Schmieder et al. (2012) reported that Kerivoulinae, Hipposideridae, Rhinolophidae, and Murininae have better echolocation calls to track and approach their prey in dense rainforest understory. Specializations of wing morphology and the ability to echolocate in clutter environments are characteristics of the species that forage in dense vegetation, which makes these taxa capable to forage in dense clutter of the forest understory (Kingston et al., 2003b). The presence of indicator species that roost in bamboos (*Tylonycteris pachypus* and *Tylonycteris robustula* (Thomas, 1915)) proved that the vegetation has massive bamboo trees and is a secondary forest (Kingston et al., 2003a). Russo et al. (2010) noted that species richness responded to availability of roosting sites (tree cavity and foliage roosting).

The urban forest shows a high evenness of bats although the individuals captured for each species was low. Five species of Megachiroptera and six species of Microchiroptera were captured. Frugivorous bats feed on fruits, leaves, and nectar of forest trees, which makes a wider food selection (Corlett, 2004; Nelson et al., 2005). Other than forest trees, fruit trees were also the main diet of frugivorous bats. The presence of fruit trees such as rambutan (*Nephelium lappaceum*) and jambu (*Psidium guajava*) promotes abundance of *C. brachyotis* (Liat, 1970). The main diet of *C. brachyotis* and *C. horsfieldii* is *Ficus* sp. but the presence of seasonal species such as *Artocarpus maingayi*, *Palaquium obovatum*, and *Payena maingayi* attracted the frugivorous bats (Tan et al., 1998). Various niches in the urban habitat have promoted the captures of species such as *Scotophilus kuhlii* which often roost under building roofs and *Myotis muricola* (Gray, 1846) in a furred central leaves of banana plants (Francis, 2019).

Forest changes caused by logging activities have increased the feeding opportunities for some species (Brosset et al., 1996). Clarke et al. (2005) found that there is no evidence that forest changes had affected species richness of bats. The density of prey or prey types may shift in the regenerating area. Habitat fragments act as corridors to maximize habitat areas that promote connectivity among large core areas of forest (Struebig et al., 2011). In the early succession, disturbed forest is dominated by keystone and late-seral vegetation such as *Macaranga*, *Mallotus*, *Callicarpa*, and *Melastoma* (Appanah, 1990). These vegetation types attract insects such as grasshoppers

(Orthoptera), bees (Hymenoptera), and butterflies (Lepidoptera) (Appanah, 1990). The abundance of insects attracted insectivorous bats to the habitat.

Anthropogenic changes to an area can create mosaics of fragmented vegetation, thereby affecting the diversity, abundance, and feeding behavior of bats (Fukuda, 2009). According to Levey (1998) and Cueto and de Casenava (1999), mammals' distribution, diversity, species richness, and activity were determined by vegetation structure and abiotic factors (temperature, rainfall, and humidity). The difference in bat diversity may be due to various other factors including variation in sampling methods, duration of study, type of the capture method employed, and suitability of the forest to support a great diversity of bats (Azlan et al., 2000). This reflects the complexity of factors that can influence directly or indirectly the distribution and species richness of animal species (Cueto and de Casenava, 1999).

4.4. Capture rate

Mist-nets are specified to capture frugivorous bats while harp traps are designed for insectivorous bats, but are sometimes effective for both frugivorous and insectivorous bats. Frugivorous bats that were caught in the harp traps in the primary forest were *Balionycteris maculata*, *Cynopterus brachyotis*, and *Chironax melanocephalus*. In the secondary forest, the species of bats that were caught in the harp traps were *B. maculata*, *C. brachyotis*, *C. horsfieldi*, and *Macroglossus minimus*. Harp trap is especially effective in capturing small bats that weigh less than 30 g. However, certain species such as hovering and gleaning bats appear to be better at avoiding harp traps than heavy, larger-bodied frugivorous bats (Kunz and Kurta, 1988). In the secondary forest, one individual of *Rhinolophus affinis* (Horsfield, 1823) and one individual of *Rhinolophus sedulus* (Andersen, 1905) were caught in the mist-net. This could have happened because bats that fly through familiar areas often navigate by special memory and do not listen to their acoustic and visual input (Tuttle, 1974). The capture rate using mist-net was the highest in the urban forest. All frugivorous bats in the urban forest habitat were captured in the mist-nets. The cause of these high capture rates was

the presence of many fruiting trees and the abundance of flowers in the vicinity. Capture rates using harp traps were relatively high in the primary and the secondary forests. Sedlock (2008) stated that harp traps greatly increased the capture rate of largely insectivorous species. Harp trap is very effective when placed across narrow paths or between trees (Payne, 1985) suggesting that a garden-like urban forest is not very suitable for this method to be employed.

5. Conclusion

This study has determined that the bat species diversity was higher in the primary forest, followed by the secondary forest and the urban forest, while species abundance was much higher in the secondary forest compared to the primary forest and the urban forest. In comparison to Microchiropteran, the Megachiropteran individuals were abundantly caught in the three habitat types. Food sources and roost sites may have influenced the species richness and evenness in a habitat type. Since the primary forest is located at close proximity to the secondary forest, and the urban forest is adjacent to the fragmented forest, it encourages the increase of various microhabitats. This can attract more forest bat species to utilize the resources in the secondary forest and the urban forest and help stabilize the diversity in a disturbed habitat. The result obtained from this study can be useful to determine the important factors that influenced the distribution and habitat suitability of bat species in a habitat type. Application of Geographical Information System (GIS), which constructs a database and develops maps, should be considered in future studies.

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