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## Fruit bat assemblage in different lowland forest types in the Northern Sierra Madre Mountains, Philippines

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Prior studies of species assemblages of fruit bats in the Philippines have focused on primary and disturbed habitats as the point of comparison. No studies to date have been conducted on assemblages of fruit bats within primary lowland forest vegetation types. This study aimed to determine the fruit bat assemblage in dipterocarp, mangrove and lowland ultramafic forest and their association with these vegetation types. We hypothesize that difference in the diversity and abundance of fruit-producing plants in these habitat types would influence the abundance and diversity of bats. The study was conducted in the Northern Sierra Madre Natural Park, Philippines from April to October 2017. Eleven species of fruit bats were captured during the study, in order of decreasing abundance: *Rousettus amplexicaudatus*, *Ptenochirus jagori*, *Cynopterus brachyotis*, *Macroglossus minimus*, *Haplonycteris fischeri*, *Eonycteris robusta*, *Desmalopex leucopterus*, *Eonycteris spelaea*, *Pteropus vampyrus*, *Acerodon jubatus* and *Pteropus hypomelanus*. Species richness was highest in dipterocarp forest (11 species), and lowest in the mangrove area (seven species), but species diversity was highest in the lowland ultramafic forest. The study suggests that species diversity and abundance of fruit bats in the different lowland vegetation habitats can be linked to their diet and morphology. Frugivores were strongly associated with dipterocarp forest and lowland ultramafic forest where fruit-producing plant diversity is high. *Haplonycteris fischeri*, *C. brachyotis* and *P. jagori* were more abundant in the dipterocarp than in the ultramafic forest. The abundance of nectarivores varied between vegetation types. *Macroglossus minimus* was more abundant in the mangrove while *E. robusta* and *R. amplexicaudatus* were more abundant in the dipterocarp and ultramafic forest. The difference in plant species composition and abundance may explain the variation in frugivore and nectarivore abundance between vegetation types. No pattern could be discerned for the large flying foxes (*A. jubatus*, *P. hypomelanus*, and *P. vampyrus*) because of few captures in each habitat, except for *D. leucopterus*, which was frequently captured in lowland ultramafic forest. The low captures of flying foxes may be attributed to the difficulty of capturing high-flying bats. Further research on foraging behavior, fruit selection by bats and the role of forest structure in determining the abundance and distribution of fruit bats is needed.

**Key words:** Pteropodidae, flying fox, frugivore, lowland tropical forest, nectarivore, ultramafic forest, mangrove, dipterocarp forest

### INTRODUCTION

Fruit bats from the family Pteropodidae (Old World fruit bats) are important seed dispersers and pollinators of many tropical forest plants. They are known to feed on flowers and fruits of 145 genera in 56 families of paleotropical plants (Fleming, 1986). However, many of these bats are threatened with extinction due to hunting and habitat loss. It is widely recognized that forests are essential in the survival of fruit bats. Unfortunately, forest cover in the Philippines has continuously declined from 14.8 million ha of the total land area in 1950 (Bankoff, 2007) to about 6.8 million ha in 2010 (Forest Management Bureau, 2017).

There are 26 species of pteropodid bats in the Philippines, 17 of which are endemic (Heaney *et al.*, 2016). Fifteen of these pteropodids have been documented on Luzon, with one species restricted only to the island. About 58% of the Philippine fruit bats are dependent on lowland forest (Heaney and Roberts, 2009), and 12 out of the 26 (46%) are currently listed by the IUCN as vulnerable, endangered or critically endangered. Fruit bat species diversity and abundance in the Philippines reaches its maximum in the lowland forest and decreases with elevation (Heaney *et al.*, 1989, 2016; Heaney and Rickart, 1990; Heaney, 1991). These forest-dependent bats are particularly vulnerable to habitat loss, and this is often exacerbated by heavy hunting (Mickleburgh *et*

*al.*, 1992). In turn, the absence of these bats in any given forest could impact the survival of the forest and reproductive biology of their food plants because of their role in dispersing seeds (Utzurum, 1995; Ingle, 2003; Fleming *et al.*, 2009).

The lowland forest in the Philippines is the most vulnerable among the vegetation types due to accessibility and high-value timber and soil mineral content. Studies on Philippine fruit bat assemblages have included studies focused on taxonomy, phylogeny, and biogeography (Heaney and Rickart, 1990; Heaney, 1991; Heaney and Roberts, 2009). Studies of fruit bat community ecology have been confined mostly to Negros and Mindanao Islands (Heideman and Heaney, 1989; Utzurum, 1995, 1998; Hamann and Curio, 1999; Heideman and Utzurum, 2003) and one study was conducted in Mt. Makiling on Luzon Island (Ingle, 1992, 1993). These studies suggest that the quality and quantity of forest habitats influence fruit bat diversity, abundance, and community structure. However, these studies focused on primary, secondary and disturbed habitats as points of comparison. So far, no studies have been conducted comparing bat assemblages in different types of primary forest habitat in the Philippines. The Northern Sierra Madre Natural Park supports large tracts of contiguous lowland dipterocarp forest and the few remaining intact areas of mangrove and ultramafic forest in the country. In this study, we investigated the effect of vegetation types (dipterocarp, mangrove and lowland ultramafic) on fruit bat diversity and abundance. This study is part of a larger project that aims to describe bat-plant interactions in primary lowland forest and disturbed habitats across the archipelago (Ong *et al.*, 2014; Yap, 2015; Yap *et al.*, 2016; Duya *et al.*, 2017).

## MATERIALS AND METHODS

### Study Site

The study area is located on the east coast of Isabela province within the Northern Sierra Madre Natural Park (NSMNP). The NSMNP is the largest protected area in the Philippines covering 359,486 hectares that support 10 of the 12 known forest formations in the Philippines (Fernando *et al.*, 2008). Three vegetation types were selected for this study, dipterocarp forest, mangrove, and lowland ultramafic forest, all within the municipalities of Palanan and Divilacan, Isabela (Fig. 1 and Table 1). Climatic conditions in the province of Isabela belong to Type II in the Coronas climate classification where there is no pronounced dry season, but with minimum rainfall occurring between March and May and heavier rain from August to December (Corporal-Lodangco and Leslie, 2016). The rainfall pattern of the area during the study and average monthly rainfall from 1982–2012 are presented in Fig. 2.

Rainfall data during the study from January to December 2017 were taken from the portable weather station (Davis Vantage Vue DAV-6250EU) installed as part of the long term monitoring study on the impact of typhoons on forest dynamics. The unusually high rainfall observed in April 2017 was due to the presence of tropical depression 02W (locally known as ‘Crising’) by the Joint Typhoon Warning Center (JTWC), which brought heavy rain to parts of the country.

### Bat Sampling

Six netting sites, two in each vegetation type, were sampled for fruit bat diversity and abundance. Five sub-canopy and five ground mist nets measuring 6 × 12 m were used in each of the six sampling sites. Nets were operated for four consecutive nights every month in each site from April to October 2017 (Table 2). In each site, the nets were moved to different locations every two nights of netting. One net-night is defined as a net operated from 17:30 to 12:00 midnight. Two vegetation types were sampled simultaneously every month when possible. All individual bats captured were measured, identified, photographed and tagged before release. Identification of species was based on Ingle and Heaney (1992). Bats were tagged to identify individual recaptures and to avoid double counting. Adult and young bats were tagged with uniquely coded aluminum alloy rings (Porzana Ltd) attached to stainless ball chain fitted to the neck. This study was part of a larger long-term bat population study to establish a baseline for monitoring and assessing impact of disturbance caused by typhoons.

Field sampling was covered by permits issued by the Department of Environment and Natural Resources (Wildlife Gratuitous Permit Nos. 2017-07). Capture and handling of bats were conducted in accordance with animal care and use guidelines established by the American Society of Mammalogists (Sikes *et al.*, 2011).

### Vegetation Characterization

The vegetation types were selected based on the physical habitat and three primary types of soil substrate in the region; previous studies have demonstrated that plant assemblage and forest structure are influenced by soil substrate and nutrients (Potts *et al.*, 2002; Fu *et al.*, 2004; Fernando *et al.*, 2008; Condit *et al.*, 2013). Six 10 × 200 m plots, two in each vegetation type, were selected to characterize species composition and forest structure and surveyed for bat diversity and abundance. Trees and palms with greater than 5 cm diameter at breast height (DBH) were tagged, and DBH and tree height were recorded for each tree, and tree density in each vegetation type was calculated. Voucher specimens of plants were collected for proper identification and deposited at the Jose Vera Santos Herbarium (PUH) at the Institute of Biology, University of the Philippines Diliman.

### Statistical Analysis

Individual fruit bat species abundance and feeding guilds between study sites in each vegetation type were compared. Fruit bats were classified into two feeding guilds, frugivores or nectarivores based on their food preference. Bats in the Philippines that depend on fruits as a major part of their diet were classified as frugivores (Utzurum, 1995), whereas bats that

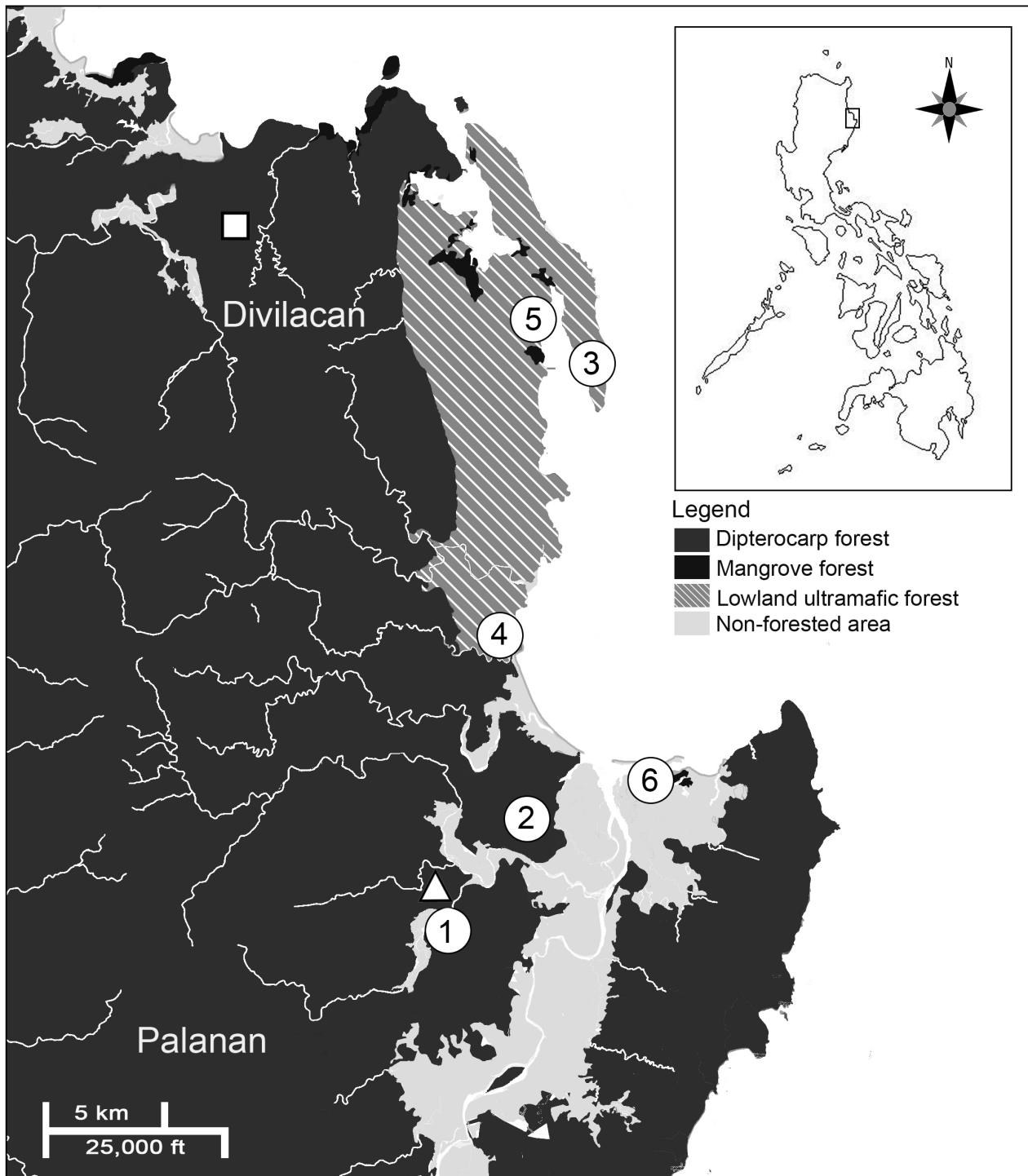


FIG. 1. Location of the study area in the Northern Sierra Madre Natural Park, province of Isabela, northeastern Luzon, Philippines. Dipterocarp forest (1 and 2), lowland ultramafic forest (3 and 4) and mangrove (5 and 6). Square indicates location of flying fox roosting site and triangle indicates location of the cave referred to in the text. Inset map indicates location of the Northern Sierra Madre Natural Park. Map adapted from NAMRIA basemap downloaded from <http://www.geoportal.gov.ph/viewer>

consume nectar as a primary source of food were classified as nectarivores (Heideman and Utzurrum, 2003). We used the capture rate per species as a measure of abundance. Capture rate was computed by dividing the total individual bat species abundance by the total netting effort in each vegetation type per month. Capture rates of each species and feeding guild between

vegetation types were compared using Kruskal-Wallis tests ( $\alpha = 0.05$ ) to determine significant differences between vegetation types. Pairwise comparison was performed using Dunn's (1964) procedure with a Bonferroni correction for multiple comparisons. Statistical analysis was done using SPSS version 20. We did not include *Acerodon jubatus*, *Pteropus vampyrus*



TABLE 1. Location of the six vegetation sampling sites in the Northern Sierra Madre Natural Park

Site	Locality	Vegetation	Coordinates	Elevation (m)	On site disturbance
Site 1	Palanan Forest Dynamics Plot, Barangay Villa Robles, Palanan municipality	Dipterocarp 1	17°02'49.8"N 122°23'13.2"E	89–159	Human trails used during forest dynamics plot re-census and research activities
Site 2	Barangay Culasi, Palanan municipality	Dipterocarp 2	17°6'55.70"N 122°27'47.00"E	50–76	Human trails and timber poaching
Site 3	Barangay Dimapnat, Divilacan municipality	Ultramafic 1	17°9'36.29"N 122°24'27.52"E	62–105	Abandoned mining road and timber poaching
Site 4	Barangay Bicobian, Divilacan municipality	Ultramafic 2	17°15'22.82"N 122°25'22.6"E	57–65	Trails used by indigenous people
Site 5	Barangay Bicobian, Divilacan municipality	Mangrove 1	17°15'46.96"N 122°25'2.70"E	10–12	Trapping of crabs and seashell gathering by local community
Site 6	Barangay Maligaya, Palanan municipality	Mangrove 2	17°6'55.70"N 122°27'47.00"E	6–8	Timber poaching and access trails used by the local community

and *Pteropus hypomelanus* in all the analyses because of the small sample size.

To quantify species diversity of fruit bats in the dipterocarp, mangrove and lowland ultramafic forest, we followed the method proposed by Chao *et al.* (2014) using the iNEXT package (Chao *et al.*, 2016) in the R statistical software v. 3.2.2 (R Core Team, 2015). A sample-size-based rarefaction (interpolation) and extrapolation curves for Hill numbers of  $q = 0, 1$ , and 2 with a 95% confidence interval based on bootstrap method were constructed up to a base sample size. Hill numbers are the number of equally abundant species that are equivalent to the value of a diversity measure. Hill numbers include the three most widely used species diversity measure: Species richness ( $q = 0$ ), Shannon's entropy index ( $q = 1$ ) and the inverse of Simpson's index ( $q = 2$ ). Converting these indices to true values of diversity facilitates comparison between communities (Jost, 2006). An accumulation curve was constructed by doubling the highest observed number of bat captures (reference sample) between vegetation types to extrapolate species richness and abundance in each sampling site. Doubling the number of the highest reference sample lessens the bias and ensures the reliability of the extrapolation of the asymptotic estimator for species richness and species diversity indices (Chao *et al.*, 2014). The generated accumulation curves were used to compare the fruit bat assemblages between the vegetation types. A non-overlapping confidence interval between the diversity indices indicates a significant difference.

Completeness of sampling per vegetation type surveyed was determined by comparing the actual number of species recorded to the estimated species richness. Chao 1 was used in estimating species richness based on bat abundance data in each vegetation type sampled; this is the default species estimator in the iNEXT package. This was done to allow comparison of species richness between vegetation types. Sampling efficiency greater than 90% was considered appropriate (Moreno and Halffter, 2000).

A bipartite network analysis was used to visualize the association of fruit bat species with dipterocarp, mangrove, and lowland ultramafic forest. The bipartite graph was drawn as an adjacency matrix, in which species of bats were represented as vertices on one side and vegetation types as vertices on the other side of the network. The interactions are drawn as links with higher abundance represented by wider bands indicating the degree of association. Bipartite network analysis has been used successfully in studying ecological interactions (Gotelli and Graves, 1996; Dormann *et al.*, 2009; Tur *et al.*, 2013; Crea *et al.*, 2016; Dale, 2017). The analysis was done using Community Ecology package ('vegan' v. 2.3-2) (Oksanen *et al.*, 2016) and Bipartite package v2.11 (Dormann *et al.* 2009; Dormann, 2011), and 'plotweb' was used (Tylianakis *et al.*, 2007) in the R statistical software v. 3.2.2 (R Core Team, 2015) to visualize the bipartite interaction matrix.

## RESULTS

### *Fruit Bat Diversity and Abundance*

A total of 1,260 individual fruit bats were captured from 1,650 net-nights from April to October 2017 belonging to 11 species of fruit bats. Among these, five species are endemic to the Philippines and six are non-endemics (Table 3). These bats

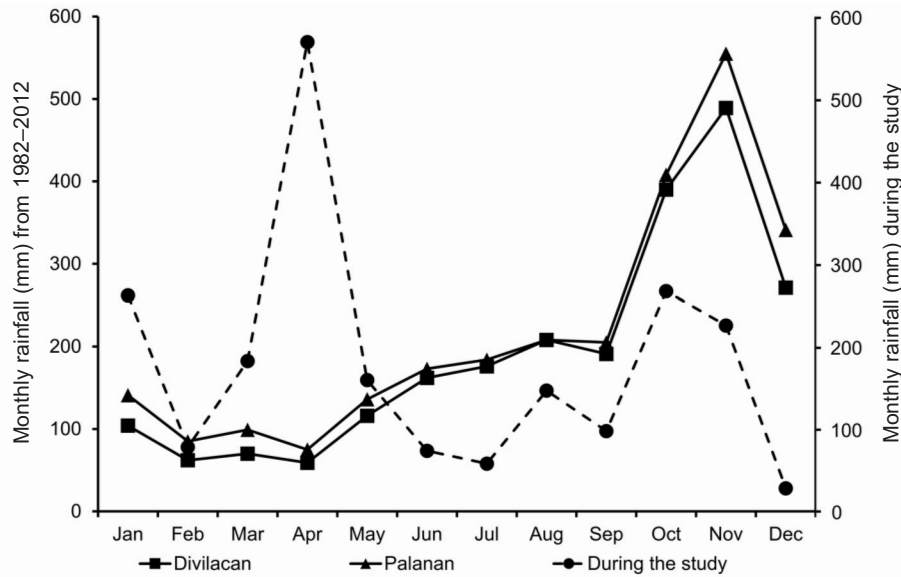


FIG. 2. Average monthly rainfall pattern (solid lines) in the municipality of Palanan and Divilacan on the eastern side of Northern Sierra Madre Natural Park from 1982–2002 (<https://en.climate-data.org>). Rainfall pattern (broken lines) in Palanan during the study was taken from a portable weather station (Davis Vantage Vue DAV-6250EU) installed in the Palanan Forest Dynamic Plot (PFDP) during the study

included eight primarily frugivores and four nectarivores. Frugivorous bats included *Acerodon jubatus*, *Cynopterus brachyotis*, *Desmalopex leucopterus*, *Haplonycteris fischeri*, *Ptenochirus jadori*, *Pteropus hypomelanus*, and *Pteropus vampyrus* while nectarivorous bats included *Eonycteris robusta*, *Eonycteris spelaea*, *Macroglossus minimus*, and *Rousettus amplexicaudatus*. The most abundant species was *R. amplexicaudatus*, followed by *P. jadori* and *C. brachyotis*. Large flying foxes (*A. jubatus*, *P. vampyrus* and *P. hypomelanus*) were not included in all the subsequent analyses due to small sample size.

Sampling was considered adequate (i.e. sampling completeness > 90%) in all vegetation types except for ultramafic site 4 (Table 4 and Fig. 3). Extrapolation of species richness indicates an increase of one species of fruit bat in the ultramafic study site 4. Based on the diversity profiles, the dipterocarp forest and ultramafic 1 (site 3) had the highest number of species (Fig. 3). However, Shannon

diversity was higher in the ultramafic 1 (site 3) than in the dipterocarp forest study sites and ultramafic 2 (site 4), and species diversity was lowest in the mangrove. A significant difference was observed in species diversity between dipterocarp 1 (site 1) and mangrove 1 (site 5) and ultramafic 1 (site 3) and mangrove forest based on the non-overlapping confidence intervals.

#### Fruit Bat Abundance Variation by Vegetation Type

A comparison of capture rates between feeding guilds in the different vegetation types showed a significant difference (Fig. 4), with the capture rate of fruit bats higher in the dipterocarp forest study sites and in the ultramafic forest site 3, while there were more nectarivores than frugivores in the mangrove forest. Individual species of fruit bats also differed significantly between vegetation sampling sites with the exception of *C. brachyotis* and *E. spelaea* (Fig. 5). Among the small frugivorous bats, *P. jadori*

TABLE 2. Summary of sampling dates in each lowland forest vegetation type in the Northern Sierra Madre Natural Park

Sites	Vegetation	April	May	June	July	August	September	October
Site 1	Dipterocarp 1	19–22	28–31	27–30	22–25	27–30	22–26	21–24
Site 2	Dipterocarp 2	Apr 30–May 02	18–21	17–20	26–29	22–24	18–21	21–23
Site 3	Ultramafic 1	Apr 30–May 02	18–21	17–20	26–28	22–24	18–21	25–27
Site 4	Ultramafic 2	20–23	23–26	22–24		18–21	Sept 28–Oct 01	
Site 5	Mangrove 1	24–27	23–26	22–24		18–21	Sept 28–Oct 01	
Site 6	Mangrove 2	24–27	28–31	27–30	22–25	26–29	23–25	21–24

TABLE 3. Body mass and capture rates of 11 species of fruit bats in the different vegetation types surveyed in the lowland forest of the Northern Sierra Madre Natural Park. Numbers in parentheses indicate the capture rate of individual species of fruit bat. Average mass was based on 20 adult individuals unless otherwise indicated (in brackets)

Species	Average mass (g)	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Total individuals	Capture rate
<b>Frugivores</b>									
<i>P. jagori</i>	73	93 (0.34)	47 (0.21)	50 (0.13)	4 (0.01)	6 (0.03)	17 (0.06)	217	(0.13)
<i>C. brachyotis</i>	36	55 (0.20)	42 (0.19)	44 (0.12)	13 (0.04)	20 (0.10)	21 (0.06)	195	(0.12)
<i>H. fischeri</i>	20	61 (0.23)	31 (0.14)	55 (0.15)	1 (0.003)	0	0	148	(0.09)
<i>D. leucopterus</i>	417	10 (0.04)	4 (0.02)	22 (0.06)	1 (0.003)	1 (0.01)	5 (0.02)	43	(0.03)
<i>A. jubatus</i>	777 [1]	0	1 (0.01)	0	0	0	0	1	(0.001)
<i>P. vampyrus</i>	742 [2]	0	1 (0.01)	5 (0.01)	3 (0.01)	0	0	9	(0.01)
<i>P. hypomelanus</i>	390 [1]	0	0	0	0	1 (0.01)	0	1	(0.001)
<b>Nectarivores</b>									
<i>M. minimus</i>	16	14 (0.05)	5 (0.02)	56 (0.15)	7 (0.02)	47 (0.24)	34 (0.12)	163	(0.10)
<i>E. robusta</i>	76	38 (0.14)	9 (0.04)	34 (0.09)	4 (0.01)	14 (0.07)	3 (0.01)	102	(0.06)
<i>R. amplexicaudatus</i>	87	119 (0.44)	37 (0.17)	145 (0.38)	6 (0.02)	4 (0.02)	58 (0.21)	369	(0.22)
<i>E. spelaea</i>	51 [1]	5 (0.02)	2 (0.01)	4 (0.01)	0	0	1 (0.004)	12	(0.01)
Total captures per vegetation type		395 (1.46)	179 (0.81)	415 (1.09)	39 (0.13)	93 (0.47)	139 (0.50)	1,260	(0.76)
Total net-nights		270	220	380	300	200	280	1,650	

and *H. fischeri* showed significant differences, with  $H = 16.71$ ,  $d.f. = 5$ ,  $P = 0.005$  and  $H = 28.58$ ,  $d.f. = 5$ ,  $P < 0.001$ , respectively. *Desmalopex leucopterus* also showed a significant difference between vegetation sampling sites ( $H = 13.47$ ,  $d.f. = 5$ ,  $P = 0.019$ ), with a higher number of captures in the ultramafic forest site 3 than in the dipterocarp and mangrove forest. The number of individuals of *P. jagori* in the dipterocarp forest was about two times greater than in the ultramafic forest and six times greater than in the mangrove forest. Almost twice as many *H. fischeri* were captured in the dipterocarp as in the ultramafic forest and the species was absent in the mangrove forest. *Macroglossus minimus* ( $H = 17.32$ ,  $P = 0.004$ ), *E. robusta* ( $H = 17.92$ ,  $P = 0.003$ ) and *R. amplexicaudatus* ( $H = 13.26$ ,  $P = 0.021$ ; in all cases  $d.f. = 5$ ) were among the nectarivorous bats that differed significantly between vegetation study sites. *Macroglossus minimus* was three times more abundant in the mangrove area than in the dipterocarp forest, while *E. robusta* and *R. amplexicaudatus* were almost twice as abundant in the dipterocarp forest as in the mangrove. A low abundance of fruit bats was observed in the ultramafic forest site 4.

TABLE 4. Species richness and diversity of fruit bats observed with nonparametric species estimator (Chao1) for fruit bats in each sampling site in the Northern Sierra Madre Natural Park (Large flying foxes, *Acerodon* and *Pteropus* excluded; see Materials and Methods)

Vegetation types/Sites	Diversity	Observed	Chao1	Sampling efficiency (%)
Dipterocarp forest				
Site1	Species richness	8	8	100
	Shannon diversity	5.79	5.85	
	Simpson diversity	4.98	5.03	
Site 2	Species richness	8	8	100
	Shannon diversity	5.55	5.66	
	Simpson diversity	4.87	4.98	
Lowland ultramafic forest				
Site 3	Species richness	8	8	100
	Shannon diversity	6.13	6.19	
	Simpson diversity	5.05	5.1	
Site 4	Species richness	7	7.92	88
	Shannon diversity	5.32	5.94	
	Simpson diversity	4.5	5	
Mangrove forest				
Site 5	Species richness	6	6	100
	Shannon diversity	3.76	3.87	
	Simpson diversity	2.96	3.03	
Site 6	Species richness	7	7	100
	Shannon diversity	4.44	4.54	
	Simpson diversity	3.66	3.73	



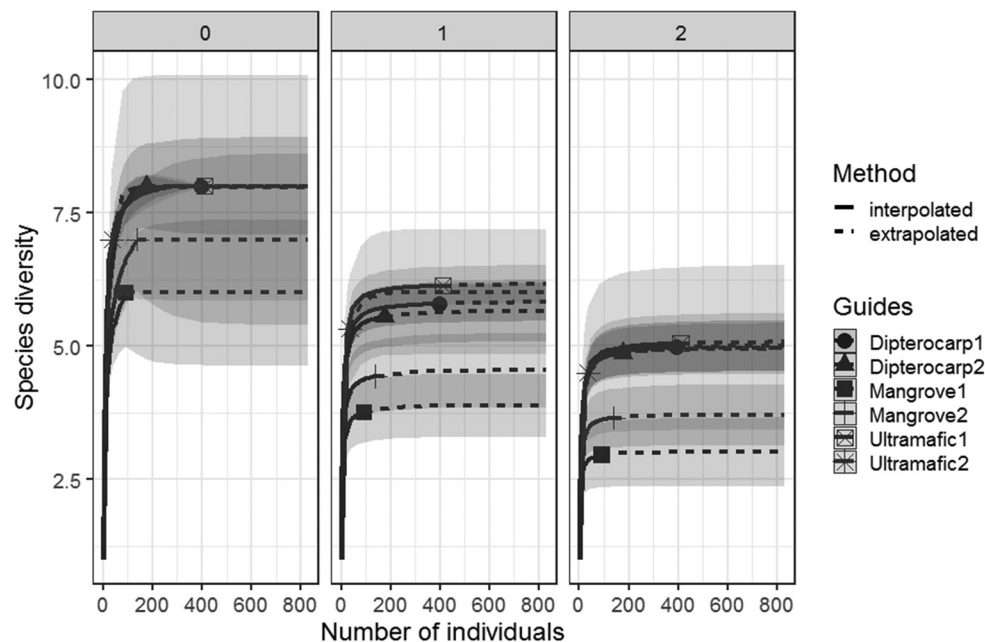


FIG. 3. Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the largest reference sample size) of fruit bat species diversity based on hill numbers ( $q = 0$  = species richness,  $1$  = exponential of Shannon's entropy index,  $2$  = inverse of Simpson's concentration index) for the dipterocarp, mangrove and lowland ultramafic forest. The grey-shaded regions represent the confidence interval obtained by bootstrap method based on 200 replications. Reference samples are denoted by shapes (Large flying foxes, *Acerodon* and *Pteropus* excluded; see Materials and Methods)

### Vegetation Composition and Structure

Plant species diversity and abundance differed between vegetation types (Table 5). In order of abundance, the dipterocarp forest study sites were dominated by families Dipterocarpaceae, Lauraceae, Meliaceae and Putranjivaceae. The lowland ultramafic forest was dominated by the families

Myrtaceae, Cannabaceae, Dilleniaceae, Theaceae, and Dipterocarpaceae. Mangrove forest was dominated by Rhizophoraceae and Lythraceae species, comprising about 91% of the species in the area. At the genus level, the most common genera in the dipterocarp forest were *Drypetes*, *Dysoxylum*, *Strombosia*, and *Albizia*, but in terms of number of individuals per species, *Drypetes megacarpa*, *Shorea*

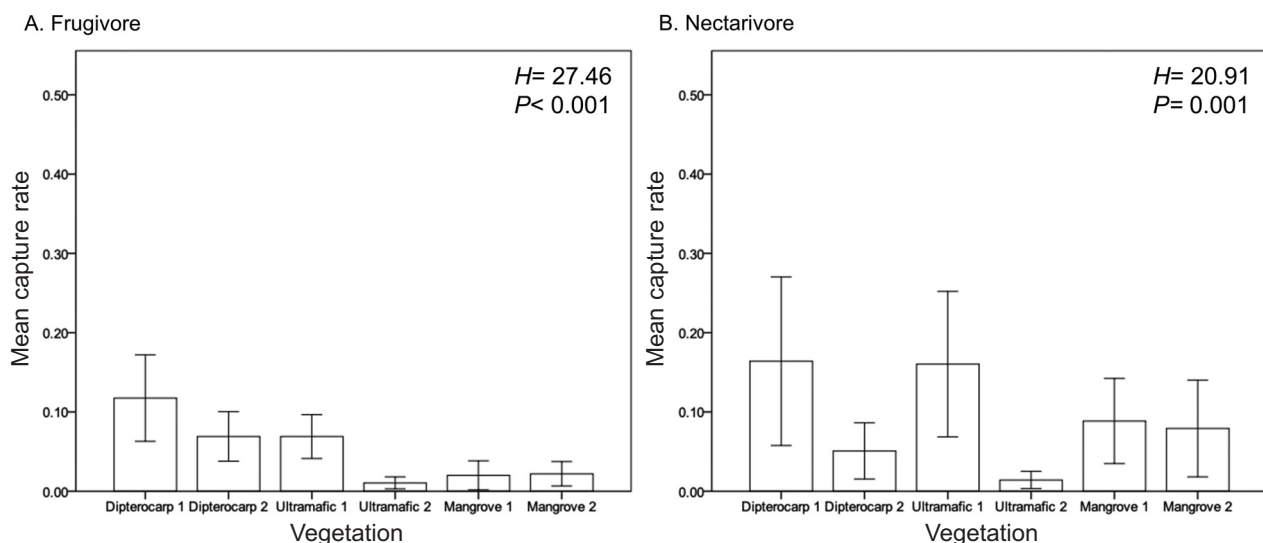


FIG. 4. Average monthly capture rates of (A) frugivores and (B) nectarivores in the different vegetation types in the Northern Sierra Madre Natural Park. Bars indicate standard errors. Statistics refer to Kruskal-Wallis tests (Large flying foxes, *Acerodon* and *Pteropus* excluded; see Materials and Methods)

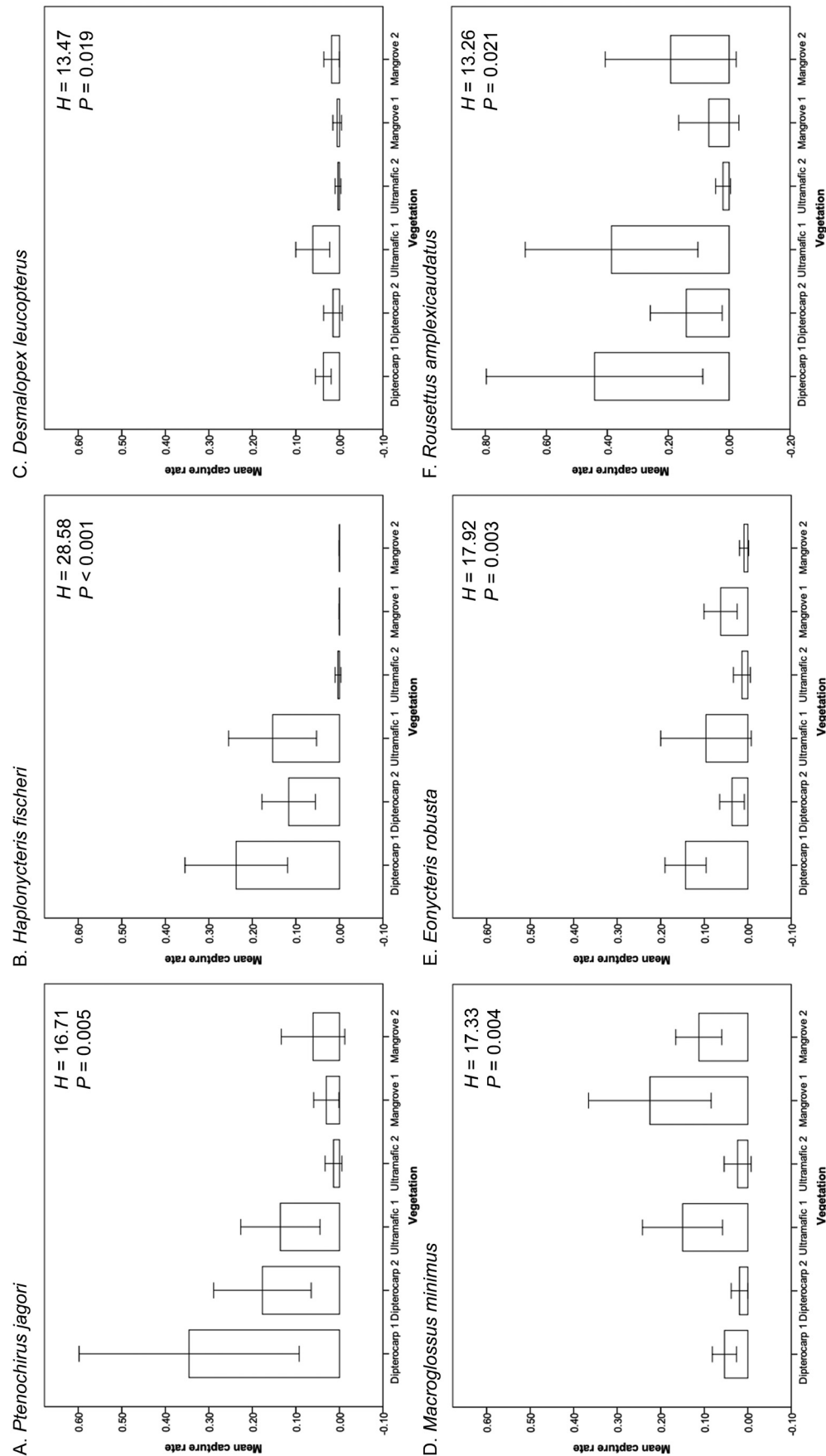


FIG. 5. Average monthly capture rates of six fruit bat species (A–F) that showed significant difference between vegetation types. Bars indicate standard errors. Statistics refer to Kruskal-Wallis tests. Note the different y-axis scale for (F) *E. robusta*

TABLE 5. Ranking of top 30 most abundant families and genera of plants in each vegetation type surveyed in the Northern Sierra Madre Natural Park (A = abundance; R = species richness)

Site 1					Site 2				
Family	A	Genus	A	R	Family	A	Genus	A	R
Dipterocarp forest									
Dipterocarpaceae	41	<i>Shorea</i>	38	4	Dipterocarpaceae	43	<i>Shorea</i>	36	4
Meliaceae	23	<i>Drypetes</i>	21	2	Meliaceae	43	<i>Drypetes</i>	24	4
Arecaceae	22	<i>Albizia</i>	12	1	Putranjivaceae	24	<i>Dysoxylum</i>	23	7
Putranjivaceae	21	<i>Pinanga</i>	12	2	Lauraceae	22	<i>Strombosia</i>	20	1
Lauraceae	20	<i>Xanthophyllum</i>	11	1	Erythraliaceae	20	<i>Endiandra</i>	14	1
Malvaceae	14	<i>Ficus</i>	10	3	Euphorbiaceae	18	<i>Enicosanthum</i>	13	1
Fabaceae: Mimosoideae	12	<i>Syzygium</i>	9	6	Malvaceae	17	<i>Albizia</i>	12	1
Polygalaceae	11	<i>Aglaia</i>	8	2	Annonaceae	15	<i>Pterocarpus</i>	12	1
Moraceae	10	<i>Dysoxylum</i>	8	2	Arecaceae	12	<i>Ficus</i>	10	4
Myrtaceae	9	<i>Endiandra</i>	8	1	Fabaceae: Mimosoideae	12	<i>Xanthophyllum</i>	10	3
Erythraliaceae	8	<i>Strombosia</i>	8	1	Fabaceae: Papilionoideae	12	<i>Areca</i>	9	1
Melastomataceae	6	<i>Chisocheton</i>	7	1	Moraceae	12	<i>Chisocheton</i>	9	2
Sapindaceae	6	<i>Leptonychia</i>	7	1	Burseraceae	10	<i>Aglaia</i>	8	3
Annonaceae	5	<i>Litsea</i>	7	3	Polygalaceae	10	<i>Celtis</i>	8	1
Euphorbiaceae	5	<i>Areca</i>	6	1	Anacardiaceae	9	<i>Microcos</i>	8	1
Fabaceae: Caesalpinioideae	4	<i>Nephelium</i>	6	1	Apocynaceae	9	<i>Dillenia</i>	7	3
Burseraceae	3	<i>Sterculia</i>	5	2	Phyllanthaceae	9	<i>Diospyros</i>	7	2
Clusiaceae	3	<i>Cryptocarya</i>	4	1	Cannabaceae	8	<i>Canarium</i>	6	3
Sapotaceae	3	<i>Cynometra</i>	4	1	Dilleniaceae	7	<i>Flueggea</i>	6	1
Theaceae	3	<i>Haplostichanthus</i>	4	1	Ebenaceae	7	<i>Kibatalia</i>	6	2
Dilleniaceae	2	<i>Macaranga</i>	4	2	Sapindaceae	7	<i>Leptonychia</i>	6	1
Gesneriaceae	2	<i>Astronia</i>	3	2	Clusiaceae	5	<i>Semecarpus</i>	6	2
Lamiaceae	2	<i>Calophyllum</i>	3	2	Myrtaceae	5	<i>Syzygium</i>	5	5
Cornaceae	1	<i>Camellia</i>	3	1	Myristicaceae	4	<i>Claoxylon</i>	4	1
Elaeocarpaceae	1	<i>Caryota</i>	3	1	Lamiaceae	3	<i>Dacryodes</i>	4	1
Fabaceae: Papilionoideae	1	<i>Dipterocarpus</i>	3	2	Myrsinaceae	3	<i>Dehaasia</i>	4	1
Myrsinaceae	1	<i>Memecylon</i>	3	1	Rubiaceae	3	<i>Discocalyx</i>	4	1
Oleaceae	1	<i>Palaquium</i>	3	1	Sapotaceae	3	<i>Hopea</i>	4	1
Rubiaceae	1	<i>Cyrtandra</i>	2	1	Actinidiaceae	2	<i>Croton</i>	3	1
Stemonuraceae	1	<i>Dacryodes</i>	2	1	Asteraceae	2	<i>Dimocarpus</i>	3	1
Lowland ultramafic forest									
Site 3					Site 4				
Theaceae	67	<i>Camellia</i>	66	1	Myrtaceae	58	<i>Syzygium</i>	44	8
Dilleniaceae	66	<i>Dillenia</i>	66	4	Pentaphylacaceae	31	<i>Ternstroemia</i>	31	1
Apocynaceae	61	<i>Alstonia</i>	59	1	Anacardiaceae	30	<i>Shorea</i>	29	1
Myrtaceae	49	<i>Gironniera</i>	47	1	Dipterocarpaceae	30	<i>Casuarina</i>	27	1
Cannabaceae	47	<i>Artocarpus</i>	39	1	Annonaceae	29	<i>Gironniera</i>	27	1
Moraceae	40	<i>Decaspermum</i>	27	1	Cannabaceae	27	<i>Xylopia</i>	27	1
Sapotaceae	40	<i>Syzygium</i>	22	8	Casuarinaceae	27	<i>Buchanania</i>	24	1
Dipterocarpaceae	36	<i>Palaquium</i>	17	1	Clusiaceae	26	<i>Calophyllum</i>	20	4
Lauraceae	21	<i>Buchanania</i>	14	3	Ebenaceae	19	<i>Teijsmanniodendron</i>	20	1
Clusiaceae	16	<i>Madhuca</i>	13	1	Lamiaceae	19	<i>Diospyros</i>	19	2
Primulaceae	15	<i>Teijsmanniodendron</i>	12	1	Polygalaceae	15	<i>Xanthophyllum</i>	15	1
Anacardiaceae	14	<i>Vatica</i>	12	1	Rubiaceae	10	<i>Tristanopsis</i>	13	1
Rubiaceae	13	<i>Calophyllum</i>	11	3	Symplocaceae	10	<i>Symplocos</i>	10	2
Lamiaceae	12	<i>Shorea</i>	11	2	Violaceae	9	<i>Rinorea</i>	9	1
Rutaceae	11	<i>Discocalyx</i>	9	1	Combretaceae	7	<i>Antirhea</i>	7	2
Annonaceae	9	<i>Haplostichanthus</i>	9	2	Bignoniaceae	6	<i>Terminalia</i>	7	1
Symplocaceae	9	<i>Symplocos</i>	9	1	Lythraceae	6	<i>Garcinia</i>	6	2
Fabaceae: Papilionoideae	7	<i>Actinodaphne</i>	8	1	Meliaceae	6	<i>Lagerstroemia</i>	6	1
Lythraceae	7	<i>Pouteria</i>	8	1	Celastraceae	5	<i>Mangifera</i>	6	3
Bignoniaceae	5	<i>Lagerstroemia</i>	7	1	Oleaceae	5	<i>Radermachera</i>	6	1
Calophyllaceae	5	<i>Nauclea</i>	7	1	Thymelaeaceae	5	<i>Aglaia</i>	5	3
Pentaphylacaceae	5	<i>Anisoptera</i>	6	1	Primulaceae	4	<i>Chionanthus</i>	4	1
Polygalaceae	4	<i>Ardisia</i>	6	1	Sapotaceae	4	<i>Artocarpus</i>	3	2
Sapindaceae	4	<i>Cryptocarya</i>	5	2	Lauraceae	3	<i>Exocarpos</i>	3	1

TABLE. 5. Continued

Site 3					Site 4				
Family	A	Genus	A	R	Family	A	Genus	A	R
Chrysobalanaceae	3	<i>Garcinia</i>	5	3	Moraceae	3	<i>Pleioluma</i>	3	1
Putranjivaceae	3	<i>Kayea</i>	5	1	Salicaceae	3	<i>Salacia</i>	3	1
Cardiopteridaceae	2	<i>Litsea</i>	5	5	Santalaceae	3	<i>Wikstroemia</i>	3	1
Euphorbiaceae	2	<i>Melicope</i>	5	1	Apocynaceae	2	<i>Alstonia</i>	2	1
Pandaceae	2	<i>Radermachera</i>	5	1	Burseraceae	2	<i>Aquilaria</i>	2	1
Phyllanthaceae	2	<i>Ternstroemia</i>	5	1	Chrysobalanaceae	2	<i>Brackenridgea</i>	2	1
Mangrove forest									
Site 5					Site 6				
Rhizophoraceae	558	<i>Ceriops</i>	293	1	Rhizophoraceae	52	<i>Heritiera</i>	41	1
Lythraceae	16	<i>Rhizophora</i>	265	2	Lythraceae	41	<i>Sonneratia</i>	38	1
		<i>Sonneratia</i>	16	1	Malvaceae	39	<i>Rhizophora</i>	33	2
					Meliaceae	2	<i>Bruguiera</i>	19	2
							<i>Xylocarpus</i>	2	1

*negrosensis*, *Strombosia philippinensis* and *Albizia* sp. (locally known as 'butarek') were the most common. Based on Co *et al.* (2006), species of *Syzygium* and *Ficus* were among the most common species in the dipterocarp forest. In the lowland ultramafic forest, *Gironniera*, *Dillenia*, *Camellia*, *Syzygium*, and *Alstonia* were the most common genera. *Gironniera subaequalis*, *Camellia lanceolata*, *Alstonia macrophylla* and *Dillenia* sp. were the most common species encountered. Mangrove forest was dominated by Rhizophoraceae species composed mainly of *Ceriops tagal* and *Rhizophora apiculata*. *Sonneratia alba* was the third most common species in the mangrove study site and was most abundant at mangrove site 6.

Among the plant species, family Anacardiaceae (*Mangifera*), Arecaceae (*Pinanga*, *Areca*, *Caryota*), Burseraceae (*Canarium*, *Dacryodes*), Calophyllaceae (*Calophyllum*), Combretaceae (*Terminalia*), Dilleniaceae (*Dillenia*), Ebenaceae (*Diospyros*), Gesneriaceae (*Cyrtandra*), Lauraceae (*Litsea*), Lythraceae (*Sonneratia*), Meliaceae (*Chisocheton*, *Dysoxylum*), Moraceae (*Ficus*, *Artocarpus*), Myrtaceae (*Syzygium*, *Decaspermum*), Putranjivaceae (*Drypetes*), Rubiaceae (*Diplospora*, *Nauclea*, *Psychotria*), Sapindaceae (*Nephelium*) and Sapotaceae (*Madhuca*, *Palaquium*, *Pouteria*) have been reported to be part of fruit bat diets (Marshall 1985; Utzurrum, 1995; Hamann and Curio, 1999; Hodgkinson *et al.*, 2003) (Table 6). These plants have either flowers or fruits located at the outer tip of branches, clustered along tree trunks and branches such *Ficus* (cauliflory or ramiflory) or suspended in long stalks like *Chisocheton* and *Dysoxylum* (flagelliflory), with tubular or symmetrical flowers with several stamens such as *Syzygium*, all

of which are characteristics of bat-visited plants (Marshall, 1983; Kalko *et al.*, 1996; Fleming *et al.*, 2009).

Forest structure also differs between vegetation types (Table 7 and Fig. 6). A total of 154, 135 and eight species of plants were recorded in the dipterocarp, lowland ultramafic and mangrove forest, respectively. Dipterocarp forest had the highest plant species richness and had the largest basal area and tallest trees averaging at 8.25 m but had the lowest tree density. Lowland ultramafic forest had the second highest number of species and had the highest tree density and tree height averaging 6.5 m. Mangrove forest had the lowest plant species richness, and tree density was intermediate between dipterocarp and lowland ultramafic forest, and average tree height was 4.9 m.

#### Habitat Association

A bipartite graph was used to examine the association of the different fruit bat species with the three vegetation types (Fig. 7). As indicated by the weight of the bands in the graph, endemic species such as *H. fischeri*, *P. jagori*, and *D. leucopterus* were highly associated with dipterocarp and lowland ultramafic forest. Moreover, *D. leucopterus* was more strongly associated with lowland ultramafic than with dipterocarp forest, while *P. jagori* and *H. fischeri* were more strongly associated with dipterocarp forest than ultramafic forest. *Eonycteris robusta* was encountered in all three forest formations but was highly associated with the lowland ultramafic and dipterocarp forest. Non-endemic species such as *C. brachyotis*, *E. spelaea*, *R. amplexicaudatus*, and *M. minimus* were found in all

TABLE 6. List of plant genera that are potential food plants of fruit bats in the three vegetation types sampled in the Northern Sierra Madre Natural Park

Family/Species	Food type	Dipterocarp	Ultramafic	Mangrove
Anacardiaceae				
<i>Mangifera</i>	Fruit	x	x	
Arecaceae				
<i>Areca</i>	Fruit	x		
<i>Pinanga</i>	Fruit	x		
<i>Caryota</i>	Fruit	x		
Burseraceae				
<i>Canarium</i>	Fruit	x		
<i>Dacryodes</i>	Fruit	x		
Calophyllaceae				
<i>Calophyllum</i>	Fruit	x	x	
Combretaceae				
<i>Terminalia</i>	Fruit/Flower	x	x	
Dilleniaceae				
<i>Dillenia</i>	Fruit	x	x	
Ebenaceae				
<i>Diospyros</i>	Fruit	x	x	
Fabaceae: Mimosoideae				
<i>Albizia</i>	Flower	x		
Gesneriaceae				
<i>Cyrtandra</i>	Fruit	x		
Lauraceae				
<i>Litsea</i>	Fruit	x	x	
Lythraceae				
<i>Sonneratia</i>	Flower			x
Meliaceae				
<i>Chisocheton</i>	Flower	x		
<i>Dysoxylum</i>	Flower	x		
Moraceae				
<i>Artocarpus</i>	Fruit	x	x	
<i>Ficus</i>	Fruit	x	x	
Myrtaceae				
<i>Decaspermum</i>	Flower/Fruit		x	
<i>Syzygium</i>	Flower/Fruit	x		
Putrajivaceae				
<i>Drypetes</i>	Fruit	x		
Rhizophoraceae				
<i>Ceriops</i>	Flower			x
Rubiaceae				
<i>Nauclea</i>	Fruit		x	
<i>Psychotria</i>	Fruit		x	
<i>Diplospora</i>	Fruit	x	x	
Sapotaceae				
<i>Madhuca</i>	Fruit		x	
<i>Palaquium</i>	Fruit	x	x	
<i>Pouteria</i>	Fruit		x	
Sapindaceae				
<i>Nephelium</i>	Fruit	x		

vegetation types surveyed, but *M. minimus* was more strongly associated with mangrove and ultramafic forest than with dipterocarp forest, while *C. brachyotis* was more strongly associated with the dipterocarp forest than ultramafic and mangrove forest. There were also very few captures of *E. spelaea* in all the vegetation types sampled, and most of the

captures were young individuals. In addition, very few individuals of flying foxes were captured during the study. Among the large flying foxes, one individual of *A. jubatus* was captured in the dipterocarp forest, and one *P. hypomelanus* in the mangrove forest. *P. vampyrus* was captured in both dipterocarp and lowland ultramafic forest.



TABLE 7. Summary of species richness and forest structure of each vegetation type surveyed in the Northern Sierra Madre Natural Park

Site	Total no. of species	No. of species	Average tree ( $\bar{x} \pm SD$ )		
			Density (trees/ha)	Height (m)	Basal area (m <sup>2</sup> )
Site 1	154	123	1230 $\pm$ 218	7.81 $\pm$ 4.55	0.027 $\pm$ 0.074
Site 2		69	1838 $\pm$ 464	8.68 $\pm$ 5.00	0.035 $\pm$ 0.096
Site 3		82	2185 $\pm$ 851	6.20 $\pm$ 2.03	0.009 $\pm$ 0.014
Site 4		102	2975 $\pm$ 680	6.87 $\pm$ 3.04	0.012 $\pm$ 0.035
Site 5	8	4	2870 $\pm$ 911	4.12 $\pm$ 0.85	0.007 $\pm$ 0.008
Site 6		7	777 $\pm$ 437	5.85 $\pm$ 1.94	0.001 $\pm$ 0.001

## DISCUSSION

The total number of fruit bat species captured during the study comprised 73% (11) of all the known fruit bats on Luzon Island. The species

known from other parts of Luzon that were not recorded include the Philippine endemic species *Dyacopteris rickarti*, *Harpyionycteris whiteheadi*, *Pteropus pumilus* and *Otopteropus cartilagonodus*. *Dyacopteris rickarti* is known on Luzon only from



FIG. 6. Forest structure of the three vegetation types surveyed in the study in the Northern Sierra Madre Natural Park: A — Dipterocarp 1, B — Dipterocarp 2, C — Ultramafic 1, D — Ultramafic 2, E — Mangrove 1, F — Mangrove 2

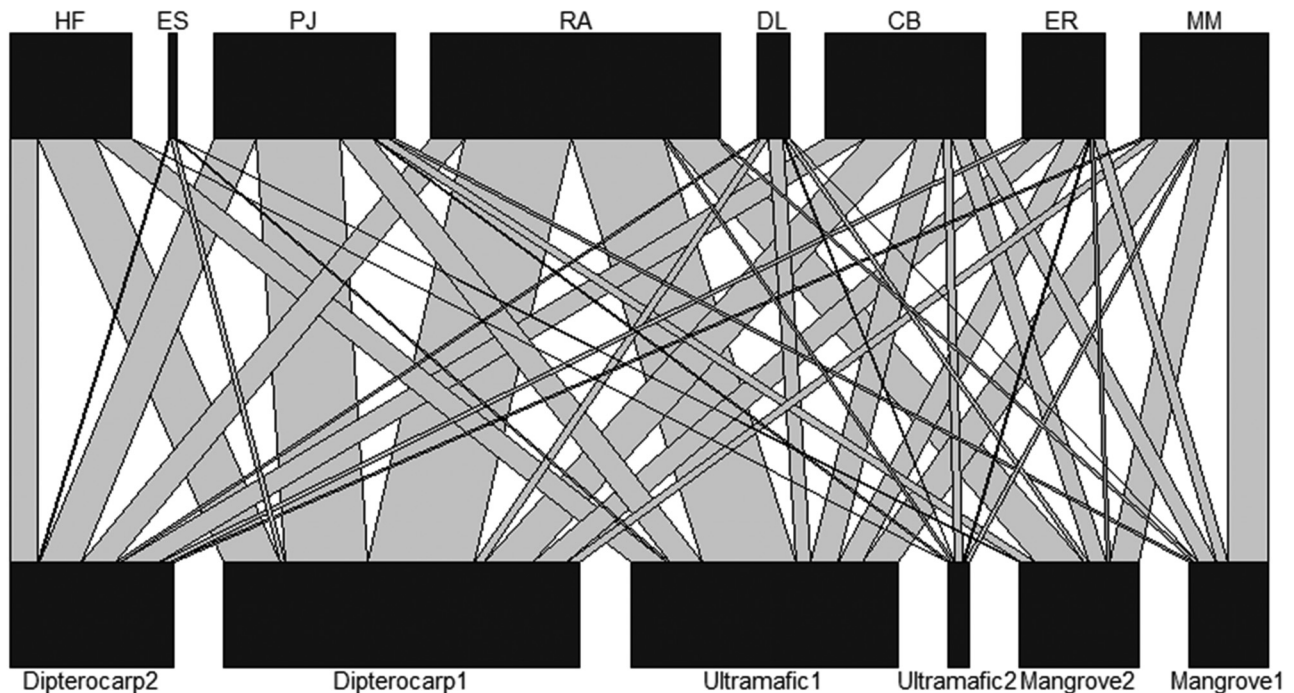


FIG. 7. A bipartite network graph showing the fruit bats species association with the three vegetation types. The wider the band, the higher the capture rate in the given habitat. (CB = *C. brachyotis*; DL = *D. leucopterus*; ER = *E. robusta*; ES = *E. spelaea*; HF = *H. fischeri*; MM = *M. minimus*; PJ = *P. jagori*; RA = *R. amplexicaudatus*)

Abra province. *Harpyionycteris whiteheadi* is known on Luzon only from the Bicol Peninsula; both of these are distant from the study area. *Otopterus cartilagonodus* are uncommon in lowland forest and relatively common in primary montane and mossy forest throughout Luzon Island (Ruedas *et al.*, 1994; Duya, 1999; Heaney *et al.*, 2010, 2016). *Pteropus pumilus* is associated with primary and secondary lowland forest and are common on small islands and rare on larger Islands (Heaney *et al.*, 2016); their absence in our study area despite extensive netting efforts using ground and sub-canopy/canopy nets suggests that they may be rare on Luzon Island compared to other islands in the country. So far, only one individual was recorded at Dalton Pass in Nueva Vizcaya province (Heaney *et al.*, 2016). In other words, for species presence, our sampling may have been complete for NE Luzon, with the exception of *O. cartilagonodus*.

Prior studies of the association of Philippine fruit bats with forest types has suggested that endemic species are associated with primary forest while non-endemics are associated with disturbed forest (Heaney *et al.*, 1989; Heideman and Heaney, 1989). So far, there has been no study to our knowledge on the abundance of fruit bats in the different vegetation types in the Philippines. The observed patterns of fruit bat abundance in the three vegetation types

in our study suggest that species have varied vegetation preferences that may be linked to their diet and morphology.

There was no difference in species richness and diversity of fruit bats between dipterocarp and lowland ultramafic forest. Dipterocarp and ultramafic forest differ significantly with mangrove forest, which may be attributed to the abundance of fruit producing plants in the dipterocarp and ultramafic forest compared to mangrove (Table 6). Despite the presence of a large colony of flying foxes composed of *P. vampyrus*, *P. hypomelanus*, and *A. jubatus* located about 10 kilometers northwest from our ultramafic study site 3 in Barangay Dimapnat and ultramafic study site 4 and mangrove study site 5 in Barangay Bicobian, we only captured a few individuals of flying fox. The few captures of these large flying foxes may be attributed to the difficulty of capturing the species, as they usually fly high above the canopy.

On the other hand, *D. leucopterus* was most frequently captured in lowland ultramafic forest. The species is thought to roost in small groups or solitarily (Heaney *et al.*, 2010, 2016). They may prefer to roost in more cluttered vegetation than in less cluttered understory to lessen exposure to predators, in contrast to the large flying foxes which roost in large colonies and open canopy, but there is no direct



information on the roosting site of *D. leucopterus* or the size of their colonies. The capture of *A. jubatus* in dipterocarp forest and *P. hypomelanus* in the mangrove forest is consistent with observations of Mildenstein *et al.* (2005) and Heaney *et al.* (2016) that the former species prefer high diversity forest while the latter is associated with low diversity forest. The low fruit bat abundance in the ultramafic site 4 may be due to its distance from the contiguous forest and food availability may be low in the area. This indicates that fruit bats may choose to forage in adjacent forest areas when food resources are abundant. A phenology study in the ultramafic forest site 4 indicated low food availability compared to the ultramafic study site 3 (M. R. Duya, unpublished data).

Among the small primarily fruit-eating bats, the most common species was *P. jagori* in all vegetation types sampled except in the mangrove forest, followed by *C. brachyotis* which was the most common fruit bat in the mangrove forest. *Haplonycteris fischeri*, which was the smallest among the fruit bats and the third most common species of fruit bat, was absent in the mangrove forest. *Ptenochirus jagori* and *C. brachyotis* occur in both forest and highly disturbed habitats. However, *P. jagori* usually occurs in low numbers in disturbed habitats where *C. brachyotis* is more common, while *H. fischeri* is usually strongly associated with forest areas (Heaney *et al.*, 2010, 2016).

Our dipterocarp and ultramafic forest sites share many of the species of plants that are potential food plants for bats. However, the difference in individual plant species abundance between the vegetation types could have accounted for the variation in the abundance of fruit bats. The higher number of *C. brachyotis*, *H. fischeri* and *P. jagori* in the dipterocarp sites may be attributed to the high abundance of *Ficus*. Studies on the diet of all of these species indicate that *Ficus* is usually a major component of the species' diet (Utzurum, 1995; Tan *et al.*, 1998; Hamann and Curio, 1999). Bats chew the *Ficus* fruit and expel the pellets rather than swallow the whole fruit while feeding. Thus, other fleshy fruits with larger seeds such as *Dillenia*, *Drypetes*, *Mangifera*, *Pinanga*, and *Syzygium* which are also common in the dipterocarp forest, may also be part of the species diet. However, gape width of this small bat could limit the size of fruit the bat can hold (Kalko *et al.*, 1996). Understory plants such as Arecaceae, Melastomataceae, and Rubiaceae are also found in our dipterocarp study sites. Although the latter species have fruits on their leaf axils, they produce

small colorful fruits that are conspicuous to fruit bats. Species of these plant families may be a potential source of food for smaller bats such as *H. fischeri*.

*Ptenochirus jagori* and *C. brachyotis* dispersed seeds of mostly *Ficus* species and other early-successional species such as *Bischofia javanica* from family Phyllanthaceae (Hamann and Curio, 1999), which have relatively large fruits compared to the fruit of other understory plants. Given the small size of *H. fischeri* (15–20 grams) and the width of its gape, *Ficus* may not be the primary food of the species; rather, they may prefer the small colorful fruits of the understory plants such as *Litsea* and *Psychotria* or probably fruits from understory vines such as *Freycinetia* and *Piper* that were observed in the dipterocarp study sites. Both species have been reported as food plants of *H. fischeri* in the montane forest of Negros Island (Utzurum, 1995). Seeds of *Piper* were collected in the fecal samples of *H. fischeri* in the study site (J. Rey, personal communication).

Lowland ultramafic forest was dominated by families Myrtaceae, Dilleniaceae, Anacardiaceae, Sapotaceae, and Moraceae. Trees that produce fleshy fruits, such as species of *Syzygium*, *Dillenia*, and *Artocarpus*, were the most commonly recorded in the ultramafic forest. The lesser abundance of species of *Ficus* (Moraceae), *Areca* (Arecaceae), and *Litsea* (Lauraceae) among other fruit-bearing plants in the ultramafic forest might explain the variation of frugivore abundance between dipterocarp and ultramafic forest. However, further studies are needed to test this assertion as other factors may have influenced the fruit bat behavior such as forest structure and phenology of their food plants. Furthermore, *Palaquium* and *Madhuca* of the family Sapotaceae are among the sub-canopy trees common in the area, and their fruits are large and fleshy. We observed three individuals of *D. leucopterus* feeding on the fruit of a *Madhuca* tree near our campsite and we also observed the species visiting a *Palaquium* tree in the study area. These food plants could have attracted *D. leucopterus* to frequent the area. Both genera have been suspected to be dispersed by bats because of the position of their flowers and fruits (van der Pijl, 1957).

The presence of *P. jagori* and *C. brachyotis* in the mangrove forest, albeit in low numbers, maybe due to the continuous availability of flowers rather than fruits. Both species of bats have been reported to feed on leaves and flowers of other plants (Tan *et al.*, 1998; Reiter and Tomaschewski, 2002). *Cynopterus brachyotis* have been shown to feed on

flowers (Tan *et al.*, 1998). Pollen samples from *S. alba* were collected from individual specimens of *C. brachyotis* and *P. jagori* caught in the mangrove forest of Palanan and Divilacan (D. Fajardo, personal communication). The presence of pollen from fruit-eating bats suggests that they visit flowers and probably eat parts of the flowers. The absence of *H. fischeri* in the mangrove may be due to the large size, hardness, and irregular shape of mangrove fruits that makes handling of fruit difficult for small bats. Smaller bats usually carry their food away from the source and feed on nearby trees (Utzurum, 1995; Kalko *et al.*, 1996). Studies also suggest that body size, wing and cranial morphology of bats limit food items that can be accessed by fruit bats (Aguirre *et al.*, 2003; Dumont, 2003; Dumont and O'Neal, 2004).

The abundance of nectarivorous bats varied between vegetation types. *Macroglossus minimus* was the most common species in mangrove forest. The presence of *S. alba* and *C. tagal* species in the mangrove could have attracted this bat. Although *S. alba* was less common than *C. tagal*, the species has previously been associated with *M. minimus* (Winkelman *et al.*, 2003), as we found in this study. Based on studies in other countries, the flowers of both species bloom only at night and produce a fragrant smell which is a typical characteristic of bat-visited flowers; both species also flower throughout the year (Tomlinson *et al.*, 1979; Steinke *et al.*, 1995; Wang'ondou *et al.*, 2013; Duke and Schmitt, 2015;

Sarno *et al.*, 2017). The availability of abundant food for long periods in the mangrove forest may have attracted *M. minimus* to favor mangrove forest over dipterocarp and ultramafic forest.

We found a higher proportion of *E. robusta* and *R. amplexicaudatus* in dipterocarp and lowland ultramafic forest than in mangrove. This variation likely reflects differences in size, wing morphology, and proximity of food plants. The former two species are four and five times heavier than *M. minimus*, respectively. *Sonneratia alba* and *C. tagal* species are absent in the dipterocarp and lowland ultramafic forests. However, other species with flower characteristic similar to *Sonneratia* occurred abundantly in the dipterocarp and lowland ultramafic forest, such as *Syzygium* from family Myrtaceae; this was the most abundant family in lowland ultramafic forest in our study area, and among the most common species in the dipterocarp forest (Co *et al.*, 2006). Meliaceae, which was the second most common family in the dipterocarp forest in the study sites, have flowers located along the main trunk of the tree or located terminally on the branches or suspended on long stalks. Species belonging to this family such as *Dysoxylum parasiticum*, *Chisocheton pentandrus*, and *Chisocheton patens* were common in the dipterocarp forest study sites (Co *et al.*, 2006). In addition, species of *Ficus* from family Moraceae that exhibit cauliflory were common in the dipterocarp forest (Co *et al.*, 2006). These tree species are relatively larger compared to *S. alba* and *C. tagal*

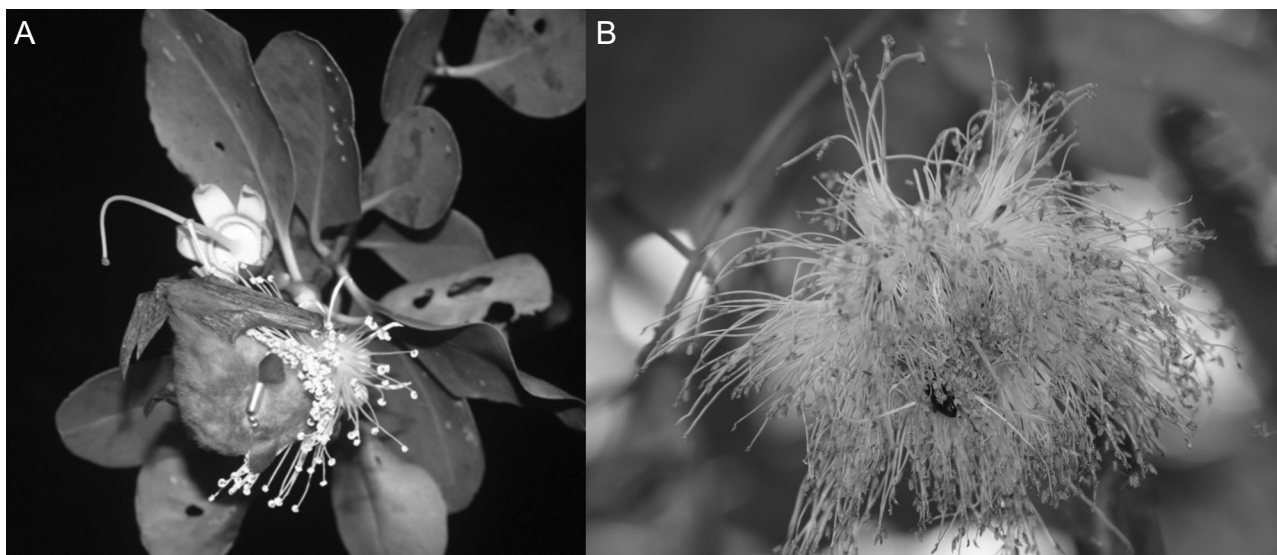


FIG. 8. A — *Macroglossus minimus* observed feeding on *S. alba* on the seaward side of the mangrove forest. Photography by M. R. Duya on May 2017; B — Photo of flower on the right is from the *Syzygium* cf. *everetti* belonging to family Myrtaceae that has a similar flower structure as *S. alba*. Photo taken from the dipterocarp forest study site by R. Tubale on April 2018

and the locations of their flowers are well suited for the pteropodid bats. Unlike the New World nectarivorous bats, which hover while feeding, Old World fruit bats land on the flowers before feeding (Fleming *et al.*, 2009). We observed such behavior in *M. minimus* when we released the bat near a flowering *S. alba* tree: the bat immediately landed on the flower and started feeding on it (Fig. 8). *Eonycteris robusta* and *R. amplexicaudatus* roost in caves, and their abundance in the dipterocarp forest and lowland ultramafic forest could be attributed to the presence of a cave near the study area. Although their long and narrow wings (Duya *et al.*, 2017) allow them to travel a great distance in search of food, the abundance of food resources in a particular site may have limited their movement (Bonaccorso *et al.*, 2002; Bianconi *et al.*, 2006). *Macroglossus minimus*, on the other hand, has short and broad wings (Duya *et al.*, 2017) compared to the other two species. This allows the species to easily maneuver in the understory or cluttered spaces (Norberg and Rayner, 1987), which are the characteristics of the mangrove and ultramafic forest in our study site.

We captured few individuals of *E. spelaea* compared to its congeneric *E. robusta* in all our vegetation sampling sites. The latter species is endemic to the Philippines while the former is widespread throughout Southeast Asia (Heaney *et al.*, 2016). *E. spelaea* is known to inhabit highly disturbed habitats and agricultural areas (Heideman and Heaney, 1989; Heaney *et al.*, 2010, 2016), which could explain the low capture rate of *E. spelaea* in our relatively undisturbed sampling sites. The two species have similar body size and have a long rostrum, a typical characteristic of a nectar-feeding bat, but they differ significantly in wing morphology (Duya *et al.*, 2017). *Eonycteris robusta* have a higher aspect ratio and wing loading compared to *E. spelaea*. Different habitat preferences indicate different food resources and forest structure, which could require different feeding behavior. The latter species forages mostly in agricultural areas and along forest edges while the former species forage in primary and secondary forest near their roost (Heaney *et al.*, 2016).

This study is the first survey of a fruit bat assemblage in old-growth lowland tropical forest in the Philippines. The data presented here, which include fruit bats in relatively intact dipterocarp, ultramafic and mangrove forest, can be considered a baseline for future studies. Our study indicates that small frugivorous bats prefer dipterocarp and ultramafic forest more than mangrove forest. On the other hand, mangrove forest is an important habitat for

small nectarivorous bats. The pattern of fruit bat abundance between vegetation types observed could be attributed to the presence of preferred food plants of the species. More extensive sampling in these vegetation types may reveal species-specific preferences. Studies on the vertical distribution of fruit bats and food plants in these forests will allow us to understand how these forest-dwelling bats partition the vast resources in the forest. Further research on foraging range and behavior and fruit selection are needed to understand further the role of fruit bats in seed dispersal and pollination, and the role of forest structure in determining the abundance and distribution of these ecologically important members of Philippine forest communities.

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