

Research Article

Patterns of fruit bat diversity in forest fragments and exotic tree species-based reforestation areas within highly modified karst areas in the Philippines

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ABSTRACT

Karst forests are important habitat for many karst-associated species such as bats. However, there is paucity of comprehensive studies exploring the long-term responses of bats to fragmentation or conversion of their natural habitat in the karst ecosystems of Southeast Asia. In this study, we assessed the diversity, composition, abundance, and vertical stratification of fruit bats in forest fragments and exotic species-based reforestation areas within limestone quarries in Luzon and Mindanao sub-regions of the Philippines. Bats were sampled over a five-year period using mist nets set in the understory (0–3 m) and sub-canopy (4–15 m). A total of 15,332 individuals of fruit bats from 10 species were recorded from a total sampling effort of 4,014,878.4 mist-net hours (m²h). Each forest type exhibited uniqueness in bat composition, with some forest-associated species observed only in forest fragments whereas disturbance-tolerant species were more abundant in reforestation areas. Bat assemblage also differed between the vertical strata within each habitat type, with capture rates about six and two times higher in sub-canopy than understory in forest fragment and reforestation area, respectively. Lastly, abundance of bats showed relationship with area of forest fragment but not with reforestation age. These findings highlight the importance maintaining and expanding the forest patches within and adjacent quarry sites for bat conservation. Additionally, enhancing plant diversity in reforestation areas is crucial to attract fruit bats and expedite the process of forest regeneration in these degraded environments

Key words: Karst forest, Pteropodidae, Southeast Asia, mining areas, vertical stratification

INTRODUCTION

Southeast Asia is home to a disproportionate amount of biodiversity, deeming it one of the most biologically rich regions in the world (Sodhi *et al.*, 2004). The region is also teeming with high level of endemism, owing in part to the presence of unique habitats such as karst forests. These landscapes' unique chemistry, geological, and hydrological characteristics provides numerous unique microhabitats and strong selective forces for the evolution of many species (Kruckeberg & Rabinowitz, 1985; Hamilton-Smith, 2001; Clements *et al.*, 2006).

Karst forests encompass nearly 12% of the total land area of the Philippines (Fernando *et al.*, 2008). However, these landscapes are largely understudied and continually threatened primarily by large-scale mining of limestone, an important material in manufacturing of cement (Clements *et al.*, 2006; Tolentino *et al.*, 2020). Unfortunately, mining activities often result to the fragmentation of the forest landscape (Fahrig, 2003; ELAW, 2010). The formation of isolated forest patches makes the dispersal of wildlife fauna and flora difficult to impossible and ultimately leads to decline in their population, especially those that are not resilient to such

conditions (*i.e.*, habitat and dietary specialists) (Clavel *et al.*, 2011). Many mining companies in the country often conduct reforestation activities as a means to offset the biodiversity loss resulting from their operations. Unfortunately, a common practice involves the use of fast-growing exotic tree species, most common of which were gmelina (*Gmelina arborea*) and mahogany (*Swietenia macrophylla*). While this approach is believed to rapidly increase forest cover compared to native tree reforestation, the use of exotic tree species has garnered negative perceptions as it provides very few benefits to ecosystem services as well as its potential threat to the conservation of numerous forest-dependent flora and fauna species (Lamb *et al.*, 2005; Wingfield *et al.*, 2015). For instance, D'Antonio and Meyerson (2002), in their review, emphasized that areas restored with a monoculture of exotic tree species may hinder the thriving of native tree species and wildlife. This is attributed to alterations in topography, vegetation, and ecosystem biogeochemistry. Furthermore, plantations dominated by only one or two exotic tree species have limited available resources, creating challenges in attracting diverse wildlife populations due to the lack of variability in vegetation structure (D'Antonio & Meyerson, 2002; Norton & Forbes, 2013).

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Bats comprise the second largest mammalian order globally with over 1300+ species recognized and represent approximately 30% of Southeast Asia's mammalian species (Kingston, 2008; Burgin *et al.*, 2018). The Philippines hosts a diverse community of this vertebrate group with 79 known species, 16 of which are endemic to the country (Heaney *et al.*, 2010; Amberong *et al.*, 2021). Bats are of great importance because they maintain ecosystem balance in tropical forests (Kunz & Parsons, 2009). In particular, members of the Old World fruit bats (Pteropodidae) play a significant role in dispersing seeds and pollen of various plant species. Recent studies have provided evidence suggesting that some bat species exhibit a strong preference for pioneer plants (Muscarella & Fleming, 2007; Andrade *et al.* 2013). This behaviour is a crucial feature in promoting forest regeneration, especially in disturbed areas (Farneda *et al.*, 2018). Moreover, bats have extensively been used as bioindicator species to assess effects of fragmentation in many tropical forests because of their sensitivity to human-induced disturbances (Jones *et al.*, 2009; Park, 2015; De Conno *et al.*, 2018; Meyer, 2016).

Since many bat species largely depend on caves and karst outcrops for roosting and shelter, protection of karst forests is crucial for their survival (Clements *et al.* 2006; Duco *et al.* 2021). However, data and comparative studies of bats and their responses to fragmentation or conversion of their natural habitat in Southeast Asian karst ecosystems are still very limited (Kingston, 2008). This highlights the immediate need to conduct studies on their behavior and ecology in highly modified karst landscapes to provide a basis for implementing efficient conservation strategies.

Here, we describe the community composition, spatial heterogeneity, and relative abundance of fruit bats in reforestation areas and remaining forest fragments within limestone quarries in two biogeographic sub-regions in the Philippines. This study provides

insights to responses of bats to anthropogenic disturbances and contribute to enhancement of mitigation plans and restoration initiatives undertaken by mining companies in the Philippines.

METHODOLOGY

Study Sites

The study was conducted in seven (7) sites, with three situated in the Luzon sub-region (La Union, Agno, and Bulacan) and four in the Mindanao sub-region (Lugait, Bunawan, Mati, and Initao) (Figure 1). Except for Initao, which is a designated protected area, all the

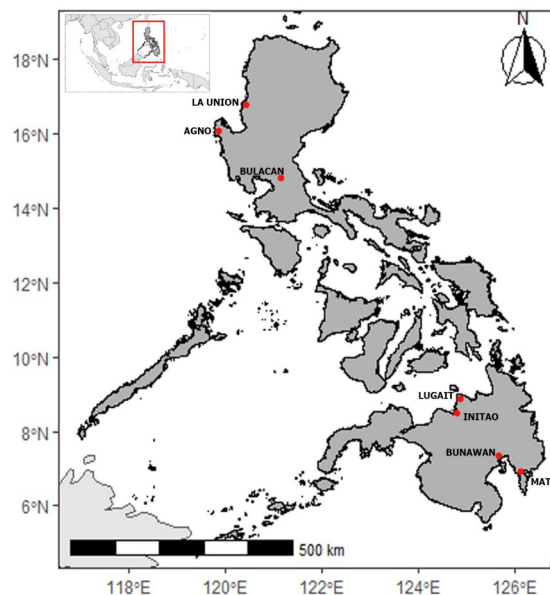


Figure 1. Location of sampling sites across the two biogeographic sub-region in the Philippines.

Table 1. Classification of each sampling area based on forest type, including the duration of sampling and sampling effort.

Study Sites	Sub-site	Forest Condition	Forest fragment size/ Year the reforestation area established	Sampling Years	Total Sampling Effort (m ² h)
Luzon Sub-region					
La Union	Carisquis	Forest fragment	5.7 ha	2013-2017	168,480.0
La Union	Quirino	Forest fragment	15.4 ha	2013-2017	224,640.0
La Union	Paraoir	Forest fragment	9.4 ha	2013-2017	224,640.0
Agno	Gayusan	Forest fragment	4.3 ha	2013-2017	230,256.0
Agno	Magsaysay	Forest fragment	4.4 ha	2013-2017	230,256.0
Agno	Namatucan	Forest fragment	2.6 ha	2013-2017	228009.6
Bulacan	Bayabas	Forest fragment	4.6 ha	2013-2017	193,003.2
Bulacan	Quarry 1	Reforestation	1996	2013-2017	163,987.2
Bulacan	Quarry 2	Reforestation	2000	2013-2017	163,987.2
Mindanao Sub-region					
Lugait	Dalipuga	Reforestation	1995	2013-2017	215,280.0
Lugait	Poblacion	Reforestation	1995	2013-2017	224,640.0
Initao	Site A	Forest fragment	36 ha	2014-2017	185,328.0
Initao	Site B	Forest fragment	14 ha	2014-2017	159,494.4
Initao	Site C	Forest fragment	14 ha	2014-2017	213,408.0
Bunawan	Bunawan	Reforestation	1997	2013-2018	217,900.8
Bunawan	Mahayag	Reforestation	1993	2013-2018	219,024.0
Bunawan	Kiotoy	Reforestation	1997	2013-2018	219,024.0
Mati	Lampasan-A	Reforestation	1998	2013-2016	168,480.0
Mati	Lampasan-B	Reforestation	1998	2013-2016	168,480.0
Mati	Tagamot	Reforestation	1993	2013-2016	196,560.0

sampling sites are characterized as active limestone quarry areas. We classified our sites to two distinct forest habitat conditions, forest fragments and reforestation areas (Table 1), following prior vegetation assessment conducted by Galindon *et al.* (2017).

Bat Sampling

Sampling was done from 2013 to 2018. Bats were captured using 12 x 2.6 m mist nets with 4-shelf and 36 mm mesh. For each site, twenty nets were set in understory level, about 0-3 m above ground, in a series of five nets. Meanwhile, five mist nets (two and three nets stacked on top of the other) were set in the sub-canopy layer (10-15 m above ground) using a rope and pulley system (Ingle, 1993). Bats were captured from 1800h until 0600h, with the exception of periods of extreme weather conditions, such as rains or thunderstorms, during which the nets were closed. Thus, actual netting hours were carefully recorded for analysis.

Nets were checked every hour to retrieve any captures. Bats were identified following field guides and identification keys (Ingle & Heaney, 1992; Heaney *et al.* 2016). Captures were measured then tagged with uniquely numbered aluminum alloy rings attached to stainless steel ball chains fitted to the bat's neck prior to release. Following Moreno and Halffter (2000), total sampling effort for each site were calculated. Since the total sampling effort between understory and sub-canopy nets for both reforestation and forest fragment are unequal, capture rate of bats were standardized as the number of individuals captured per mist net hour (m²h) of sampling effort. Field sampling and collection was covered by the following Department of Environment and Natural Resources (DENR) Wildlife Gratuitous permits: 2013-004, 2016-03, III-2013-06, III-2016-01, III-2018-06, R10 2013-23, R10 2014-36, R10 2018-07, RXI-2013-07, RXI-2013-08, RXI-2015-06, and RXI-2017-07.

Data Analysis

We compare species richness between forest type within each sub-region by providing an estimated species richness using the mean of four selected non-parametric species richness estimators (Chao, Jack1, Jack2, and Bootstrap). This was done using the Community Ecology package ('vegan' v. 2.4-1) (Oksanen *et al.*, 2016) in the R statistical software (v. 3.5.0) (R Core Team, 2016). Sampling completeness was also assessed by comparing the actual number of species sampled with the total estimated species richness, with a value greater than 90% considered sufficient (Moreno & Halffter, 2000). Species accumulation curves with 95% confidence interval were also generated based on the expected species richness.

Using generalized linear model (GLM) with Poisson error structure, we determined the relationship of forest fragment size and reforestation age with the relative abundance of bats in the quarry areas. Analysis was also performed using R software, using the capture rate of bats as a response variable. For each species, capture rate was also subjected as response variable to determine which species have significant result for the model.

Permutational MANOVA (PERMANOVA) analysis was performed using the "adonis" function of the "vegan" package in R to compare differences in bat

assemblage between forest type and between vertical strata. Non-metric multidimensional scaling (NMDS) ordinations based on Bray Curtis similarity matrix was also constructed using the function 'metaMDS' of 'vegan' in R. Capture data were log+1 transformed to reduce the contribution of the most abundant species (Duco *et al.*, 2021). Similarity Percentage (SIMPER) was used to determine which species provide the highest contribution to any dissimilarity observed while Mann-Whitney U-test was performed to compare the capture rates of each species between forest types and strata. SIMPER was conducted using PRIMER (v 6.4.7) (Clarke & Gorley, 2006) whereas Mann-Whitney U test was performed using IBM SPSS Statistics for Windows v 20.0 (2011).

RESULTS

Bat Community

A total of 15,332 individuals of fruit bats belonging to 10 species was recorded from a total sampling effort of 4,014,878.4 mist-net hour (m²h). We captured nine species in Luzon while eight species were captured in Mindanao. Notably, flying foxes (*i.e.*, *Acerodon jubatus* and *Pteropus hypomelanus*) were caught exclusively in forest fragments sites in Luzon, whereas *Ptenochirus minor* was captured exclusively in Mindanao. All species were recorded in forest fragment sites while eight species were recorded in reforestation area.

The most abundant species recorded was *Cynopterus brachyotis*, making up 41.19% of the total number of individuals captured, followed by *Rousettus amplexicaudatus* (34.99%) and *Ptenochirus jagori* (14.75%). These species were also the most commonly captured for both forest types. Of the 10 species recorded, four were endemic to the Philippines, including one that is endemic to the Mindanao faunal region (Table 2). Additionally, two species are categorized Near Threatened based on IUCN Red list (2022), one is classified Vulnerable, and another recognized Endangered (Table 2).

Species Richness and Composition

Sampling efficiency was above 90% for all sites, except for reforestation area in Luzon (Table 3). Moreover, both species accumulation curves for reforestation area in Luzon and forest fragment in Mindanao did not reach an asymptote, indicating that additional species will likely be captured with additional sampling effort (Figure 2).

Species accumulation curves indicate that forest fragment sites accumulated higher number of species compared to the reforestation area for both Luzon and Mindanao sub-region (Figure 2). Among Luzon, mean of the four non-parametric species richness estimators indicates that forest fragment is more species than the reforestation area (Table 3). Meanwhile, the two forest types in Mindanao have the same number of species. However, given an equivalent sampling effort, forest fragment yielded more species compared to the reforestation area based on the accumulation curve generated (Figure 2b). Further, no significant difference in mean capture rates between the two forest types in Luzon ($U=30,608.00$, $p=0.321$) and Mindanao ($U=50,840.00$, $p=0.849$) was observed.

Table 2. Species list of bats recorded including their endemcity and conservation status based on IUCN (2020), and the number of individuals mist-netted in each forest type within Luzon and Mindanao sub-region.

Species	Endemcity	Conservation Status*	Luzon		Mindanao	
			Forest frag- ment	Reforesta- tion area	Forest fragment	Reforesta- tion area
<i>Acerodon jubatus</i>	Philippine Endemic	EN	3	0	0	0
<i>Cynopterus brachyotis</i>	Non-endemic	LC	1827	267	542	3987
<i>Eonycteris robusta</i>	Philippine Endemic	VU	4	1	2	4
<i>Eonycteris spelaea</i>	Non-endemic	LC	104	20	102	214
<i>Macroglossus minimus</i>	Non-endemic	LC	28	1	39	446
<i>Pteropus hypomelanus</i>	Non-endemic	NT	96	0	0	0
<i>Ptenochirus jagori</i>	Philippine Endemic	LC	158	86	481	1537
<i>Ptenochirus minor</i>	Mindanao Endemic	LC	0	0	3	7
<i>Pteropus vampyrus</i>	Non-endemic	NT	5	0	1	1
<i>Rousettus amplexicaudatus</i>	Non-endemic	LC	349	231	1789	2997

*EN – Endangered; LC – Least Concern; NT – Near Threatened; VU – Vulnerable

Table 3. Observed and mean estimated species richness (\pm SE), total number of captures, mean capture rate, and completeness of sampling for bats caught in forest fragment and reforestation sites in Luzon and Mindanao sites.

-	Luzon		Mindanao	
	Forest fragment	Reforestation area	Forest fragment	Reforestation area
Number of species recorded	9	6	8	8
Mean estimated species richness	9.03 \pm 0.03	7.73 \pm 0.54	8.48 \pm 0.16	8.83 \pm 0.37
Total number of captures	2574	606	2959	9193
Mean capture rate (capture/m ² ·h)	0.008 \pm 0.001	0.009 \pm 0.002	0.021 \pm 0.003	0.023 \pm 0.002
Total Sampling Effort (m ² ·h)	1,499,284.8	327,974.4	558,230.4	1,827,259.2
Sampling Completeness	99.62%	77.64%	94.29%	90.62%

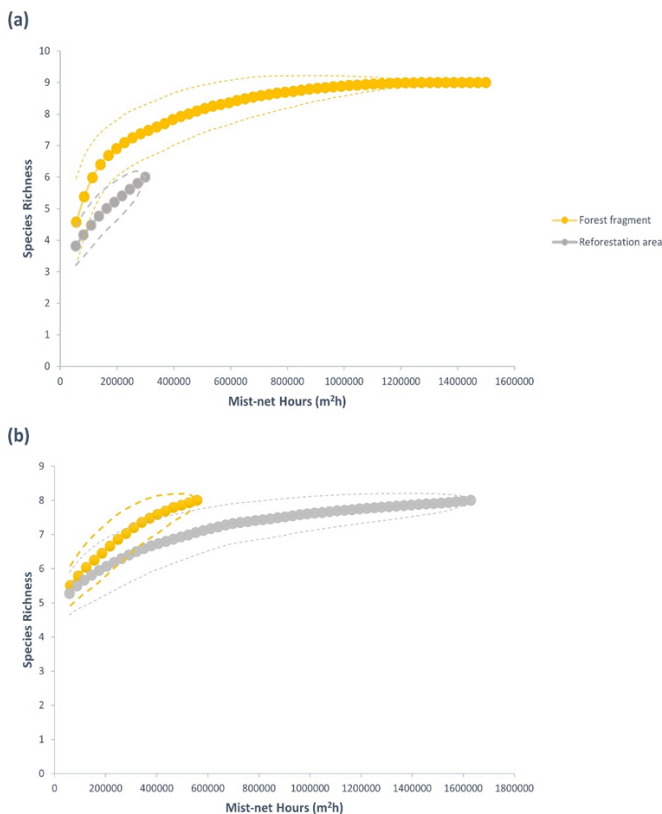


Figure 2. Species accumulation curves based on mist-netting of bats in two forest types in a) Luzon and b) Mindanao sub-region, Philippines. Dashed lines indicate 95% confidence intervals.

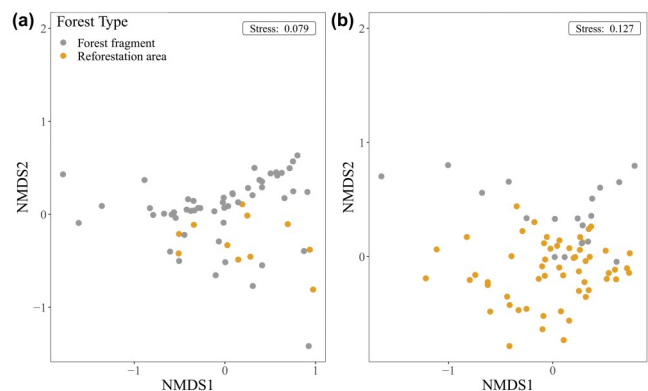


Figure 3. NMDS ordination plots showing bat assemblage based on mist net captures between forest fragment and a reforestation area in (a) Luzon and (b) Mindanao sub-regions.

Result of the PERMANOVA showed significant difference in bat assemblage between the two forest types for both Luzon (F=3.55, p=0.01) and Mindanao sub-region (F=8.56, p=0.001). These results were also supported by the NMDS plot generated (Figure 3).

Based on SIMPER analysis, five species (*Cynopterus brachyotis*, *Ptenochirus jagori*, *Eonycteris spelaea*, *Pteropus hypomelanus*, and *Rousettus amplexicaudatus*) contributed 98.23% to the observed dissimilarity between the two forest types in Luzon. Of these, *Ptenochirus jagori* and *Rousettus amplexicaudatus* were significantly more abundant in reforestation area

($U=516.00$, $p=0.000$ and $U=487.00$, $p=0.000$, respectively) while *Pteropus hypomelanus* had significantly higher capture rate in forest fragment ($U=143.00$, $p=0.003$) (Figure 4).

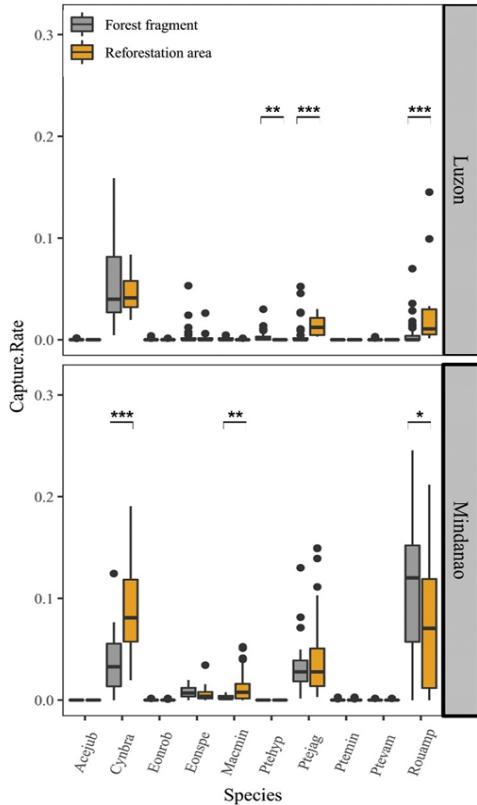


Figure 4. Comparison of mean capture rate (individuals/m²h) between forest fragment and reforestation area in Luzon and Mindanao sub-regions. Error bars represent 95% confidence interval while asterisks indicate significant differences at $\alpha = *0.05$, $**0.01$, or $***0.001$.

Acejub: *Acerodon jubatus*; Cynbra: *Cynopterus brachyotis*; Eonrob: *Eonycteris robusta*; Eonspe: *Eonycteris spelaea*; Macmin: *Macroglossus minimus*; Ptehyp: *Pteropus hypomelanus*; Ptejag: *Ptenochirus jagori*; Ptemin: *Ptenochirus minor*; Ptevam: *Pteropus vampyrus*; Rouamp: *Rousettus amplexicaudatus*.

Meanwhile, 95.96% of the observed dissimilarity between the two forest types in Mindanao sub-region were explained by four bat species. Of these, *Cynopterus brachyotis*, *Ptenochirus jagori*, and *Macroglossus minimus* have higher capture in the reforestation area, although only that of *C. brachyotis* and *M. minimus* were found to be significant ($U=848.00$, $p=0.000$ and $U=731.00$, $p=0.004$, respectively) (Figure 4). *Rousettus amplexicaudatus* meanwhile characterizes the forest fragment in Mindanao sub-region, having significantly

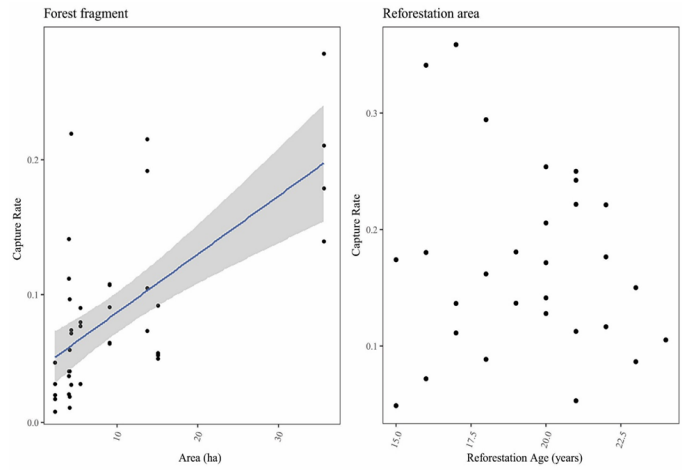


Figure 5. Regression relationship between capture rate of bats and forest fragment size (left) and reforestation age (right). Plot with shaded region indicating significant relationship at $\alpha = 0.001$.

higher capture rate in the forest fragment ($U=350.50$, $p=0.029$).

Abundance of fruit bats in relation to forest fragment size and reforestation age

Results from GLM indicates that the abundance of bats, as measured by capture rate, showed a clear relationship with the area of forest fragment, but not with reforestation age (Figure 5). In general, capture rates of bats increase with larger forest fragment areas. We also assessed if the same pattern was observed at the species level. Five species showed relationship with their capture rates and the area of forest fragment in the regression model generated (Figure 6). Of these, three species (*Macroglossus minimus*, *Ptenochirus jagori*, and *Rousettus amplexicaudatus*) showed an increase in capture rate with an increase in forest fragment area while two species of flying fox (*Acerodon jubatus* and *Pteropus hypomelanus*) showed a significant decrease in their capture rate (Figure 6).

Vertical Stratification

The capture rate of fruit bats is approximately six times higher in the sub-canopy than in the understory in forest fragments and two times higher in reforestation areas despite of the higher sampling effort for the understory (Table 4). Mann-Whitney U-tests showed that the differences in the mean capture rate between understory and sub-canopy was significant in forest fragment ($U = 19,962.50$, $p = 0.000$) but not for the reforestation area ($U=15,947.5$, $p=0.077$).

Table 4. Sampling effort, capture rate, and number of species recorded in the two vertical strata within forest fragment and reforestation areas in Luzon and Mindanao.

	Forest fragment		Reforestation area	
	Understory	Sub-canopy	Understory	Sub-canopy
Sampling Effort (m ² h)	1,690,228.80	367,286.40	1,560,499.20	396,864.00
Number of Captures	1736	3797	5612	4187
Mean Capture Rate (capture/m ² h)	0.005 + 0.001	0.030 + 0.005	0.015 + 0.002	0.036 + 0.005
Number of Species	7	10	7	8

Results from both PERMANOVA and NMDS also showed a significant difference in bat assemblage between the two vertical strata for both forest fragment ($F = 27.78$, $p = 0.001$) and reforestation area ($F = 33.61$, $p = 0.001$) (Figure 7).

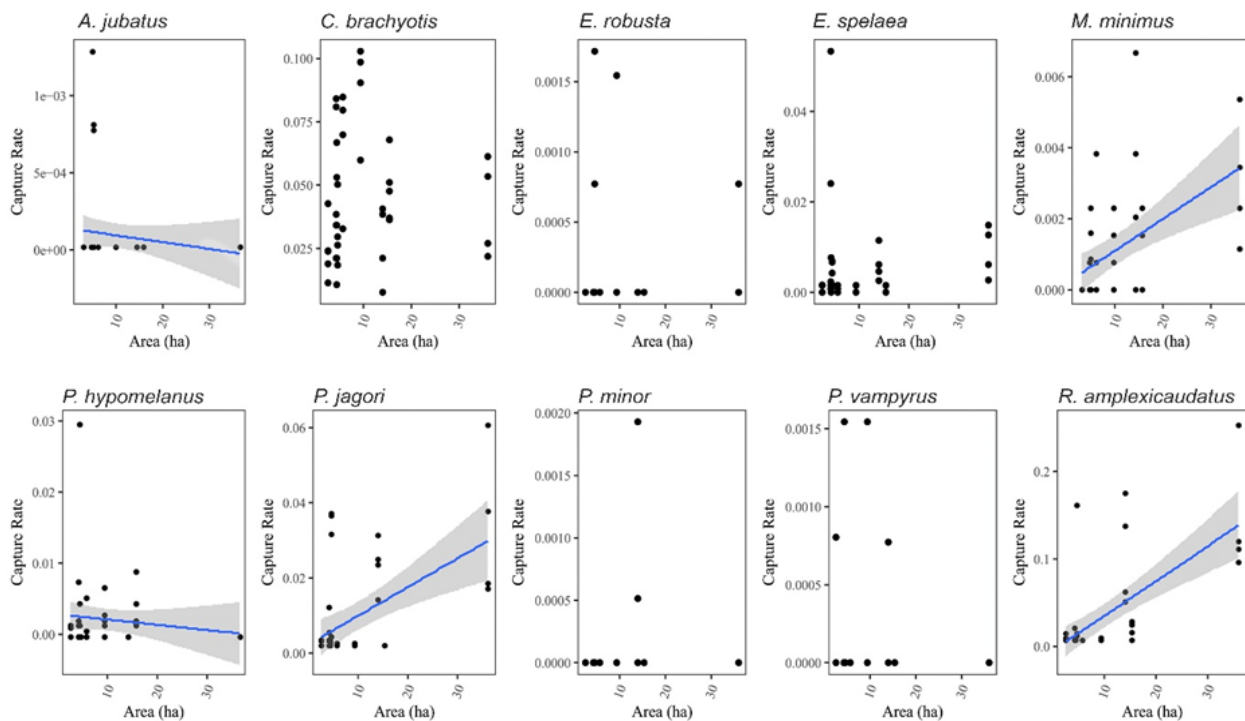


Figure 6. Regression relationship between capture rate of the 10 species of fruit bats and forest fragment size. Plots with shaded region indicates significant relationships at alpha= 0.001.

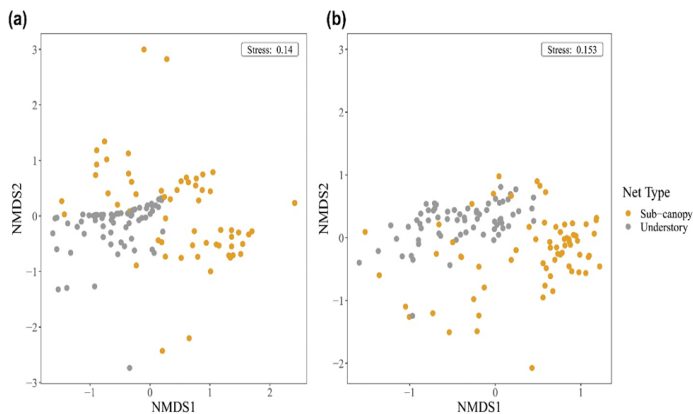


Figure 7. NMDS ordination of bat assemblage in two vertical strata present in (a) forest fragment and (b) reforestation area.

Within forest fragment, the difference in assemblage between the two strata was largely contributed by four species (*C. brachyotis*, *E. spelaea*, *P. hypomelanus*, and *R. amplexicaudatus*), all of which had significantly higher capture rate in the sub-canopy (Figure 8). Likewise, three species (*E. spelaea*, *R. amplexicaudatus*, and *P. jagori*) which were identified by SIMPER analysis to have the highest contribution to the observed difference in composition between the two strata in the reforestation area had significantly higher capture in the sub-canopy (Figure 8).

DISCUSSION

Our study revealed patterns of diversity and composition of bat community in active limestone quarries in the Philippines. Even in its degraded state, our sites still hosted a total of ten species of fruit bats which accounts

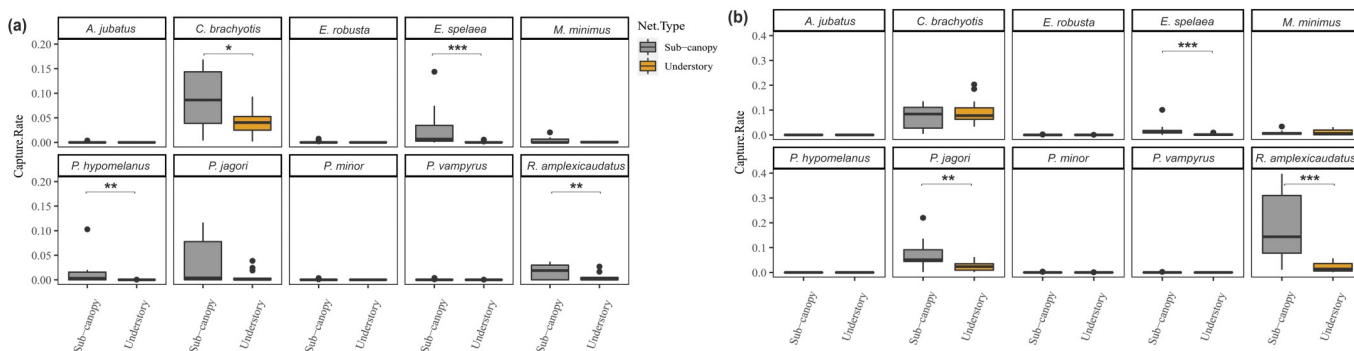


Figure 8. Mean capture rate of each species in the understory and sub-canopy in (a) forest fragment and (b) reforestation sites. Error bars represent 95% confidence interval while asterisks indicate significant differences at alpha= *0.05, **0.01, or ***0.001.

for 40% of the total number of fruit bat species present in the Philippines, or about half of the number of species occurring in Luzon and Mindanao faunal region (Heaney *et al.*, 2010). All of the species recorded were widespread throughout the country, except for *Ptenochirus minor* which is restricted to the Mindanao faunal region.

Cynopterus brachyotis was the most abundant species captured probably due to its high tolerance for disturbance. This species is widespread throughout the country and commonly found in agricultural and secondary growth forests. Further, this bat is considered among the most abundant in habitats with a considerable degree of disturbance (Heaney *et al.*, 2010; Heaney *et al.*, 2016).

Fruit bat assemblage in forest fragments and exotic species-based reforestation areas

The bat assemblage was found to be significantly different between the two forest types for both sub-regions. The study by Galindon *et al.* (2017) on the same sites found that the forest fragments and exotic species-based reforested areas significantly differ in floristic species composition. Thus, the differences in resource availability and environmental conditions between two forest types could have influenced the composition of the bat community. For instance, two species of flying foxes, *A. jubatus* and *P. hypomelanus*, were exclusively captured in the forest fragment. Both species are known to roost in large and tall trees and the availability of food resources and roosting sites in the forest fragment may explain the presence and abundance of both species in these areas (Heideman & Heaney, 1992; IUCN, 2022). Meanwhile, *C. brachyotis*, *M. minimus*, and *P. jagori* had significantly higher capture rate in reforestation sites because of the adjacent coconut and banana plantations in the area where these species usually feed and roost (Richarz & Limbrunner, 1993; Gunnell *et al.*, 1996; Crichton & Krutzsch, 2000). Moreover, these species are known to occupy a wide range of habitats and have high tolerance to disturbance which could explain their abundance in the reforestation sites which are mostly situated near active limestone quarry areas (Heaney *et al.*, 2016).

Lastly, *R. amplexicaudatus* exhibited a significantly higher capture rate in the forest fragment in Mindanao but was also more abundant in the reforestation area in the Luzon sub-region. Given that this bat is a known strict cave-dwelling species, its abundance across different forest types may be influenced by the presence and proximity of suitable caves in the sampling areas. Indeed, areas with a higher abundance of caves, known to host this species, were in closer proximity in the reforestation area in Luzon. Conversely, among the Mindanao sites, caves were only identified in the forest fragment site (i.e., Initao). This suggests that the abundance of *R. amplexicaudatus* is associated with the availability and proximity of suitable caves, regardless of whether the sites are classified as forest fragments or reforestation areas.

Abundance of fruit bats in relation to forest fragment size and reforestation age

The loss and fragmentation of forests have been a major threat to biodiversity, causing an increase in risks of local extinctions (Janzen, 1994; Laurance *et al.*, 2011).

In this study, the abundance of fruit bats was significantly affected by size of forest fragment (Figure 5). This is in accordance with previous studies showing an increase in rate of capture of bats in larger fragments compared to smaller ones. For instance, in Yucatan Peninsula, Montiel *et al.* (2006) found that although species richness was similar between large and small fragments, the capture rate of bats was significantly higher in larger fragments. Gehrt and Chesvig (2003) and Medlin *et al.* (2010) also found that the size and density of forest patches are major predictors of bat captures. This observation may be explained considering that larger forest fragments would offer more foraging grounds and roosting sites for bats.

The two species of flying fox (*Acerodon jubatus* and *Pteropus hypomelanus*) showed a decrease in capture rate with an increase in the size of the forest fragment (Figure 6). However, our data suggests that the proximity of their roosting sites to the sampling areas with relatively smaller forest fragment area could have influenced the result. Moreover, these bats could have been frequently flying over and using these small fragments as flyways or stepping stones towards larger forest fragments. Both of these species were large-bodied bats and have high wing load (proportion of bat weight to wing area), which allows them to travel long distances to find food (Norberg & Reyner, 1987; Cosson *et al.*, 1999 Duya *et al.*, 2017). *Acerodon jubatus* was known to forage as far as 12 km from their roosting site while *P. hypomelanus* has a foraging range of up to 8 km (Heideman & Heaney, 1992; Mildenstein *et al.*, 2005). Ideally, these bats would prefer larger forest fragments over the smaller fragments since the former would offer a more abundant supply of fruit or nectar to compensate for the high energy needed for flying long distances.

In this study, the abundance of fruit bats was not affected by reforestation age. Since reforestation areas were mainly planted with a monoculture of exotic tree species, we hypothesize that the constant abundance of bats in these areas even after years after establishment may have been caused by the lack of variability in vegetation structure and the limited resources it offers. Studies have provided evidence of an increase in abundance and species richness of vertebrates, such as birds and bats, with an increase in habitat's structural complexity and tree diversity of as these areas presumably offer a wider range of roosting sites and food resources (Hughes *et al.*, 2002; Harvey *et al.*, 2006; Munro *et al.*, 2011). Nonetheless, Galindon *et al.* (2017) reported that there was an apparent increase in native tree species richness and a significant decline in the number of exotic tree species in older reforested sites. In addition, our data suggests that some of the species of fruit bats recorded were particularly abundant in the reforestation areas despite the limited food resources in these habitats. Moreover, some forest-dependent and threatened species such as *E. robusta* and *P. vampyrus* were recorded in the reforestation areas, albeit in low numbers. We speculate that these areas are utilized by forest-dependent bat species mainly as corridors between foraging habitats. These observations underline the importance of reforestation sites for conservation of fruit bats by allowing movement and gene flow between remaining areas of high habitat quality (Estrada *et al.*, 1993; Harvey *et al.*, 2006).

Vertical stratification of fruit bats

We observed differential use in vertical space among fruit bats for both forest types in terms of both capture rate and composition. Our results are in accordance with most of the studies done in other tropical forests that showed similar pattern of vertical stratification. Factors such as diet, feeding and roosting behavior of bats, as well as the differential amount or availability of resources in the vertical layer contribute to the observed pattern of vertical stratification in bats (Bernard, 2001; Kalko & Handley, 2001; Gregorin *et al.*, 2017).

In our study, all species which showed significant difference in their capture rate between the two strata clearly showed preference for the sub-canopy layer. The response of fruit bats favoring the sub-canopy can be explained by their preference for less-cluttered, open space for flying. In Luzon Island, bat distribution along the vertical forest strata was largely influenced by the amount of clutter present (Duya *et al.*, 2017). For instance, most flying foxes are rarely caught in the understory because cluttering would reduce maneuverability and limit the access of bats with relatively larger size and higher wing load to the forest understory (Ingle, 1993; Duya *et al.*, 2017). Our study sites can be characterized to be highly fragmented and still in the early stages of vegetation succession, dominated by species from the bean family (Fabaceae), coffee family (Rubiaceae), fig family (Moraceae), grass family (Poaceae) and palms (Arecaceae). Moreover, the abundance of small trees and herbs caused the understory vegetation to be highly cluttered. This cluttering therefore deters most of the fruit bat species to fly or forage in the understory layer, compared to the open canopy that allows for greater movement.

In contrast, *C. brachyotis* and *M. minimus* were found to have higher capture rate in the understory of our reforestation sites, although the difference was not significant. While most of our reforestation sites are monoculture of exotic species such as *Acacia auriculiformis*, *Gmelina arborea*, *Swietenia macrophylla*, and *Mangifera indica*, other fruiting plant species such as figs and banana are common in the area that may attract both *C. brachyotis* and *M. minimus* in the lower strata.

Interestingly, two individuals of *Pteropus hypomelanus* and one individual of *Pteropus vampyrus* were caught using understory nets in one forest fragment site in Luzon. Flying foxes, characterized by high wing load and aspect ratio, are typically limited to flying in less cluttered areas within the lower forest layer (Schunk *et al.*, 2017). The capture of these individuals may be attributed to the setup of our understory nets on ridgetops, which aligns with the canopy height of a nearby forest fragment where they might have been foraging.

Conservation Implications

Our results demonstrate that highly disturbed habitats still harbor a substantial amount of fruit bat species and still have high biological potential, notably due to the presence of endemic and threatened species with high conservation value, stressing the importance of these habitats for bat conservation. Furthermore, our study underscores the importance of extensive and long-term biodiversity monitoring in quarry areas to better understand diversity patterns of fruit bats as consequences of reforestation efforts of mining companies. These data are crucial, not only for revealing patterns and

thresholds of species colonization as reforestation sites age but also for properly designing future restoration projects (Gardali *et al.*, 2006; Taki *et al.*, 2010; Derhé *et al.* 2016).

Based on our results, forest fragment size is an important predictor of abundance in fruit bats. We therefore recommend that conservation strategies should focus on increasing the area of remaining forest fragment rather than establishing a reforestation area planted with a monoculture of exotic tree species. Increasing the area of these forest patches would be beneficial for fruit bats, especially those that are disturbance-sensitive and forest specialists of high conservation value. This approach would enhance their foraging grounds and roosting areas, attracting a greater diversity and abundance of fruit bat species. Consequently, this could facilitate faster rate of seed dispersal and contribute to a more rapid process of forest regeneration.

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