

## The role of fruit bats in plant community changes in an urban forest in Indonesia

Sheherazade<sup>1,2</sup>, Yasman<sup>2</sup>, Dimas H. Pradana<sup>2</sup>, Susan M. Tsang<sup>3,4,5\*</sup>

**Abstract.** Urban forests are important for alleviating the impact of environmental stress in intensely developed cities and play a role in maintaining natural interactions in urban ecosystems. Two of the most densely populated cities in Southeast Asia: Jakarta and Depok, Indonesia, have seen a dramatic decrease in green spaces, despite the importance of such spaces in making these cities more liveable and sustainable. One of the few remaining green spaces in the greater Jakarta area is the urban forest at Universitas Indonesia, yet little is known about its native biota, especially its bats. A host plant association study was conducted to determine the role of fruit bats in the urban forest ecosystem, which are suspected to be seed dispersers and pollinators. Eight fruit bat species (*Cynopterus brachyotis*, *C. horsfieldii*, *C. minutus*, *C. sphinx*, *C. titthaecheilus*, *Macroglossus minimus*, *M. sobrinus*, and *Rousettus amplexicaudatus*) consumed plant products from 26 plant species. Bat-plant species pairs were significantly associated (Cramer's  $V = 0.51$ ,  $p < 0.05$ ). *Ficus* species comprised the highest percentage of plants consumed (25%), yet they were never deliberately planted, suggesting that fruit bats introduced them from other areas. Additionally, introduced plants were found outside the introduction area. By acting as seed dispersers and pollinators, fruit bats potentially contribute to the current plant diversity in the urban forest and connect distant plant populations. Fruit bats facilitated seed dispersal of species important to forest regeneration, an important insight for future plans to increase green spaces to mitigate the negative effects of anthropogenic change in urban environments.

**Key words.** fragmented landscape, Indonesia, pollination; Pteropodidae, seed dispersal; urban ecology

### INTRODUCTION

Green spaces serve an important role in making cities more liveable and sustainable (Kusratmoko et al., 2002; Raciti et al., 2014). In rapidly developing nations, such as Indonesia, green spaces are often forgotten in urban planning and have subsequently dramatically decreased in total area covered (Ramdani, 2013; Zain et al., 2015). This trend has been especially prevalent in one of the most densely populated areas in all of Southeast Asia—the greater capital area of Indonesia, where Jakarta and the adjoining city of Depok has seen intense growth in both area and population size for the past two decades (Krank et al., 2009; Zain et al., 2015). The intense urbanisation of both cities highlights many of the rapid changes and challenges to natural systems in West Java and Southeast Asia as a whole (Zain et al., 2015). Infrastructure expansions often do not retain sufficient

drainage, and exacerbates damage caused by annual flooding (Muis et al., 2015). The high concentration of vehicles and factories throughout the greater Jakarta area causes heavy air pollution, which reduces the quality of living and often causes loss of human life (Santoso et al., 2013). Of the existing green spaces in the greater Jakarta area, a small percentage of them would be considered an urban forest. An urban forest is considered a distinctive type of ecosystem, where, in addition to plants and animals, people and artificial structures within it interact and contribute significantly to the ecosystem to provide a wide range of ecosystem services that can affect the quality of urban life (Bolund & Hunhammar, 1999; Nowak et al., 2010). These interactions are an essential component to the utility of urban forests as a carbon sink and water reservoir (Alvey, 2006). Urban forests are often deliberately established through greening programs to alleviate the environmental stress caused by intense development (Jim, 2013; Lubis et al., 2013). The absence of green areas is an important issue near most metropolitan areas in Indonesia and Southeast Asia, many of which now lack natural buffers to ameliorate the effects of flooding and heavy air pollution (Muis et al., 2015; Zain et al., 2015). One of the few remaining green spaces in the greater Jakarta area is the urban forest at Universitas Indonesia (UI) in Depok (Lubis et al., 2013; Ramdani, 2013). Prior to the existence of the UI urban forest, the campus was comprised of paddy fields and lawns, but the Technical Unit of Campus Security (Unit Pelaksana Teknis, Pengamanan Lingkungan Kampus, UPT PLK) at UI decided to initiate a greening program in the 1980s to 2000s. The

<sup>1</sup>Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA

<sup>2</sup>Department of Biology, University of Indonesia, Depok, West Java, Indonesia

<sup>3</sup>Department of Mammalogy, American Museum of Natural History, New York, USA

<sup>4</sup>Department of Biology, City College and the Graduate Center, The City University of New York, New York, USA

<sup>5</sup>Mammalogy Section, National Museum of the Philippines, Manila, Philippines; Email: [stsang@amnh.org](mailto:stsang@amnh.org) (\*corresponding author)

program introduced new, economically important plants, such as *Hevea brasiliensis* (rubber tree), to ensure that the local people can benefit from the new forest. Over the past 30 years, the UI urban forest has grown to include a plethora of plants, many of which were never deliberately planted (Lubis et al., 2013). With minimal to no human intervention, plant diversity in the UI urban forest has now increased to 150 angiosperm species from 45 different families (Lubis et al., 2013). The plants are predominantly species from Myrtaceae, Moraceae, Musaceae, and Fabaceae (Nurhayati, 2009; Toni, 2009). It is unclear what caused the increase in plant diversity, but fruit bats (family Pteropodidae) are the most probable seed disperser causing these changes in the plant community of the UI urban forest. Since the UI urban forest is located in the middle of a highly urbanised area with limited green space and no connective corridors, animals with the ability for directed and long flight are the most likely source for the introduction of new species, and the known traits of resident plants suggest that these dispersers are fruit bats. The overlap in fruit diet for birds and bats is low (Fleming, 1979) and plants tend to exhibit characteristics that would attract a specific disperser taxa, especially since previous studies suggest birds and bats are not redundant seed dispersers (Jacomasa & Pizo, 2010; Sarmiento et al., 2014). In the UI urban forest, many plants exhibit morphological and physiological traits that are generally associated with a chiropterophilous syndrome to attract bats to the plant. Their fruits tend to be pale in colour, produce a distinct odour, and their flowers bloom at night (Goltenboth et al., 2006; Willmer, 2011). These attributes specifically attract fruit bats, not birds, to the plants, resulting in pollination or seed dispersal. The mechanism for the seed dispersal is either: 1) after undergoing endozoochory and seeds are dropped via bat guano, or 2) when the bat spits out chewed fruit and seeds, creating a mass called the ejecta (Tan et al., 2000). Furthermore, fruit bats are known to be long-distance seed dispersers and pollinators due to their ability to forage and fly over large areas (Fleming et al., 2009; Abedi-Lartey et al., 2016). This study aims to determine which plant species are most closely associated with fruit bats in order to understand the role of fruit bats in plant community changes in an urban forest. Our hypothesis is that increased plant diversity in UI is a result of natural plant-fruit bat associations, primarily driven by the diversity of fruit bat species and the breadth of the niche of some fruit bat species. Understanding these interactions is important for promoting natural links between plants and animals in a fragmented, heavily developed landscape by preferentially planting certain species of plants that may be attractive to fruit bats and having these species bring in seeds from other native species. These findings may provide important insights for future plans to increase the percentage of green space in metropolitan areas in Indonesia and other Southeast Asian countries facing similar challenges due to deforestation and development.

## METHODS

The study was conducted during the rainy season from December 2013 to March 2014 (temperature 26°C and

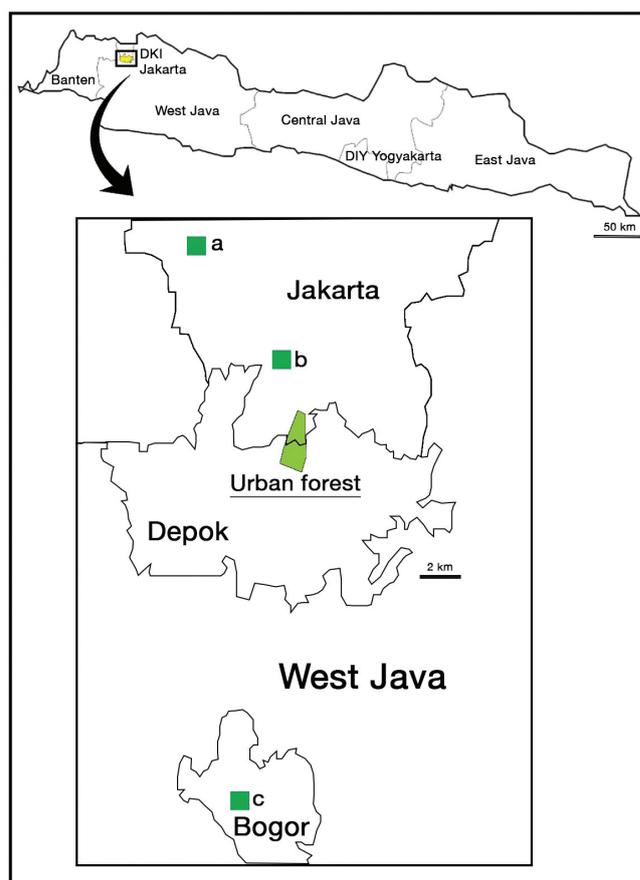


Fig. 1. Location of the Universitas Indonesia urban forest in South Jakarta, which extends into Depok, Indonesia. Fruit bats connect plant population among green areas in Jakarta and West Java. a) Serengseng Forest; b) Ragunan Zoo Forest; c) Bogor Botanical Garden.

humidity 86%) in the UI urban forest. The UI urban forest consists of 130 hectares of contiguous forest, and 190 hectares of buildings mixed with patchy stands of trees. The urban forest is primarily located in Jakarta and extends into Depok (Fig. 1). Initial observations were conducted to find either chiropterophilous plants or plants that were actively recorded as being visited by fruit bats (Table S1). Fruiting and flowering plants were recorded and mapped in the study area. Individual plants were selected randomly within the study area with two consecutive nights of observations for each plant. The bat capture method followed Kunz et al. (2009), with mild modifications to increase the accuracy and precision for capturing Palearctic bats. The two mistnets were set up in front of the canopy of each plant where fruits and flowers were located. The height of the mistnet was approximately 6–9 m. The nets were manned from 1700 hours to 2200 hours and checked every 15 minutes. The bats captured were identified using Suyanto (2001) by measuring the forearm, ear, hind foot, and body length, and then they were weighed. Sex, age (juvenile or adult) and reproductive status for female bats were identified following Racey (2009). Additionally, each individual was examined closely for ejecta or pollen on their fur and mouth to ensure that the fruit bats directly interacted with the flowering and fruiting plants. Relationships between bat and plant species was determined by the abundance of foraging bats in preselected trees. For

Table 1. All plant species found to be associated with fruit bats, along with phenology during the study period of December 2013 to March 2014. Plant identities were verified by examination of plant anatomy by a local botanist. However, bats are likely not foraging on *Acacia mangium*, *Macaranga*, and *Swietenia mahagoni*, but instead using these species as feeding trees after foraging elsewhere.

Family	Species	Phenology
Moraceae	<i>Ficus benjamina</i>	Fruiting
	<i>F. binnendijkii</i>	Flowering and Fruiting
	<i>F. callosa</i>	Fruiting
	<i>F. excelsa</i>	Fruiting
	<i>F. hispida</i>	Fruiting
	<i>F. septica</i>	Fruiting
	<i>F. excelsa</i>	Fruiting
Sapindaceae	<i>Filicium decipiens</i>	Fruiting
	<i>Nephelium lappaceum</i>	Fruiting
	<i>Pometia pinnata</i>	Fruiting
Fabaceae	<i>Acacia mangium</i>	Flowering
	<i>Calliandra</i> sp.	Flowering
Myrtaceae	<i>Syzygium polyanthum</i>	Flowering
	<i>Syzygium</i> sp.	Fruiting
Arecaceae	<i>Roystonea regia</i>	Flowering
Cecropiaceae	<i>Cecropia</i> sp.	Fruiting
Ebenaceae	<i>Diospyros</i> sp.	Fruiting
Euphorbiaceae	<i>Macaranga</i>	Fruiting
Lamiaceae	<i>Gmelina arborea</i>	Fruiting
Meliaceae	<i>Swietenia mahagoni</i>	Fruiting
Muntingiaceae	<i>Muntingia calabura</i>	Fruiting
Musaceae	<i>Musa paradisiaca</i>	Fruiting
Phyllanthaceae	<i>Antidesma</i> sp.	Fruiting
Sapotaceae	<i>Mimusops elengi</i>	Fruiting
Rubiaceae	<i>Morinda citrifolia</i>	Flowering and Fruiting
Tiliaceae	<i>Microcos tomentosa</i>	Fruiting

each plant species, all the fruit bat species that used this particular species were recorded. Then, the abundance of each fruit bat species for one plant species was calculated and expressed as number of individuals per mistnet hour. This information was used to determine specific associations between bat-plant species pairs. They were analysed using Cramer's V in vcd package in R i386 2.15.2 (Zeileis et al., 2007; Meyer et al., 2013). Correlation between the average forearm length and average fruit diameter consumed was tested using Spearman correlation test in R version 2.15.2. The forearm length (mm) of individual bats was a proxy for body size in fruit bats, and fruit diameter (mm) was a proxy for fruit size (Seidler & Plotkin, 2006; Safi et al., 2013).

**RESULTS**

A total of 273 individuals from eight species of bats were captured and identified during 426 mistnet hours. Bats of the genus *Cynopterus* comprised 95% of bats captured. *Cynopterus brachyotis* was the most abundant species, followed by *C. sphinx* (Fig. 2). In comparison, *Rousettus amplexicaudatus*, a cave-roosting bat species (Fajri et al.,

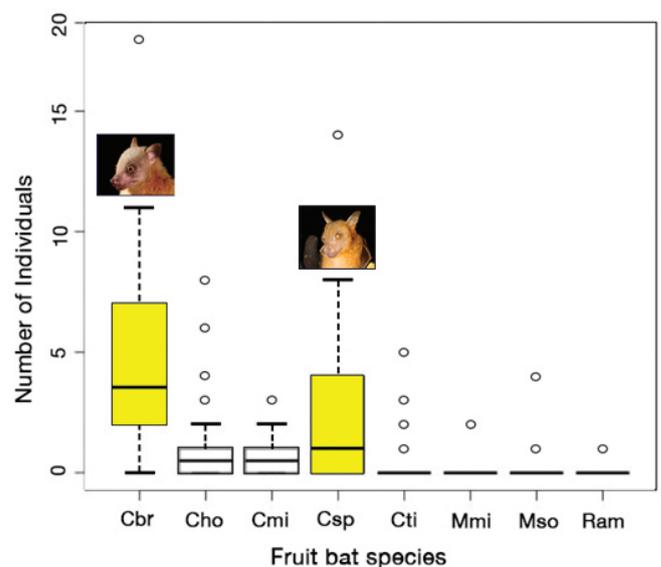


Fig. 2. Total number of fruit bats captured in this study from the UI urban forest. Species are abbreviated as follows: Cbr = *C. brachyotis*; Cho = *C. horsfieldii*; Cmi = *C. minutus*; Csp = *C. sphinx*; Cti = *C. titthaechellus*; Mmi = *M. minimus*; Mso = *M. sobrinus*; Ram = *R. amplexicaudatus*.

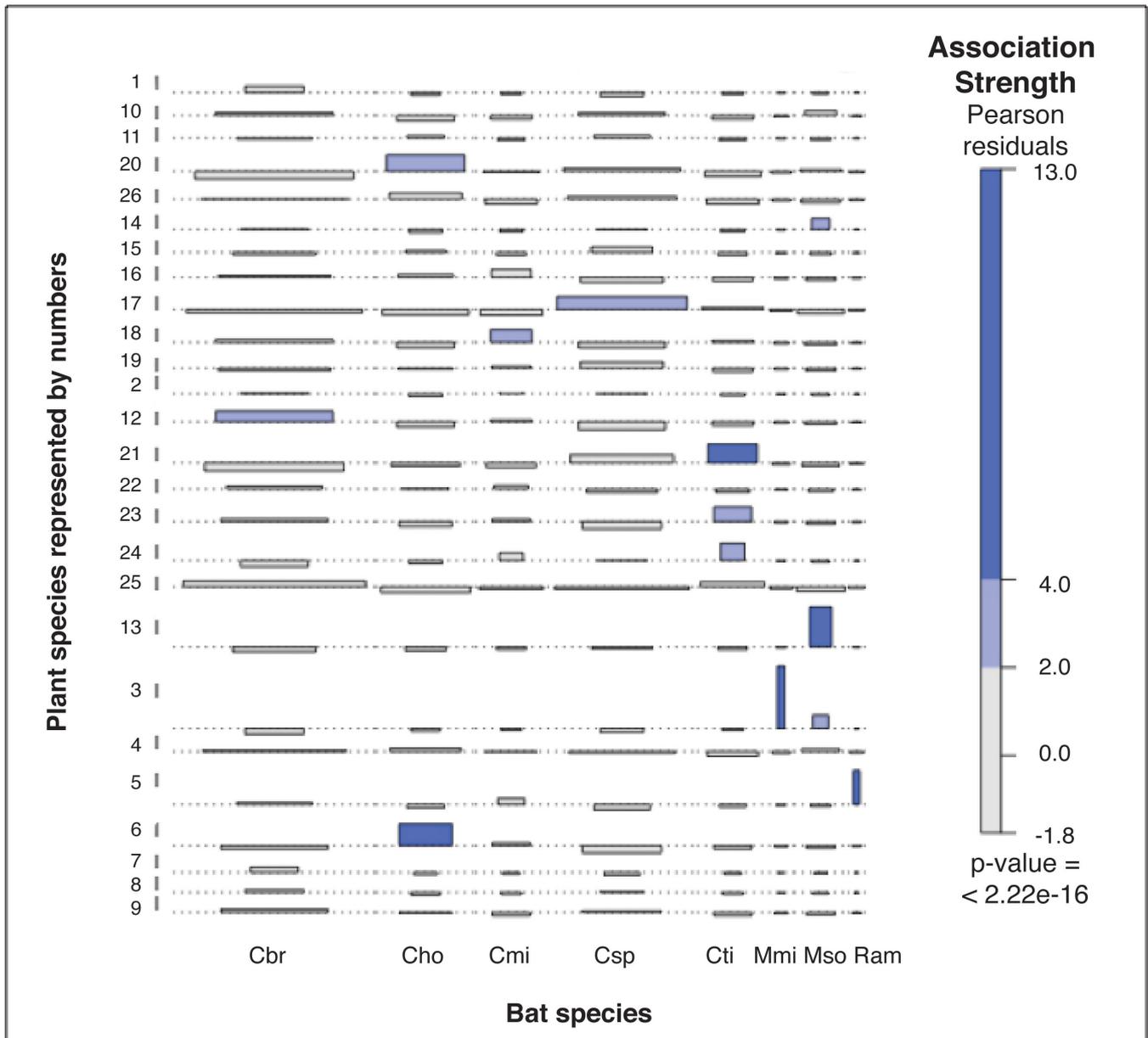


Fig. 3. Association results from *vcd* between bats and plants. Strength of bat-plant associations are indicated by the height and colour of the bars (Zeileis et al. 2007). The thickness of each bar suggested the number of fruit bats used certain plant species. The length of the bar showed the general diet breadth of each fruit bat species. Each of the plant species is represented by a number (1=*Filicium decipiens*, 2=*Nephelium lappaceum*, 3=*Syzygium* sp., 4=*Morinda citrifolia*, 5=*Musa paradisiaca*, 6=*Pometia pinnata*, 7=*Cecropia* sp., 8=*Calliandra* sp., 9=*Muntingia calabura*, 10=*Ficus benjamina*, 11=*Mimusops elengi*, 12=*Ficus septica*, 13=*Roystonea regia*, 14=*Acacia mangium*, 15=*Microcos tomentosa*, 16=*Antidesma* sp., 17=*Gmelina arborea*, 18=*Ficus callosa*, 19=*Syzygium polyanthum*, 20=*Macaranga* sp., 21=*Swietenia mahagoni*, 22=*Ficus hispida*, 23= *F. racemosa*, 24= *F. excelsa*, 25= *F. binnendijkii*, 26=*Dyospiros* sp.). Each of it has a single bar, which depicts the association strength with each of the bat species. The bar graph with darker blue and wider indicates strong association.

2014), exhibited the lowest abundance in our captures, likely due to the lack of caves in surrounding areas. *Macroglossus* species were also captured at low abundances, likely due to fieldwork occurring during the low season for flowering plants. *Macroglossus* species are primarily nectarivores; consequently, species abundance is determined by the availability of flowering plants (Soegiharto et al., 2010). The high number of plant species visited by the six most common fruit bat species in this study suggested that they are generalists. There were 44 plant species from 22 families recorded in the preliminary observation (Table S1). Fruit bats were observed foraging on 26 plant species in total (Table

1). However, bats may not be foraging on *Acacia mangium*, *Macaranga*, and *Swietenia mahagoni*, but instead using these species as feeding trees. Bats often forage in a particular tree then bring and eat the fruits in another tree, which is called a feeding tree. *Cynopterus brachyotis* was found to coexist with congeners, including *C. sphinx*, *C. horsfieldii*, *C. titthaecheilus*, and *C. minutus*. Bat-plant associations varied between species (Fig. 3). Associations among species pairs were significant (Cramer’s V = 0.51,  $p < 0.05$ ). *Cynopterus horsfieldii* was associated with *Pometia pinnata*, while *C. minutus* and *C. titthaecheilus* were associated with *F. callosa* and *F. excelsa* respectively. There was only a weak

correlation between average forearm length and average fruit diameter (Spearman's correlation test,  $r = 0.15$ ,  $df = 175$ ,  $p < 0.05$ ) (Fig. S1). Both small and large fruit bat species mostly consumed fruits with a diameter of less than 70 mm. However, larger fruit bats could feed on larger fruits; for example, *C. horsfieldii* foraged the most on *Pometia pinnata*, which produces large and hard fruits. *Cynopterus sphinx*, the second most abundant bat captured in this study, had a high degree of resource overlap with *C. brachyotis*. However, *C. sphinx* is a larger species (forearm length 64–79 mm) that could eat larger fruits, such as *Gmelina arborea* (diameter of ~25 mm), whereas *C. brachyotis* (forearm length 54.7–66.7 mm) exploited smaller fruits more often, such as *F. septica* (diameter of ~15–20 cm). Fruit bats were directly observed dropping ejecta and seeds, suggesting their role as seed dispersers. For example, *C. brachyotis* dropped seeds in the ejecta of *Felicium decipiens*. *Macroglossus minimus* and *M. sobrinus* are nectarivores and were found only in association with flowering plants, such as *Syzygium polyanthum* and *Roystonea regia*. The pollen of these plant species was found on the fur of nectarivores, suggesting that these bats may provide pollination services.

## DISCUSSION

The associations, though weak, between plant and fruit bat species highlights the importance of bats for maintaining biotic interactions as part of the forest community composition in the isolated UI urban forest. To understand the specific relationships between certain bats and certain fruits, more precise pollination and seed dispersal experiments will be needed. Differential associations between bats with plant species allowed multiple *Cynopterus* species to live and exploit different plant species in the UI urban forest. This association depends on the variation in adaptability of fruit bat species to urbanised areas. Compared to its congeners, *C. brachyotis* exhibits high ecological plasticity, allowing it to occupy a broad niche and is distributed more widely, even in highly disturbed areas (Benda, 2010). This species is able to fly through manmade structures while foraging (Campbell et al., 2004; Fukuda et al., 2009). Kinjo et al. (2006) also found *C. brachyotis* to be the most common species in nearby areas in West Java, which are also undergoing development. It foraged on 24 of the 26 plants observed in this study, suggesting a generalist diet. *Cynopterus brachyotis* is able to exploit both steady state resources (fruits available throughout the year) and big bang resources (fruits available in high abundance only in certain seasons). These resources allow *C. brachyotis* to maintain a high relative abundance throughout the year in habitats that have both, such as an urban forest. Another aspect which determines the plant species that the fruit bat is associated with is body size. The body size of the bat is positively correlated to gape size, which determines the maximum diameter of fruits that can be eaten (Dumont & O'Neal, 2004). The results of this study suggest that fruit bats with larger body size could exploit larger fruits. This is consistent with bat-plant studies in peninsular Southeast Asia, where *C. sphinx* is generally associated with plants that produce larger fruits compared to the plants exploited by *C. brachyotis* (Bumrungsri et al., 2007). Our additional

observations suggested that *C. brachyotis* was active earlier in the evening (1800 hours to 2000 hours) compared to *C. sphinx* (1930 hours to 2100 hours), which allowed both species to exploit some of the same resources, but maintain temporal separation. Differential dominant host plant exploitation between bat species suggested that they co-exist in the same habitats without competitively excluding each other. This result is consistent with findings in other part of Asia where *C. sphinx* has later peak foraging times (Elangovan et al., 2001).

As generalists, fruit bats can disperse seeds from many plant species, which can promote higher plant diversity in depleted ecosystems (Herrera et al., 2008). The genus *Ficus* (figs) was the most commonly consumed group of plants. Figs are early successional plants (Whitten et al., 1996) and often make up a majority of the diet of other pteropodids (Marshall, 1985; Dumont et al., 2004; Muscarella & Fleming, 2007; Lomascolo et al., 2010). Our findings suggested that fruit bats introduced them to the urban forests, as they were not planted in the original set of species by the UI greening program. Most of the figs consumed by bats in this study exhibited chiropterophilous syndrome traits, having relatively larger (>1 cm in diameter) and harder fruits on average, and are visually inconspicuous compared to ornithochorous figs. Some species of figs have bright colours and are relatively small (<1 cm in diameter) in size, suggesting that they may be dispersed by birds. However, as noted earlier, the avifauna in small fragmented areas, particularly in highly developed urban landscapes in Southeast Asia, are often depleted, and makes it more likely that bats play a larger role in seed dispersal. Out of the 50 species of birds previously recorded in UI urban forest (*pers. obs.*), 15 species have been recorded as frugivorous (Pradana et al., 2010). This is in contrast to the total West Javan avian assemblage of approximately 200 bird species, with about 50 being partially or fully frugivorous (MacKinnon & Phillipps, 1993; Eaton et al., 2016). To rule this possibility out, additional observations and experiments will be needed.

The results suggest that fruit bats likely contributed to the plant diversity of the UI urban forest over a relatively short period of time through the ecological services these species provided. Plants from the original greening program, such as *Filicium decipiens* and *Pometia pinnata* were found outside the introduction area, suggesting that seed dispersers presumably expanded the distribution of some plant species as well. In other studies in similar environments in Southeast Asia, fruit bats were shown to be more important seed dispersers than birds for reforesting previously cleared areas (Sritongchuay et al., 2014). Additionally, in Indonesia and other similar habitats in Southeast Asia, heavy declines in forest bird populations have been documented in isolated forest stands (Diamond et al., 1987; Castelletta et al., 2000; Sodhi et al., 2010). Fruit bats can act as long-distance seed dispersers from nearby green areas, as has been shown in other studies with even greater distances (Shilton et al., 1999; Hodgkison et al., 2003; Oleksy et al., 2015). The reduced avifauna and high dispersal capability of bats suggests that fruit bats likely connected plant populations that have been

fragmented by human development, though this conclusion requires more population genetic research on plants in the area to confirm. In this study, the closest green areas from which fruit bats can bring seeds are the Bogor Botanical Garden (25–30 km away), another urban forest in Ragunan Zoo in Jakarta (10 km away) or Serengseng (30 km away) (Fig. 1). The UI urban forest is also far from a stream system, which could potentially bring in seeds. For example, bats were recorded foraging on a non-native species of *Cecropia* was found in the UI urban forest, yet it was only planted in Bogor Botanical Garden. *Cecropia* species exhibit traits commonly associated with chiropterophily, suggesting that bats are the most likely dispersers that expanded the distribution of this species. The role of frugivorous bats has also previously been recognised in urban forest in South Tangerang city, approximately 24 km northwest of Depok (Meidiyanto, 2016). Additionally, the occurrence of *Macroglossus* as long-distance pollen dispersers has been shown to help maintain the genetic continuity of plant populations (Fleming et al., 2009), and this is likely the role they play in fragmented landscapes in West Java. In other parts of Java, bats have been shown to play an important role in maintenance of important urban forests. Multiple *Cynopterus* species and *Macroglossus sobrinus* are known to utilize 28 plant species in city gardens and urban forests in Situ Gintung, Bambu Apus, and Bumi Serpong Damai (Meidiyanto, 2016). The ecosystem services (seed dispersal and possibly pollination) provided by *Pteropus vampyrus* in Bogor Botanical Garden are recognised by the designated green space planner and promotes planting seeds of chiropterophilous plant species for enrichment of the plant community in the Bogor Botanical Garden (Suyitno, 2012). Maintaining urban forests is vital for intensely developed areas beyond Depok and Jakarta. The role that urban forests play has been shown to have an impact in other intensely developed spaces that can benefit human society. Urban forests have been used to reduce the concentration of air pollutants and regulating temperature in large metropolitan areas in China (Weng & Yang, 2004; Luo et al., 2014). Open green spaces have also been shown to mitigate the increased prevalence of stress, anxiety, and depression, particularly those symptomatic of urban environments (Kondo et al., 2015). The UI urban forest is also a critical source of oxygen to inhabitants in the Depok area (Afrizal et al., 2010). Considering the importance of the urban forest as a water reservoir and to prevent flooding, preservation of the urban forest should be prioritised as the severity of floods in the Jakarta area has increased in the past decade (Schanz & Wang, 2015). Among the ways in which city planners can promote the growth of urban forests is to preserve its biodiversity (Alvey, 2006), especially fruit bats, which are shown in this study to be key seed dispersers and potential pollinating agents for the plant community. This study highlights the value of fruit bats as seed dispersers and pollinators in establishing habitat connectivity in fragmented landscapes (de la Pena-Domene et al., 2014; Sritongchuay et al., 2014). On a regional scale, fruit bats are one of the most important seed dispersers for degraded habitat in the tropics (Corlett, 2002). Small, generalist bat species such as *Cynopterus* are some of the only animals that can travel over long distances and thrive in human-dominated

landscapes (Shilton et al., 1999; Kinjo et al., 2006). This allows them to facilitate the introduction of seeds between patches and gaps throughout a widespread area (Corlett, 2002; Gorresen & Willig, 2004; Tang et al., 2007; Sritongchuay et al., 2014). Moreover, many early successional plants, such as figs, depend on bats to disperse their seeds, which in turn promotes forest regeneration (Lomascolo et al., 2010). The benefits of urban forests in metropolitan areas are crucial to coping with environmental problems such as annual flooding and heavy air pollution in Indonesia, and should be considered as part of city planning. As these cities expand, the creation and maintenance of green spaces such as urban forests should be considered of paramount importance to both the health of its human and non-human inhabitants. Our study highlights the importance of fruit bat populations to the maintenance of natural interactions in urban landscapes and forest regeneration in surrounding areas. Urban planning schemes should incorporate planting of chiropterophilous species in greening programs in order to promote foraging by bats. The creation of green spaces also provides natural roosts for these urban bat species. This can reduce the likelihood of urban bats roosting in human structures, decreasing the potential for bat-human pathogen transmission as concerns of bats as natural reservoir hosts to emerging infectious pathogens linger (Calisher et al., 2006). Reducing the likelihood of contact between bats and humans will also reduce the potential for persecution of the bats by humans.

The utility of fruit bats to connect patchy forests may be important to other developing countries in Southeast Asia as well, as many face similar challenges from development as they expand. The fruit bat species from this study are widespread throughout the region, and their importance to reconnecting plant communities may not have been fully recognised due to the limited studies on bat-plant interactions in the Paleotropics. In looking towards a more sustainable urban environment in the future, city planners will need to consider the role of fruit bats in these ecosystems and determine what is a safe way for bats and humans to co-exist in human-dominated landscapes.

#### ACKNOWLEDGMENTS

We are grateful for comments and guidance during the study from Wisnu Wardhana M.Si., Erwin Nurdin M.Si., and Adi Basukriadi M.Sc. We thank the Technical Unit of Security (*Pengamanan Lingkungan Kampus*) at UI, which kindly granted us permission to conduct this study in the urban forest. All research protocols were approved by Universitas Indonesia. Funding was provided by the Nagao Natural Environmental Foundation Programme to Sheherazade and the Fulbright Student Research Fellowship to SMT.

#### LITERATURE CITED

Abedi-Lartey M, Dechmann DKN, Wikelski M, Scharf AK & Fahr J (2016) Long-distance seed dispersal by straw-coloured fruit bats varies by season and landscape. *Global Ecology and Conservation*, 7: 12–24.

- Afrizal EI, Fatimah IS & Sulistyantara B (2010) Study of urban forest oxygen production in University of Indonesia, Depok. *Jurnal Lanskap Indonesia (Journal of Indonesian Landscape)*, 2: 23–29.
- Alvey AA (2006) Promoting and preserving biodiversity in the urban forest. *Urban Forestry and Urban Greening*, 5: 195–201.
- Benda P (2010) On a small collection of bats (Chiroptera) from western Sabah (North Borneo, East Malaysia). *Vespertilio*, 13(14): 45–76.
- Bolund P & Hunhammar S (1999) Ecosystem services in urban areas. *Ecological Economics*, 29: 293–301.
- Bumrungsri S, Leelapaibul W & Racey PA (2007) Resource partitioning in sympatric *Cynopterus* bats in lowland tropical rain forest, Thailand. *Biotropica*, 39: 241–248.
- Calisher CH, Childs JE, Field HE, Holmes KV & Schountz T (2006) Bats: Important reservoir hosts of emerging viruses. *Clinical Microbiology Reviews*, 19: 531–545.
- Campbell P, Schneider CJ, Adnan AM, Zubaid A & Kunz TH (2004) Phylogeny and phylogeography of Old World fruit bats in the *Cynopterus brachyotis* complex. *Molecular Phylogenetics and Evolution*, 33: 764–781.
- Castelletta M, Sodhi NS & Subaraj R (2000) Heavy extinctions of forest avifauna in Singapore: Lessons for biodiversity conservation in Southeast Asia. *Conservation Biology*, 14: 1870–1880.
- Corlett RT (2002) Frugivory and seed dispersal in degraded tropical East Asian landscapes. In: Levey DJ, Silva WR & Galetti M (eds.) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI International, Oxon. Pp. 451–465.
- de la Pena-Domene M, Martinez-Garza C, Palmas-Perez S, Rivas-Alonso E & Howe HF (2014) Roles of birds and bats in early tropical-forest restoration. *PLoS ONE*, 9: e104656.
- Diamond JM, Bishop KD & van Balen S (1987) Bird survival in an isolated Javan woodland: Island or mirror? *Conservation Biology* 1: 132–142.
- Dumont ER & O'Neal R (2004) Food hardness and feeding behaviour in Old World Fruit Bats (Pteropodidae). *Journal of Mammalogy*, 85: 8–14.
- Dumont ER, Weiblen GD & Winkelmann JR (2004) Preferences of fig wasps and fruit bats for figs of functionally dioecious *Ficus pungens*. *Journal of Tropical Ecology*, 20: 233–238.
- Eaton JA, van Balen B, Brickle NW, & Rheindt FE (2016) Birds of the Indonesian Archipelago: Greater Sundas and Wallacea. *Lynx Edicion*, Barcelona, 496 pp.
- Elangovan V, Marimuthu G & Kunz TH (2001) Temporal patterns of resource use by the short-nosed fruit bat, *Cynopterus sphinx* (Megachiroptera: Pteropodidae). *Journal of Mammalogy*, 82: 161–165.
- Fajri SR, Idrus AA & Hadiprayitno G (2014) The richness of bat species Order Chiroptera in the southern caves of Lombok Island, West Nusa Tenggara. *Bioedukasi*, 7: 5–9.
- Fleming TH, Geiselman C & Kress WJ (2009) The evolution of bat pollination: A phylogenetic perspective. *Annals of Botany*, 104: 1017–1043.
- Fleming TH (1979) Do tropical frugivores compete for food? *American Zoologist*, 19: 1157–1172.
- Fukuda D, Tisen OB, Momose K & Sakai S (2009) Bat diversity in the vegetation mosaic around a lowland dipterocarp forest of Borneo. *Raffles Bulletin of Zoology*, 57: 213–221.
- Goltenboth F, Timotius KH, Milan PP & Margraf J (2006) *Ecology of Insular Southeast Asia: The Indonesian Archipelago*. Elsevier, Oxford, 568 pp.
- Gorresen PM & Willig MR (2004) Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *Journal of Mammalogy*, 85: 688–697.
- Herrera MLG, Korine C, Fleming TH & Arad Z (2008) Dietary implications of intrapopulation variation in nitrogen isotope composition of an Old World Fruit Bat. *Journal of Mammalogy*, 89: 1184–1190.
- Hodgkison R, Balding ST, Zubaid A & Kunz TH (2003) Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. *Biotropica*, 35: 491–502.
- Jacomasa FAF & Pizo MA (2010) Birds and bats diverge in the qualitative and quantitative components of seed dispersal of a pioneer tree. *Acta Oecologica*, 36: 493–496.
- Jim CY (2013) Sustainable urban greening strategies for compact cities in developing and developed economies. *Urban Ecosystems*, 16: 741–761.
- Kinjo K, Nakamoto A, Izawa M, Baba M, Doi T & Boeadi (2006) Bat surveys in an agricultural field and an urban area in West Java, Indonesia. *Bull Kitakyushu Museum of Natural History and Human History Series A*, 4: 115–119.
- Kondo MC, South EC & Branas CC (2015) Nature-based strategies for improving urban health and safety. *Journal of Urban Health*, 92: 800–814.
- Krank S, Sarosa W & Wallbaum H (2009) Coping with growth and sustainable development? Urban management indicators in Jakarta. 8<sup>th</sup> International Symposium of the International Urban Planning and Environment Association, Kaiserslautern, Germany. Pp. 1–20.
- Kunz TH, Hodgkison R & Weise CD (2009) Methods of capturing and handling bats. In: Kunz TH & Parsons S (eds.) *Ecological and Behavioural Methods for the Study of Bats*. Johns Hopkins University Press, Baltimore. Pp. 3–35.
- Kusratmoko E, Sukanta D, Tambunan MP & Sobirin (2002) Studi hidrologi hutan kota kampus Universitas Indonesia Depok (Study of hydrology in the urban forest of Universitas Indonesia Depok). *Makara Sains (Science Makara)*, 6: 7–14.
- Lomascolo SB, Levey DJ, Kimball RT, Bolker BM & Alborn HT (2010) Dispersers shape fruit diversity in *Ficus* (Moraceae). *Proceedings of the National Academy of Sciences*, 107: 14668–14672.
- Lubis SH, Arifin HS & Samsuodien I (2013) Analisis cadangan karbon pohon pada lanskap hutan kota di DKI Jakarta (Analysis of tree carbon stocks in urban forest landscape in DKI Jakarta). *Jurnal Penelitian Sosial dan Ekonomi Kehutanan (Journal of Social and Forest Economy Studies)*, 10: 1–20.
- Luo Y, Chen H, Zhu Q, Peng C, Yang G, Yang Y & Zhang Y (2014) Relationship between air pollutants and economic development of the provincial capital cities in China during the past decade. *PLoS ONE*, 9: e104013.
- MacKinnon J & Phillipps K (1993) *A Field Guide to the Birds of Borneo, Sumatra, Java, and Bali: The Greater Sunda Islands*. Oxford University Press, Oxford, UK, 692 pp.
- Marshall AG (1985) Old World phytophagous bats (Megachiroptera) and their food plants: A survey. *Zoological Journal of the Linnean Society*, 83: 351–369.
- Meidiyanto (2016) Struktur komunitas dan karakteristik habitat pencarian pakan kelelawar (Megachiroptera) di tiga ruang terbuka hijau kotaTangerang Selatan. (Community structure and characteristic of bat foraging habitat in three types of green spaces in South Tangerang city). Unpublished MSc Thesis, Universitas Islam Negeri Syarif Hidayatullah, Jakarta, Indonesia.
- Meyer D, Zeileis A, Hornik K, Gerber F & Friendly M (2013) Package 'vcd'. <http://cran.r-project.org/web/packages/vcd/vcd.pdf>. (Accessed 7 July 2014).
- Muis S, Guneralp B, Jongman B, Aerts JCJH & Ward PJ (2015) Flood risk and adaptation strategies under climate change and urban expansion: A probabilistic analysis using global data. *Science of The Total Environment*, 538: 445–457.
- Muscarella R & Fleming TH (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews*, 82: 573–590.
- Nowak DJ, Stein SM, Randler PB, Greenfield EJ, Comas SJ, Carr MA, Alig RJ (2010) Sustaining America's urban forests: A

- Forests on the Edge report. General Technical Report NRS-62. Newton Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, 28 pp.
- Nurhayati (2009) Struktur komunitas vegetasi dan pola stratifikasi tanaman di ruang terbuka hijau Kampus Universitas Indonesia Depok (Community structure of vegetation and plant stratification pattern in green areas of Campus Universitas Indonesia Depok). Unpublished MSc Thesis. Universitas Indonesia, Depok, West Java, Indonesia.
- Oleksy R, Racey PA & Jones G (2015) High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. *Global Ecology and Conservation*, 3: 678–692.
- Pradana DH, Mardiasuti D, Yasman (2010) An assessment of *Ficus benjamina* and *Acacia mangium* as feeding and nesting tree for birds. Case study: University of Indonesia Depok Campus. Seminar Ornitologi Indonesia & Revitalisasi Perhimpunan Ornitolog Indonesia (Indonesian Ornithology & Revitalization of Indonesian Ornithologist Association Seminar), Bogor, Indonesia, 5 pp.
- Racey PA (2009) Reproductive assessment in bats. In: Kunz TH & Parsons S (eds.) *Ecological and Behavioural Methods for the Study of Bats*. Johns Hopkins University Press, Baltimore. Pp. 249–264.
- Raciti SM, Hutyrá LR & Newell JD (2014) Mapping carbon storage in urban trees with multi-source remote sensing data: Relationships between biomass, land use, and demographics in Boston neighbourhoods. *Science of the Total Environment*, 500–501: 72–83.
- Ramdani F (2013) Extraction of urban vegetation in highly dense urban environment with application to measure inhabitants' satisfaction of urban green space. *Journal of Geographic Information System*, 5: 117–122.
- Safi K, Meiri S & Jones KE (2013) Evolution of body size in bats. In: Smith FA & Lyons SK (eds.) *Animal Body Size: Linking Pattern and Process Across Space, Time, and Taxonomic Group*. University of Chicago Press, Chicago, USA. Pp. 95–115.
- Santoso M, Lestina DD & Hopke PK (2013) Atmospheric black carbon in PM<sub>2.5</sub> in Indonesian cities. *Journal of the Air and Waste Management Association*, 63: 1022–1025.
- Sarmiento R, Alves-Costa CP, Ayub A & Mello MAR (2014) Partitioning of seed dispersal services between birds and bats in a fragment of the Brazilian Atlantic Forest. *Zoologia*, 31: 245–255.
- Schanz K-U & Wang S (2015) Insuring flood risk in Asia's high-growth markets: A Geneva association research report. Geneva Association, Zurich, 48 pp.
- Seidler TG & Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, 4: 2132–2137.
- Shilton LA, Altringham JD, Compton SG & Whittaker RJ (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London B*, 266: 219–223.
- Sodhi NS, Wilcove DS, Lee TM, Sekercioglu CH, Subaraj R, Bernard H, Yong DL, Lim SLH, Prawiradilaga DM & Brook BW (2010) Deforestation and avian extinction on tropical landbridge islands. *Conservation Biology*, 24: 1290–1298.
- Soegiharto S, Kartono AP & Maryanto I (2010) The grouping of fruit bats based on pollen type characterized as food resources in Bogor Botanical Garden, Indonesia. *Jurnal Biologi Indonesia (Journal of Indonesian Biology)*, 6: 225–235.
- Sritongchuay T, Gale GA, Stewart A, Kerdkaeuw T & Bumrungsri S (2014) Seed rain in abandoned clearings in a lowland evergreen rain forest in Southern Thailand. *Tropical Conservation Science*, 7: 572–585.
- Suyanto A (2001) Kelelawar di Indonesia. (Bats of Indonesia). Puslitbang Biologi-LIPI, Cibinong, Indonesia, 126 pp.
- Suyitno A (2012) Perencanaan ruang terbuka hijau pendukung pelestarian satwa kalong (*Pteropus vampyrus*) di kota Bogor. (Planning for green space that supports the flying fox conservation (*Pteropus vampyrus* in Bogor city). Unpublished PhD Thesis, Bogor Agricultural Institute, Bogor, Indonesia.
- Tan KH, Zubaid A & Kunz TH (2000) Fruit dispersal by the lesser dog-faced fruit bat, *Cynopterus brachyotis* (Muller) (Chiroptera, Pteropodidae). *Malayan Nature Journal*, 54: 57–62.
- Tang ZH, Mukherjee A, Sheng L-X, Cao M, Liang B, Corlett RT & Zhang S-Y (2007) Effect of ingestion by two frugivorous bat species on the seed germination of *Ficus racemosa* and *F. hispida* (Moraceae). *Journal of Tropical Ecology*, 23: 125–127.
- Toni A (2009) Struktur komunitas vegetasi dan pola stratifikasi tumbuhan di Hutan Kota Universitas Indonesia Depok. (Community structure of vegetation and plant stratification pattern in urban forest Universitas Indonesia Depok). Unpublished MSc Thesis, Universitas Indonesia.
- Weng Q & Yang S (2004) Managing the adverse thermal effects of urban development in a densely populated Chinese city. *Journal of Environmental Management*, 70: 145–156.
- Whitten T, Soeriaatmadja RE & Afiff SA (1996) *The Ecology of Java and Bali*. Periplus Editions, Singapore, 969 pp.
- Willmer P (2011) *Pollination and Floral Ecology*. Princeton University Press, New Jersey, 778 pp.
- Zain AFM, Permatasari PA, Ainy CN, Destriana N, Mulyati DF & Edi S (2015) The detection of urban open space at Jakarta, Bogor, Depok, and Tangerang–Indonesia by using remote sensing technique for urban ecology analysis. *Procedia Environmental Sciences*, 24: 87–94.
- Zeileis A, Meyer D & Hornik K (2007) Residual-based shadings for visualizing (conditional) independence. *Journal of Computational and Graphical Statistics*, 16: 507–525.

SUPPLEMENTARY INFORMATION

Table S1. All plant species observed in preliminary survey.

Family	Species	Family	Species	
Anacardiaceae	<i>Mangifera indica</i>	Lecythidaceae	<i>Barringtonia asiatica</i>	
Apocynaceae	<i>Cerbera odollam</i>	Malvaceae	<i>Ceiba pentandra</i>	
Arecaceae	<i>Cocos nucifera</i>	Moraceae	<i>Artocarpus</i> sp.	
	<i>Livistona rotundifolia</i>		<i>Ficus fistulosa</i>	
	<i>Livistona chinensis</i>		<i>Ficus roxburgii</i>	
	<i>Ptycosperma macarthurii</i>		<i>Ficus benjamina</i>	
<i>Roystonea regia</i>	<i>Ficu excelsa</i>			
Bombacaceae	<i>Durio zibethinus</i>		<i>Ficus grossularioides</i>	
Calophyllaceae	<i>Calophyllum inophyllum</i>		<i>Artocarpus communis</i>	
			<i>Artocarpus heterophylla</i>	
Caricaceae	<i>Carica papaya</i>		<i>Ficus septica</i>	
Cecropiaceae	<i>Cecropia</i> sp.		<i>Ficus hirta</i>	
		<i>Ficus callosa</i>		
Combretaceae	<i>Terminalia catappa</i>	Musaceae	<i>Musa paradisiaca</i>	
Elaeocarpaceae	<i>Muntingia calabura</i>	Myrtaceae	<i>Psidium guajava</i>	
			<i>Syzygium cumini</i>	
Euphorbiaceae	<i>Macaranga</i> sp.		<i>Syzygium aqueum</i>	
			<i>Syzygium polyanthum</i>	
Fabaceae	<i>Acacia mangium</i>	Pinaceae	<i>Pinus</i> sp.	
	<i>Pterocarpus indicus</i>		Rubiaceae	<i>Morinda citrifolia</i>
	<i>Calliandra</i> sp.	Sapidanceae		<i>Nephelium lappaceum</i>
	<i>Parkia speciosa</i>			Sapotaceae
	<i>Acacia auriculiformis</i>	Verbenaceae	<i>Tectona grandis</i>	
<i>Delonix regia</i>				
Heliconiaceae	<i>Heliconia</i> sp.			

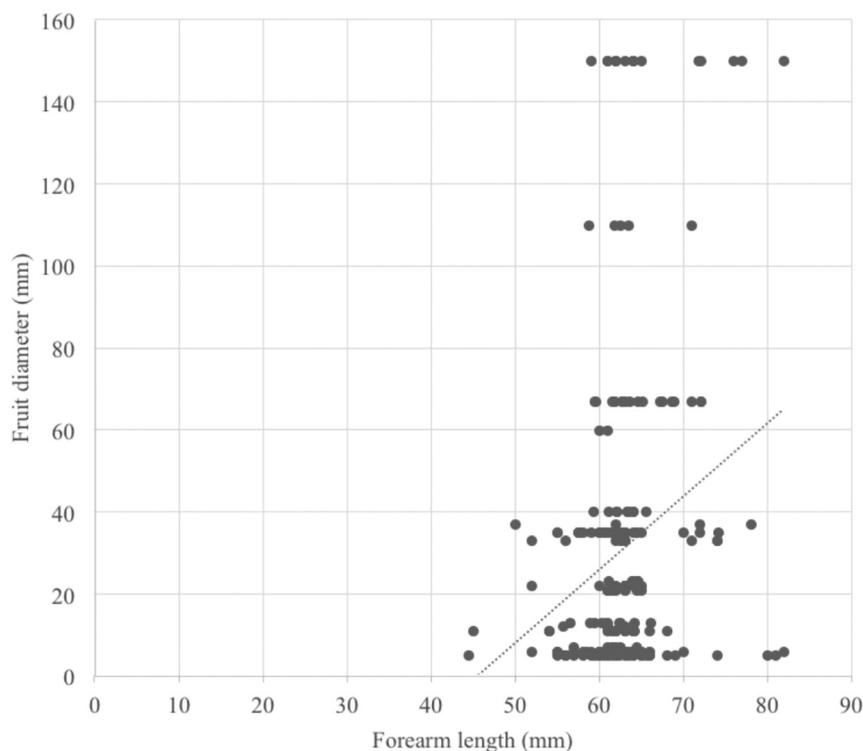


Fig. S1. Weak correlation between forearm length of fruit bats and the diameter of fruits consumed (Spearman’s correlation test,  $r = 0.15$ ,  $df = 175$ ,  $p < 0.05$ ).