Received: 28 November 2018 | Revised: 6 September 2019 | Accepted: 10 September 2019

DOI: 10.1111/btp.12712

WILEY biotropica ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

PAPER

Contributions of bats to the local economy through durian pollination in Sulawesi, Indonesia

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Abstract

Durian is economically important for local livelihoods in Indonesia. Our study investigated the identity of pollinators of semi-wild durian and subsequently estimated the economic contribution of these pollination services. We conducted pollination exclusion experiments and deployed camera traps at durian trees from October 2017 to January 2018 in an area where the local economy depends on durian production in West Sulawesi, Indonesia. Durian flowers in the experiment that were accessible to bats had significantly higher fruit set compared with flowers that were completely closed to animal visitors or those that could only be visited by insects, suggesting that bats were the primary durian pollinator. The small, highly nectarivorous cave nectar bat (*Eonycteris spelaea*) visited more inflorescences (n = 25) and had visits of much longer duration ($\bar{X}$ = 116.87 sec/visit) than the two species of flying foxes: *Pteropus alecto* (n = 7 inflorescences visited, $\bar{X}$ = 11.07 sec/visit) and *Acerodon celebensis* (n = 6 inflorescences visited, $\bar{X}$ = 11.60 sec/visit). Visits by large and small bats were influential in differentiating successful durian fruit production from unsuccessful. Using a bioeconomic approach, we conservatively estimate that bat pollination services are valued at ~$ 117/ha/fruiting season. By demonstrating an ecological link between bats and the local economy, this research provides an urgent message for Southeast Asian governments regarding the need to promote bat conservation in order to increase the production of durian grown under semi-wild conditions.

Abstract in Indonesia is available with online material.

KEYWORDS

Asia Tenggara, *bioeconomic*, jasa ekosistem, jumlah buah, kalong, Pteropodidae

1 | INTRODUCTION

Durian is one of the most economically important fruits in Southeast Asia, with an export value of up to US$254.85 million in 2013 (Indarti, 2014). Indonesia is one of the primary producers of durian: 859,118 tons were produced in Indonesia during 2014, and it commanded a higher unit price than any other fruit commodity in the country (Durian Harvests 2018; Indarti, 2014; Rafani, 2013). Durian constitutes a significant portion of Indonesia's gross domestic product and was named by the Indonesian Ministry of Agriculture as one of the five national fruit priorities, indicating its productivity and sale are national interests (Rafani, 2013). Despite the fruit's popularity, productivity of this cash crop is much lower in Indonesia than that of other fruits, and production is relatively inconsistent here compared with Thailand and Malaysia (Durian Harvests 2018; Rafani, 2013). Improvements to durian production would help Indonesia meet domestic demand and eventually grow a surplus to export to high demand consumers such as China (Indonesia Investments 2016).

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*Associate Editor: Emilio Bruna; Handling Editor: Isaac Marney

Durian is incredibly diverse, with 30 species and 76 varieties in Indonesia alone (Santoso, 2012). Durian flowers are generally self-incompatible and require animal vectors for pollination (Bumrungsri, Sripaoraya, Chongsiri, Sridith & Racey, 2009; Lim & Luders, 1998; Yumoto, 2000). To date, durian pollination studies have been limited to peninsular Southeast Asia (Aziz, Clements, McConkey, et al., 2017; Bumrungsri et al., 2009), where durian is typically grown in large plantation systems. In contrast, although plantations of some durian cultivars exist in Indonesia, most semi-wild durian sold on the market there rely on small-scale farmers who grow the fruits in agroforestry systems without direct management and intervention by local farmers (Rafani, 2013). Furthermore, the dissimilarities in wildlife species assemblages in insular Southeast Asia compared with peninsular Southeast Asia suggest that pollination systems may be quite different between the two regions.

It has been suggested that semi-wild durian may play a significant economic role in domestic and local markets (Djajanti, 2006; Kunz, de Torrez, Bauer, Lobova & Fleming, 2011). However, to the best of our knowledge, no research has yet investigated the economic contribution of specific pollinators to the semi-wild durian trade despite the known importance of pollinators to fruit set. The lack of understanding of how semi-wild durian is pollinated limits the ability of fruit producers to scale up production to increase the economic impact of durian as a cash crop.

Some durian species possess the classically defined floral traits of a plant with chiropterophilous pollinator syndrome, suggesting that bats are their primary pollinators. These floral traits include white or dull coloration, strong fragrance, and nocturnal blooming (Troll, 1975; Tschapka & Dressler, 2002). Pteropodid bats, such as *Eonycteris spelaea* (common nectar bat), *Macroglossus minimus* (lesser long-tongued fruit bat), and *Pteropus* spp., are known to be durian visitors in other parts of Southeast Asia (Aziz, Clements, McConkey, et al., 2017; Fujita & Tuttle, 1991; Gould, 1977, 1978; Marshall, 1985; Start, 1974), but the assemblage of durian visitors and its primary pollinators differ among areas and cultivars. In Malaysian Borneo, *Durio grandiflorus* and *D. oblongus* are primarily pollinated by spiderhunter birds, while *D. kutejensis* is pollinated by bees, birds, and bats (Yumoto, 2000). *Durio zibethinus* in southern Thailand relies on *Eonycteris spelaea* as their primary pollinator (Bumrungsri et al., 2009, 2013; Stewart & Dudash, 2017). In Indonesia, the primary pollinators of durian are unknown.

Additional investigation of pollination systems will be a necessary component of efforts to improve crop production rates in major semi-wild durian producing areas throughout Southeast Asia. Sulawesi is a suitable place for investigation because Sulawesi produces multiple cultivars of semi-wild durian that are of interest to the agricultural sector, and because a unique assemblage of volant wildlife occurs here relative to Peninsular Southeast Asia where durian pollination has been investigated previously. Our study aims to understand the pollination of semi-wild durian in Sulawesi, Indonesia, where durian is an essential local commodity. Thereafter, we estimate the economic significance of the primary pollinators to the local, and potentially regional, economy.

2 | METHODS

2.1 | Study site

This study was conducted in Batetangnga Village, Binuang subdistrict in Polewali Mandar Regency, West Sulawesi (Figure S1), during the flowering and fruiting season of semi-wild durian (October to November 2017 and November 2017 to January 2018, respectively). Batetangnga is the most geographically expansive village in the subdistrict (44.80 km^2), comprising 45 percent of the total area (Badan Pusat Statistik Kabupaten Polewali Mandar 2017). It extends from the coastal lowlands into inland and montane areas dominated by secondary forest mixed with various agricultural plantations. In most of Sulawesi, durian is not grown in monoculture plantations as is typical in peninsular Southeast Asia, but is instead sparsely distributed in secondary forests in managed mixed agroforestry systems along with cacao (*Theobroma cacao*), rambutan (*Nephelium lappaceum*), langsat (*Lansium parasiticum*), and mango (*Mangifera indica*). The average annual rainfall in the area is 1954 mm, with peaks usually occurring in May, June, and December. All investigative protocols in this study were approved by the University of Florida under IACUC protocol No. 201709800.

2.2 | Floral characteristic of durian

The durian species at our study site was *Durio zibethinus*. During the flowering season, each durian tree has hundreds to thousands of inflorescences (a cluster of flowers on a stem). Durian flowers are cauliflorous, meaning tens of flowers are stacked per inflorescence and grow directly on branches.

Understanding the pollination biology of durian requires an understanding of durian's floral characteristics. We observed 10 durian flowers from five inflorescences in three durian trees located in different orchards. Due to the tall stature of durian trees (15–40 m), we selected relatively shorter trees with accessible flowers. We carried out hourly observations and tests throughout the flowering period to determine five physiological attributes of the local durian species (Bumrungsri et al., 2009; Dobat & Peikert-Holle, 1985; Honsho, Yonemori, Somsri, Subhadrabandhu & Sugiura, 2004; Honsho, Yonemori, Sugiura, Somsri & Subhadrabandhu, 2004; Lim & Luders, 1998; Yumoto, 2000). We assessed (a) the time each flower opened; (b) the time each anther dehisced, determined by noting the presence of a slit on the anther as a sign that pollen grains had been released; (c) the time stigmas became receptive, determined by placing a drop of hydrogen peroxide on each stigma and noting the presence of bubbles as an indication that the stigma was receptive to pollen; (d) nectar production, using 100 μl micro-capillary tubes to draw and measure nectar; and (e) sucrose concentration of nectar using a sucrose refractometer (Extech RF10 0 to 32% Brix Refractometer). All observations and tests were conducted starting at the time durian flowers bloomed in the late evening until their corollas dropped from pedicels the next morning.

2.3 | Pollination biology of durian

We chose seven 18–20 m tall durian trees for a pollination exclusion experiment, using two criteria to select focal trees. First, a sufficient number of inflorescences per tree were required to accommodate all the treatments (described below). Second, only trees that could be climbed without safety concerns were considered (e.g., it was impractical to climb durian trees that were slippery, had extremely large trunk diameters, or had ant nests). Each durian tree in this study belonged to a different orchard but grew in a similar environment (e.g., in forests with medium canopy cover and high intensity of sunlight and rainfall). Individual trees were located 0.5 to 2.0 km apart. All trees were approximately the same height, and therefore likely of similar age.

For every target tree, we selected 3–6 durian inflorescences that had ~30 flowers each. We assigned each inflorescence to one of the three treatments: closed, insect, and open pollination (Figure S2). We attempted to install each set of three treatments (closed, insect, and open) at one height before installing the next set of three treatments at a different height within the 15–20 m height range. For example, we established one set of three treatments at the first 3 inflorescences we found meeting the above criteria at 16 m height, then another set of three treatments at 18 m height.

For the closed pollination treatment, we bagged each inflorescence before the flower bloomed with a bag made of a mesh fabric that allowed light, rain, and gas exchange between flowers and the ambient environment, but prohibited any animals from accessing the flowers. For the insect pollination treatment, inflorescences were enclosed with specialized nets made of the same garden fabric but manually perforated to allow only insects to access flowers (perforation size = 1.5 cm). For the open pollination treatment, we did not prevent access to the inflorescences by any potential visitors. We labeled all inflorescences to indicate replicate number, treatment, and experiment date. We had 36, 30, and 25 replicates (inflorescences) for open, insect, and closed treatments, respectively. Because durian flowers may have late acting self-incompatibility (Bumrungsri et al., 2009; Honsho, Yonemori, Somsri, et al., 2004) and to avoid overestimating pollination services by relying only on initial fruit set (Bos et al., 2007), we monitored and counted durian fruit set for all replicates on days 10, 20, 30, and 60 following the establishment of each treatment (Figure S3).

We used Kruskal–Wallis and Dunn's tests (Dinno, 2017) to determine whether each treatment produced significantly different amounts of durian fruit. We considered fruit set on days 20 and 60 to be indicative of pollination and reproduction success, respectively (Aziz, Clements, McConkey, et al., 2017). We visualized data using ggplot2 from the R package “ggplot2” (Wickham & Chang, 2016).

2.4 | Durian pollinators

We used camera traps to determine which animals visited durian flowers (Figure S2). We deployed a camera trap (Bushnell Trophy Cam HD Essential E2 12 MP Trail Camera) on a branch in front of each durian inflorescence that received the open pollination treatment (*n* = 36). The distance between inflorescences and camera traps ranged from 0.30 to 1.5 m. Camera traps were active during the entire flowering period for each inflorescence, recording day and night visitation rates of animals that fed on durian floral products (nectar or the whole flowers). We programmed the camera traps to capture videos with a maximum length of 15 s, with 5 min intervals between consecutive recordings. We recorded the number of interactions between each animal species and each inflorescence as well as the duration of each visit as a proxy for the contribution of each pollinator species to durian production. The videos also documented the foraging behavior of each animal visitor, which helped us determine which species contacted stigma and anthers (and presumably benefitted durian by serving as primary pollinators), which visited flowers but did not contact stigma and anthers, and which ate the whole flowers (and were thus detrimental to durian).

We used Generalized Linear Mixed-effect Models (GLMMs) to determine whether only the presence of certain animal species at inflorescences, the number of interactions between certain species and inflorescences, and/or the duration of visits of certain species to inflorescences was influential in affecting the success or failure of durian fruit production. Only those species that visited >3 inflorescences were included in these analyses. We checked for multicollinearity among variables using function “ggpairs” (package “GGally”) to extract the correlation coefficient and function “vifcor” (package “usdm”) to calculate the VIF (Variance Inflation Factor) (Naimi, 2017; Schloerke et al., 2018). We dropped variables with high correlation coefficients ($|r| > .5$)] and VIF factor > 10. Then, we used function “glmer” in R package lme 4 to test GLMMs (Bates et al., 2019), with durian tree as a random effect and a binomial distribution for our response variable that was expressed as success or failure of durian fruit production. We determined which models had the most support from the data using Multi-Model Inference with function “model.sel” in R package MuMIn (Barton, 2019).

We also assessed the temporal aspect of durian foraging of each bat species and determined whether there was temporal resource partitioning among bat species. We converted time of visitation to radians and used non-parametric kernel density estimates to display each species' temporal foraging activity as a continuous distribution over a 24-hr cycle (Frey, Fisher, Burton & Volpe, 2017). We generated the estimates and density plots using package “overlap” in R with Δ_1 estimator (Dhat1) (Meredith & Ridout, 2017a). We then used a descriptive measure of the degree of similarity to evaluate overlap between each pair of species, with values ranging from 0 (no overlap) to 1 (complete overlap) (Frey et al., 2017; Ridout & Linkie, 2009). To determine confidence intervals (CI) of the overlap, we used smoothed bootstrap with 10,000 resamples then selected basic0 output from bootCI as our CI (Meredith & Ridout, 2017b). All statistical analyses were conducted using R 1.0.136 (https://cran.r-project.org).

2.5 | Economic value of bat pollination services

We used a bioeconomic approach to estimate bat pollination services to durian, using a formula originally developed to calculate

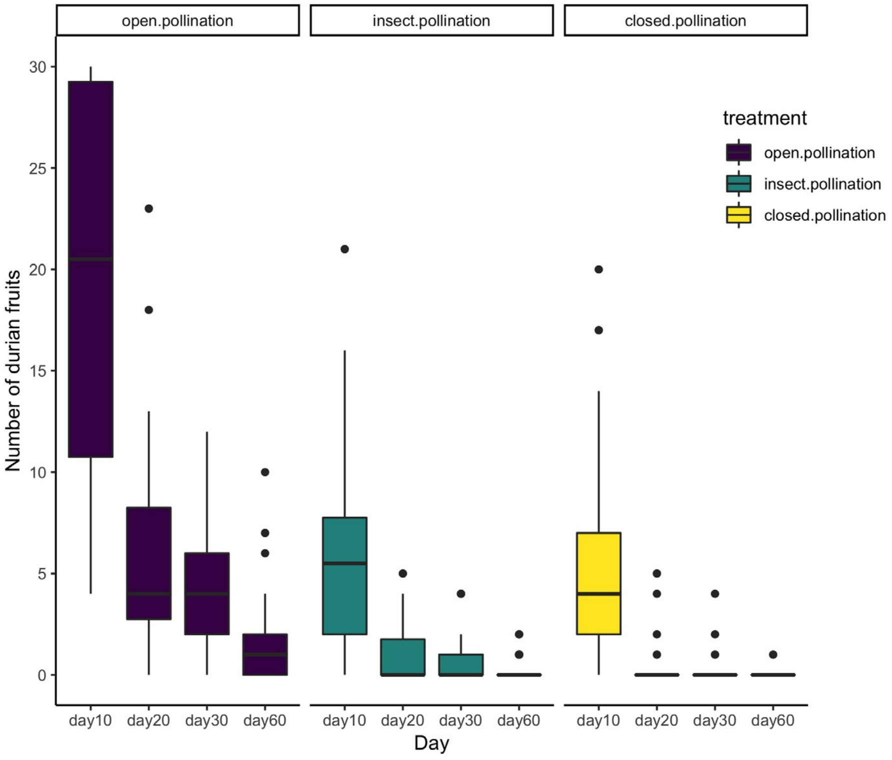

FIGURE 1 The number of durian fruit set under three pollination exclusion treatments. Box and whisker plots show the minimum, first quartile, mean, third quartile, and maximum values for each treatment

insect pollination services (Gallai, Salles, Settele & Vaissière, 2009). We modified the formula "Insect Pollination Economic Value" to "Pollination Economic Value (PEV)":

$$PEV = \sum_{i=1}^{I} \sum_{x=1}^{X} (P_{ix} \times Q_{ix} \times D_i)$$

where: i = crop; x = region; P_{ix} = price of crop i produced in x; Q_{ix} = quantity produced in region x; D_i = dependence ratio of the crop i on bat pollination.

Dependence ratio (0–1), D_i, expresses the degree of durian dependency on pollination. It is calculated by subtracting fruit set of bagged flowers (closed pollination) from fruit set of unbagged flowers (open pollination), divided by the fruit set of unbagged flowers (Kasina, Mburu, Kraemer & Holm-Mueller, 2009). In our case, we calculated durian dependence ratios in a similar manner, but we used fruit set of bagged flowers subjected to insect pollination for closed pollination treatments since insects may also pollinate durian flowers.

3 | RESULTS

3.1 | Floral characteristic of durian

Durian flowers had distinct attributes that conform to the chiropterophilous syndrome, which included dull coloration of the corolla, heavy fragrance, and night-blooming behaviors. Each flower was open and receptive for only a single night. The flowers started to open at 1530 hr and fully opened around 1800 hr. Pollen was released (anther dehiscence) after 1830 hr, about the same time when stigmas became receptive. Stigmas remained receptive until the corollas dropped early in the morning before sunrise. The average volume of nectar produced by each durian flower was 167.4 µl ± 15.11 (SE) (range: 79–240 µl, *n* = 10) (Figure S4). Nectar contained approximately 13.53% ± 0.48 (SE) (range: 9.95–16%, *n* = 10) of sucrose.

3.2 | Pollination biology of durian

Overall, durian subjected to the open pollination treatments had significantly higher fruit set compared to durian with insect and closed pollination treatments both on day 20, which represents pollination success (X^2 = 38.39, $p < .0001$), and day 60, which represents reproductive success (X^2 = 32.52, $p < .0001$) (Figure 1). The average number of fruits set in open, insect, and closed pollination treatments on day 60 was 1.69 ± 0.37 (SE) (range: 0–10 fruits, *n* = 36), 0.27 ± 0.11 (SE) (range: 0–2 fruits, *n* = 30), and 0.04 ± 0.04 (SE) (range: 0–1 fruit, *n* = 25), respectively.

3.3 | Durian pollinators

Durian visitors consisted of four vertebrate species (three species of bat and one arboreal marsupial) and two invertebrate species (one species of bee and moth). The three bat species (the small *Eonycteris spelaea* and the larger *Pteropus alecto* (black flying fox) and the *Acerodon celebensis* (Sulawesi flying fox)) were the primary visitors to durian flowers in the open pollination treatment (2, Table 1). Bats were responsible for visits to 38 of the 43 inflorescences where animal visits were recorded. We could easily differentiate these three bat species in the camera trap videos, as *E. spelaea* was distinctly smaller

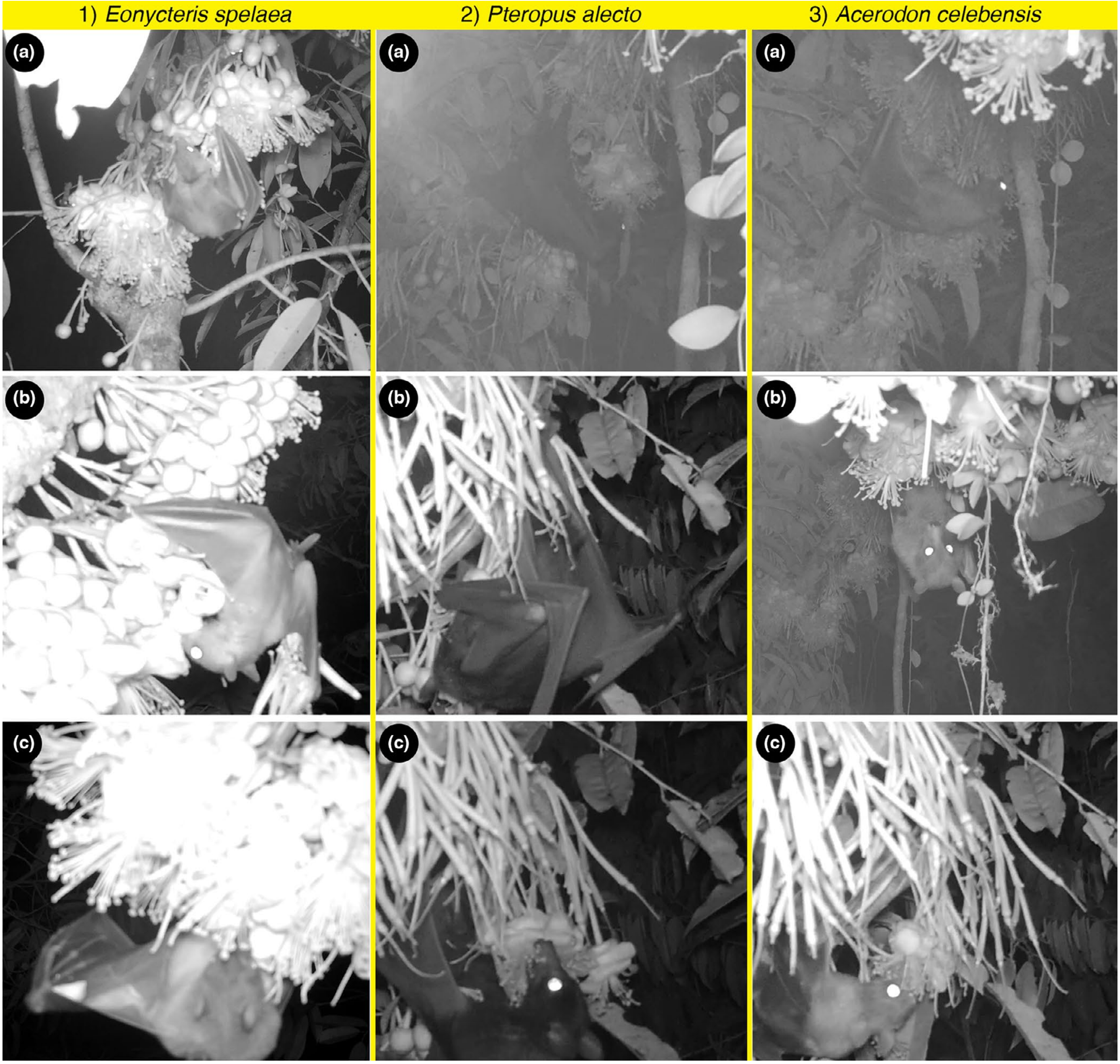

FIGURE 2 Three bat species fed on durian nectar. (1) *Eonycteris spealea* hung on durian flowers while feeding (a), sometimes accidentally pulled off flower reproductive organs (stigma and anther) (b), and convincingly served as pollinator as bat head touched lower reproductive organs while feeding on nectar (c). (2) *Pteropus alecto* hung on branches while feeding on nectar (a), grabbed a flower but did not pull it off (b), and convincingly pollinated, as its head touched flower reproductive organs (c). (3) *Acerodon celebensis* hung on branches while feeding on nectar (a), bat licked its fur (b), and convincingly served as pollinator as its head touched flower reproductive organs (c)

than the others and had brightest (grayish) fur, whereas *A. celebensis* appeared smaller and brighter than *P. alecto* due to differences in fur reflectance. All three species were observed drinking nectar from durian floral tubes without destroying the flowers. Although *A. celebensis* and *P. alecto* have large bodies relative to durian flowers, they hung from tree branches and bent their head toward the flowers when drinking and therefore did not damage the inflorescences.

Eonycteris spelaea (the smallest of the three bat species) was the most frequent visitor to the durian flowers and had visits of longer duration than *P. alecto* and *A. celebensis* (large bats/flying foxes) (Table 1). After dropping the metric describing the number of interactions of large bats with flowers due to multicollinearity, regression analyses showed that the model that received the most support given the data (model with the lowest AICc) indicated the presence of large bats was most influential to durian success (R^2 = 0.244 and marginal R^2 = 0.029) (Table 2). However, the weight of evidence in support of each of the top five models was similar, indicating that all five variables investigated explained the success of durian production (presence of large and small bats, duration of visits of large and small bats, and number of visits of small bats), and that this analysis

TABLE 1 Identity of animals that visited durian flowers in Sulawesi, the number of visits by each, the duration of their visits, and the number of inflorescences visited

Family	Species	Common names	Number of visits	Total duration of all visits (sec)	Number of inflorescences visited
Pteropodidae	*Eonycteris spelaea*	Common nectar bat	82	2474	25
	Pteropus alecto	Black flying fox	15	180	7
	Acerodon celebensis	Sulawesi flying fox	10	110	6
Phalangeridae	*Strigocuscus celebensis*	Small Sulawesi cuscus	4	2335	2
Apidae	*Apis dorsata*	Giant honey bee	5	30	2
Erebidae	Unknown	Moth	1	15	1

TABLE 2 Results of Generalized Linear Mixed-Effect Models (GLMMs) to determine which factors contribute most to the success of durian fruit production at 60 days

Model	k	loglikelihood	AICc	ΔAICc	weight
d ~ pres_lb + (1|tree)	3	−21.176	49.1	0.00	0.235
d ~ pres_sb + (1|tree)	3	−21.345	49.4	0.34	0.198
d ~ dur_lb + (1|tree)	3	−21.455	49.7	0.56	0.178
d ~ ni_sb + dur_sb + (1|tree)	4	−20.226	49.7	0.64	0.171
d ~ dur_sb + dur_lb + (1|tree)	4	−20.398	50.1	0.98	0.144
d ~ pres_sb + pres_lb + (1|tree)	4	−21.048	51.4	2.29	0.075

Note: k = number of model parameters; d = durian production (success/failure); pres_lb = presence of large bats at durian (*Pteropus alecto* or *Acerodon celebensis*); pres_sb = presence of small bats at durian (*Eonycteris spelaea*); ni_sb = number of interactions between small bats and durian; dur_lb = duration of visits of large bats to durian (min); dur_sb = duration of visits of small bats to durian (min); and random effect = tree.

lacked adequate power to conclusively determine which of these factors was most influential due to small sample size.

All three bat species showed a single nightly peak in visitation to durian. *Eonycteris spelaea* and *P. alecto* showed similar temporal foraging activity on durian nectar (overlap = 0.88), feeding on durian nectar throughout much of the night, with a peak between 2300 hr and 2400 hr. However, both of these species showed different temporal foraging activity from *A. celebensis* (overlap estimate of *E. spelaea*—*A. celebensis* = 0.45; overlap of *P. alecto*—*A. celebensis* = 0.41). *Acerodon celebensis* foraged at durian flowers earlier in the night than the other bat species, from 2000 hr to 2300 hr, with a peak between 2000 hr and 2100 hr (Figure 3). *Pteropus alecto* was always seen foraging alone and exhibiting resource defending behavior against other bats. In contrast, we once observed two individuals of *A. celebensis* feeding together on the same durian inflorescences, and on several occasions observed 2–3 individuals of *E. spelaea* feeding together on the same durian inflorescences.

A small number of inflorescences were visited by animals other than bats. While the mean duration of visits by *Strigocuscus celebensis* (small Sulawesi cuscus) were longer than that of any other animal visitor, this species destructively consumed the flowers, and flowers consumed by cuscus were no longer available to any other animal species. The cuscus is thus not acting as an effective pollinator for durian and in fact may have a negative impact on durian fruit production (Figure S5). Insects such as moths and bees were rarely documented visiting durian flowers, perhaps in part because they did not trigger the camera traps as reliably as larger

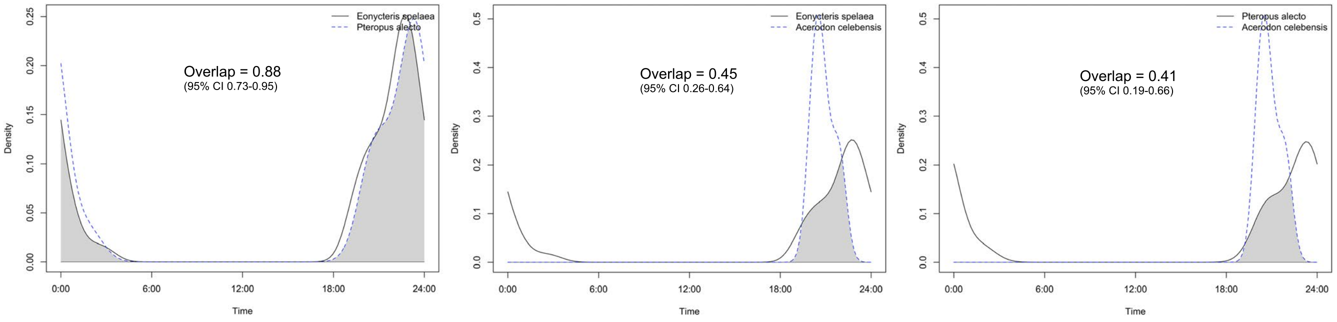

FIGURE 3 Temporal overlap of foraging activity between the three pairs of bat species that visited durian flowers. The gray shading indicates the time when pairs of species were both actively foraging at durian flowers. The y-axis shows the kernel density estimates of activity

vertebrates, or perhaps because nets used to exclude vertebrates while allowing access to insects may have inadvertently deterred insects. Regardless of documented visitation rates, inflorescences subjected to insect pollination treatments had much lower fruit set relative to the open pollination treatments, suggesting that although insects are capable of pollinating durian flowers, they are much less efficient than bats. During the day (0600–1800), camera traps also recorded bees and *Aethopyga siparaja* (crimson sunbird) visiting durian flowers. The birds visited unopened flower buds and punctured the base of the buds with their beak (Figure S6). The stigma and anthers were left untouched because the flowers were still closed, indicating it is unlikely diurnal birds could function as durian pollinators.

3.4 | Economic value of bat pollination services

The degree to which durian depends on bats as pollinators, the durian dependence ratio, was calculated as 0.84. In Batetangnga Village, durian fruiting season only occurs once per year and lasts for approximately two months. In our study, durian flowering season occurred from October to November 2017, and then the fruiting and harvesting season occurred from January to early April 2018. During this period, the total durian production in Batetangnga Village was ~1,497,600 fruits according to the locals. The villagers sold durian at a per unit price rather than by weight, with each fruit commanding IDR 5000 (~US$0.35) during our study period. Thus, we estimate that bat pollination services were worth IDR 6.3 billion (~US 450,000). Because Batetangnga Village encompasses ~44.8 km^2, bat pollination services are valued at ~117/ha in this region during this durian fruiting season.

4 | DISCUSSION

Our study provides the first evidence that durian flowers in Sulawesi, Indonesia are pollinated primarily by bats. Several observations support this evidence: (a) Each flower was open and receptive at night, which is a time of day when bats were active; (b) bats visited the greatest number of inflorescences and had the longest total duration of visits; (c) bats came into contact with anthers and stigmas without damaging flowers, whereas other visitors caused damage to flowers or did not contact anthers and stigmas; and (d) extremely low fruit set occurred via insect pollinators when vertebrates were prevented from accessing flowers during exclosure experiments. These results corroborate findings from other studies in Thailand and Malaysia in which the same durian species, *Durio zibethinus*, showed similar floral traits and also relied on bats for pollination (Aziz, Clements, Peng, et al., 2017; Bumrungsri et al., 2009). Our findings underscore the importance of bats for the pollination of this highly valuable fruit in Southeast Asia.

Among nocturnal animals, bats may increase the probability of successful durian pollination by transferring sufficient loads of pollen among different durian trees. Previous studies have documented that pteropodid bats are long-distance pollen dispersers that can deposit large loads of pollen (Acharya, Racey, Sotthibandhu & Bumrungsri, 2015). For example, *E. spelaea*, the main visitors of durian flowers in this study, travels up to 38 km while foraging (Start, 1974). Such long-distance pollen dispersers are important for low-density plant species such as the durian, especially when grown in agroforestry systems, as is typical in Indonesia (Retnowati, 2003; Salafsky, 1995). Long-distance pollination also increases the probability of pollen coming from genetically distant and distinct individuals, which is important to successful pollination and production of high quality durian fruits (Honsho et al., 2009).

4.1 | Pollinator assemblage of durian in Sulawesi

In our study area, the pollinator assemblage of durian is more diverse than those in Tioman Island, Malaysia (Aziz, Clements, McConkey, et al., 2017) and southern Thailand (Bumrungsri et al., 2009), possibly because Sulawesi has a comparatively higher diversity of pteropodid bats (Mickleburgh, Hutson & Racey, 1992; Simmons, 2005). Our study indicates that *E. spelaea*, a generalist nectarivore, is a durian pollinator in Sulawesi, much like it is in other regions (Aziz, Clements, McConkey, et al., 2017; Bumrungsri et al., 2009). Also, our study provides the first record of durian pollination services by *P. alecto* and the endemic, intensively hunted *A. celebensis*, highlighting that these endangered flying foxes are also key pollinators of durian.

Nectarivorous bat species are thought to be more important pollinators than the primarily frugivorous bat species (Stewart & Dudash, 2017). However, the potential role of all flying foxes (bats of the genera *Pteropus* and *Acerodon*) as pollinators should not be overlooked, as flowers are an important dietary component for these species and their tongue morphology indicates they are able to exploit nectar (Aziz, Clements, McConkey, et al., 2017; Banack & Grant, 2002; Brit, Hall & Smith, 1997; Palmer, Price & Bach, 2000). Our study demonstrates that *Pteropus* and *Acerodon* are important pollinators for semi-wild durian in Sulawesi, as their visitation to the flowers contributed to mature fruit set. Although our exclusion experiments unequivocally indicated bats were the primary pollinators of durian, the results of our GLMM analyses suggested our sample sizes were too small to definitively determine which aspect of bat visitations was most influential to durian fruit set. We recommend additional research with larger sample sizes in the future.

Visitation by large pteropodid bats is important to durian fruit production. Compared with smaller species, flying foxes are likely to deposit larger loads of pollen and move them over longer distances, increasing the likelihood of successful pollination. In Australia, *P. alecto* individuals are known to forage up to 20 km (Markus & Hall, 2004; Vardon et al., 2001). Other species of flying foxes are also recognized as long-distance pollinators: *P. poliocephalus* flies 17–25 km during foraging bouts (Spencer, Palmer & Parry-Jones, 1991); *Pteropus tonganus* 5–22 km (Banack & Grant, 2002); *Pteropus rufus* 1–7 km (Oleksy, Racey & Jones, 2015); and *Pteropus vampyrus* 88–363 km (Epstein et al., 2009). Further investigation to quantify pollen loads carried by various species of bats and assessments of their pollen transfer effectiveness could increase understanding of the contributions of each species to pollination for specific plant species (Sheherazade, 2018). Nevertheless, the present exclusion study provides convincing evidence regarding the need to enhance bats to increase durian production.

4.2 | Resource partitioning among bat species

Bats may partition resources either temporally or spatially. We found some evidence of temporal partitioning in durian visitation by the bats. Peak foraging occurred simultaneously for *E. spelaea* and *P. alecto*, and this peak occurred later in the night than peak activity of *A. celebensis*. The two large species appear to partition resources temporally within nights. This partition may be a function of interference, if smaller bats cannot visit the flowers that are being used by larger bats, or a function of roost location relative to the plants we monitored, which would determine the time after sunset bats start foraging at these plants.

We could not directly test whether the bats partitioned their use of nectar resources within trees by height because we deployed all the camera traps at similar heights, 15–20 m above the ground. However, we heard loud squeaking sounds and wing-clapping from the canopy of 30–40 m durian trees during the flowering season. Local people reported similar observations. We suspect these sounds were *P. alecto* and/or *A. celebensis* that foraged considerably higher in the trees compared with the smaller *E. spelaea*. Accessing flowers higher in the trees would be easier and energetically less costly for these large pteropodid bats, which are less maneuverable below the canopy than the smaller bats (Palmer et al., 2000). Previous studies corroborate this idea of spatial partitioning between species: *Pteropus hypomelanus* fed at greater heights in durian trees (6–20 m) than *E. spelaea* (<6 m) in Peninsular Malaysia (Aziz, Clements, McConkey, et al., 2017); *P. giganteus* fed at greater heights in *Madhuca latifolia* trees than *Cynopterus sphinx* (Nathan, Karuppudurai, Raghuram & Marimuthu, 2009); and *P. giganteus* foraged at greater heights (15–20 m) than *C. sphinx* in kapok trees (Singaravelan & Marimuthu, 2004). Our observations suggest that resource partitioning occurs spatially between small and large pteropodid bats (*i.e.*, larger bats forage predominantly at greater heights within trees than smaller bats), whereas it occurs temporally between two large pteropodid bats (*i.e.*, *A. celebensis* forages earlier in the night than *P. alecto*). Because durian trees grow taller with age, conservation of both small and large bat species may be important to ensure durian fruit production on trees of all ages grown under semi-wild conditions.

4.3 | Appeal for bat conservation

Our study experimentally demonstrates the importance of pollination services provided by several species of pteropodid bats for the production of semi-wild durian in Sulawesi, Indonesia. These pollination services are valued as much as US$117/ha/fruiting season for the production of 1500 tons of durian fruit in Batetangnga village. This value is similar to the direct economic benefits estimated for bee pollination services to coffee in Costa Rica and Colombia (Bravo-monroy, Tzanopoulos & Potts, 2015; Ricketts, Daily, Ehrlich & Michener, 2004). However, this valuation should be treated with caution and considered a rough estimate since our study lasted a short period and was conducted in only one village. Total durian production was based simply on an estimate provided by a knowledgeable local, because the official data about fruit production this year were not generated yet by the local government agency. We assumed all the fruits were traded locally and used a single local price to derive our estimates. Fruits sold outside the village likely commanded a higher price, so our use of the local price may have underestimated the actual value of bat pollination services to durian production in the region.

Conservation of bats in Sulawesi should be promoted to prevent loss of productivity of plant species that rely on them for pollination. This conservation is notably absent for *A. celebensis* and *P. alecto*, which are large species that are intensely hunted throughout Sulawesi to support bushmeat markets in North Sulawesi (Sheherazade & Tsang, 2015). The endemic *A. celebensis* is already listed as Vulnerable on the IUCN Red List due to declines caused by human actions (Tsang & Sheherazade, 2016). Additional loss of these bats may have a profound impact both ecologically and economically. In our study region, bat pollination services are not only important to the local economy, but also culturally valuable in the production of durian used during communal durian feasts which hold high significance for the local people.

We recommend the prioritization of bat protection by the Indonesian government and conservation NGOs. The conservation of bats should incorporate *in situ* protection of bat roosts (*e.g.*, mangroves, which are the primary roosts for flying foxes) and foraging areas (*e.g.*, primary forests and mixed plantations), reduction of hunting of bats as bushmeat in North Sulawesi, legislation for bat protection and hunting quotas, and outreach programs to raise awareness about the importance of bats.

This study provides evidence that enhanced conservation of bats could potentially improve the productivity of durian in Indonesia to fulfill the high domestic market demand. In addition, governments of Indonesia and other Southeast Asian nations should consider the potential of marketing their organic semi-wild durian pollinated by bats. Investigation of international markets for this organic fruit and engagement with relevant stakeholders would be needed to evaluate the viability of such an initiative. Organic fruits command higher prices in the market than non-organic fruits (Reganold & Wachter, 2016). An increase in perceived quality by consumers may increase the value of durian, and as a result, decrease trade deficits without the need to increase crop yield nor convert additional land from forest to agricultural production. Advertisements could also target a larger, wealthier international clientele for the sale of organic durian, thereby increasing the market reach to an audience that has more disposable income (Gasik, 2017). This “re-branding” of semi-wild durian could be advantageous to the Indonesian economy and other Southeast Asian countries, as well as to bat conservation.

ACKNOWLEDGMENTS

We are grateful for permit granted by Government of West Sulawesi, Polewali Mandar Regency, Binuang Subdistrict, and Batetangnga Village. Funding was provided by the Center for International Forestry-USAID Indonesia, Rufford Small Grant, Bat Conservation International, Tropical Conservation and Development University of Florida, and IdeaWild to Sheherazade. We thank Prof. Bette Loiselle and Prof. Todd Palmer and two anonymous reviewers for feedback that greatly improved this manuscript. We also thank the people of Batetangnga for their support; Fadli, Hamsul, Openg, and Boneng, who were great research assistants.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j74b646 (Sheherazade, Ober & Tsang, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Sheherazade, Ober HK, Tsang SM. Contributions of bats to the local economy through durian pollination in Sulawesi, Indonesia. *Biotropica*. 2019;00:1–10. https://doi.org/10.1111/btp.12712