Long-term monitoring of seed dispersal by Asian elephants in a Sundaland rainforest

Tan Wei Harn

Master of Research Thesis

Management and Ecology of Malaysian Elephants (MEME)

School of Environmental and Geographical Sciences

University of Nottingham Malaysia

Acknowledgements

This study would not have been possible without the support of many. I would like to thank my supervisors, Prof. Ahimsa Campos-Arceiz and Dr. Chin Chiew Foan for their support, guidance and feedback throughout this study. Many thanks to the members of MEME for their support; Praveena and Nurul in accommodating my logistic needs, the field team, Alicia, Param, Cherang, Husin, Ridzuan and Hamid for helping me with fieldwork, and the many others who have participated over the years; Adeline Hii, Anders, Ange, Hii Ning, Jonathan Moore, Lisa Ong, Steven Lim, Vivienne Loke. My gratitude to lab technician Siti Lin for providing me lab materials for my study. A special thanks to Dr S K Ganesan and Mr. Ali Ibrahim from Singapore Botanical Gardens in helping with the identification and accommodating me during my herbarium visit. Many thanks to Yayasan Sime Darby for funding this study as well as providing me with a scholarship along with the University of Nottingham Malaysia to pursue this degree.

Disclaimer

Being a 73-month long study, the length of this study goes well beyond the one-year period for the master's program. Thus, the author will clarify his contribution to the study as followed. My participation in the fieldwork for this study started in January 2017 as a research assistant under the project. I continued the data collection up till the last month of survey in November 2018. As for species identification, only seven species were successfully identified by other members of the working group prior to my participation of the project. Seeds of other species were identified through my own efforts in which I deduced local indigenous and my personal knowledge on plants, which I later confirmed either through comparing with herbarium specimens in Singapore Botanical Garden or DNA barcoding if necessary. Subsequent analysis of the data was done during my master program period.

Abstract

Elephants have profound effects on the functioning of the ecosystems they inhabit. Little is known, however, about the role of Asian elephants (*Elephas maximus*) as agents of seed dispersal in tropical rainforests of Southeast Asia, particularly in the Sundaland region. Sundaic forests are peculiar in their phenology, with supra-annual and highly irregular episodes of mast fruiting. Here I present a long-term (73-month) monitoring of the seeds dispersed by elephants in dipterocarp forests of northern Peninsular Malaysia. I conducted monthly dung surveys in two mineral licks (11.3 km apart) frequently visited by elephants. Additionally, I recorded haphazard observations of seeds and seedlings in elephant dung. I recorded a minimum of 45 morphospecies from at least 25 plant families dispersed by elephants. Elephant seed dispersal varies spatially, with only 39.4% of the morphospecies dispersed at both sites (Jaccard dissimilarity index = 0.45). Temporally, elephants dispersed seeds in sporadic pulses in terms of abundance and diversity, without any apparent seasonality (seeds appeared in 19.1 % of 1,284 dung piles and 49.3 % of 73 months sampled). Around 14 morphospecies exhibited the two types of megafaunal syndrome traits defined by Guimaraes et al. (2008). However, another 11 morphospecies were found to conform to a Type 3 trait; species with large fruits and moderately large (> 1.5 cm) seeds in moderately large numbers (> 15). This makes the total of 24 morphospecies exhibiting megafaunal syndrome traits. However, the current definition is over simplified, and a new definition is needed that expands beyond physical fruit traits. Over half (53%) of the plants dispersed by elephants exhibit the megafaunal dispersal syndrome, suggesting a higher level of specialized elephant-plant seed dispersal interactions than previously assumed in Asia. Sundaland's forests are undergoing a rapid loss of their rich megafaunal assemblages, with profound and long-term consequences for their function.

List of Content

1.0 Introduction 6

2.0 Aims and Objectives 11

3.0 Materials and Methods 12

4.0 Results 16

5.0 Discussion 25

6.0 References 31

7.0 Supplementary Information 39

7.1 Supplementary Graphs 39

7.2 Sequences 42

7.3 Species Profile 43

1.0 Introduction

As one of the largest megaherbivores (terrestrial animals above 1000kg; Owen-Smith 1992), elephants (mammals from the order Proboscidea) have profound impacts on the functioning of the ecosystems they inhabit (Malhi et al. 2016). Seed dispersal is the movement of seeds away from the parent plant and is an important ecological process that promotes genetic continuity and diversification within plant communities (Corlett, 2017). Seedlings dispersed away from parent plants have an increased likelihood of establishing due to the reduced negative impacts of intergenerational competition, pathogen infections and herbivory (Janzen, 1970; Connell, 1971). Many plant species in the tropical forest depend on endozoochory (seed dispersal by animals) for seed dispersal (Howe and Smallwood, 1982).

There are several factors that define the unique seed dispersal function of elephants in comparison to other vertebrates. Being so large, elephants have a high food consumption need. For example, a wild adult Asian elephant may spend up to 18 h per day feeding, consuming around 150 kg of food (Vancuylenberg, 1977). Depending on the availability of plant species, the diet of elephants can be highly diverse, consuming various forms of plant matter including fruits (e.g. McKay, 1973; Sukumar, 1990; Chen et al., 2006; Campos-Arceiz et al., 2008). Elephants have large gapes, allowing them to consume fruits or seeds without size limitations. Combining their long seed gut passage time (GPT) and their ability to travel over large distances, elephants can deposit large quantities of various sized seeds over extensive distances (Campos-Arceiz et al., 2008).

Proboscideans were once a diverse assemblage of species which flourished between the Miocene (24-5 Mya) and the Pliocene (5 to 2 Mya), whose range extended to all continents except Australia and Antarctica (Sukumar, 2003). However, human hunting resulted in the extinctions of most proboscideans species during the Late Pleistocene/early Holocene (125 kyato w12,000 BP; Surovell et al., 2005). In the present Anthropocene, there are three species of surviving proboscideans, namely *Loxodonta africana* (African bush elephants) and *Loxodonta cyclotis* (African forest elephants) which reside in the African continent, and *Elephas maximus* (Asian elephant), whose distribution ranges across several types of habitat in the Indian subcontinent,

Southeast Asia and Southern China (Blake and Hedges, 2004). While the ecological function of African forest elephants as seed dispersers is relatively well known (e.g. White et al. 1993, Feer 1995, Theuerkauf et al. 2000, Blake et al. 2009), much less is known about the role of Asian elephants (Campos-Arceiz & Blake 2011, Corlett 2017).

Previous studies suggest that Asian elephants are less frugivorous and have less specialized seed dispersal interactions than African forest elephants, especially in wet tropical rainforest (e.g. Kitamura et al. 2007, Campos-Arceiz & Blake 2011). In the tropical rainforest of Thailand, seeds were recovered at very low frequency from Asian elephant dung pile (21%, N=701; Kitamura et al. 2007). Moreover, the diversity of species consumed were also relatively low with nine and 17 species in Thailand (Kitamura et al. 2007) and Peninsular Malaysia (Oliver 1978) respectively. Interestingly, Jotish (2013) noted a higher diversity of seeds recovered from Asian elephant dung in the evergreen forest of the Western Ghats, India, though the frequency of seeds found in dung was still relatively low (28.9%, N=384). Mixed observations were recorded in other types of habitats, e.g. in the tropical dry deciduous forest, 22 species, includes cultivated crops, were found in 74% of 145 dung piles in Sri Lanka (Samansiri and Weerakoon, 2008) while eight species were recovered from 15.8% of 72 dung piles in India (Baskaran and Desai, 2013). A possible reason for these mixed observations is that Asian elephants frugivory studies in Sundaland forest failed to account for the irregular general flowering and mast fruiting phenomenon. This is evident in the supra-annual variations in frugivory habits of Bornean sun bears (*Helarctos malayanus*) (Fredriksson et al., 2006).

These unique communal flowering and fruiting events have been documented all over the predominantly Dipterocarp forests of the Sundaland (i.e. the Malay Peninsula and the islands of Sumatra, Borneo, Java, and Bali; e.g. Appanah 1985, Ashton et al. 1988, Sakai 2002). This mega-diverse region contains approximately 20% to 25% of the earth's higher plant species (Myers et al., 2000). These forests undergo mast reproductive events in which trees from many families synchronize their flowering and fruiting. General flowering followed by mast fruiting episodes occur at supra-annual and irregular intervals of 2-10 years with very little to no reproductive activity in between (Medway 1972, Appanah 1985, Ashton et al. 1988). The scale and intensity of this phenomenon can vary substantially, with affected area ranging from a river valley or a small

forest patch to an entire region like Peninsular Malaysia (Numata et al., 2013). Several climatic cues for these masting episodes are either periods of high photosynthetic radiation (Azmy et al. 2016), low temperature or drought that are usually associated with supra-annual El Niño/Southern Oscillation (ENSO) events (e.g.Chen et al. 2018, Kurten et al. 2018). During mast fruiting events, fruits are overabundant for a short period of time, which is typically followed by periods of low productivity and, in some occasions, an almost complete absence of crops, hence creating highly distinguishable periods of mast and non-mast years. This disparity in spatial and temporal fruit production in Sundaland results in lower overall productivity than tropical forest Africa and South America (Appanah, 1985).

Sundaland's forests include a range of tree species from several families that exhibit the so-called megafaunal dispersal syndrome. These are trees with overbuilt fruits and other traits adapted for seed dispersal by very large frugivores, such as elephants (Janzen & Martin 1982). Janzen and Martin's (1982) original definition was precise in terms of qualitatively describing this phenomenon but was considered as too broad and lacking quantitative support, thus, subjugating the validity of the theory to controversy and criticism (Howe, 1985). Guimaraes et al. (2008) quantified the traits by defining two megafaunal fruit types: Type I are fleshy fruits 4-10 cm in diameter with up to five large (generally ≥ 2.0 cm diameter) seeds, and Type II are fleshy fruits more than 10 cm in diameter and with numerous (> 100) small seeds. Sundaland's megafaunal-syndrome trees include *Mangifera* spp. (Anacardiaceae), *Dillenia indica* (Dilleniaceae), and *Irvingia malayana* (Malvaceae), to name just a few (e.g. Fredriksson et al. 2006, Campos-Arceiz et al. 2012; Ong et al. 2019). The presence of the megafaunal dispersal syndrome among Sundaland trees suggests a relevant role of large herbivores in seed dispersal processes. Large fruiting species, namely *Artocarpus heterophyllus*, *Careya arborea*, *Elaocarpus serratus* and *Mangifera indica,* were poorly dispersed by other non-elephant mammalian frugivores in Silent Valley, India, indicating some level of mutualism between elephants and these megafaunal syndrome species (Jotish, 2013). However, to our knowledge, no study has been conducted to examine the ecological role of elephants or other large herbivore as agents of seed dispersal in the dipterocarp forests of Sundaland (but see Ong et al. 2019).

Peninsular Malaysia is home to an estimated population of ~1500 wild elephants (Saaban et al. 2011). Given the dramatic change in forest cover that Peninsular Malaysia has experienced in the past century – from ~80% forest cover in the 1940s (Aiken, 1994) to less than 40% in 2010 (Miettinen et al. 2011) – elephants have inevitably lost range and population numbers as a consequence of habitat loss and the subsequent increase in human-elephant conflicts. Current populations are highly fragmented, populations present in seven of the 11 states, with populations being concentrated in pockets within the states of Perak, Kelantan, Terengganu, Pahang, and Johor, while Kedah is home to a small population, and only one individual being present in Negeri Sembilan (Saaban et al., 2011). In Malaysia, the foraging habits of Asian elephants impact the structure, composition, and diversity of vegetation through a strong preference for monocot (Terborgh et al., 2018). The extinction of the Sumatran rhino (*Dicerorhinus sumatrensis*) in the last decade and the crippled population of Malayan Gaur (*Bos gaurus hubbacki*; n=270–300; DWNP. 2012) leaves Asian elephants as the only true surviving megaherbivore in the region. Campos-Arceiz et al. (2012) showed that Malayan tapirs (*Tapirus indicus*) cannot replace elephants in terms of their effectiveness to disperse large-seeded plants, and Ong et al. (2019) found that elephants were the only effective dispersers of *Irvingia malayana*, a Type I megafaunal-syndrome plant, in a dipterocarp forest of northern Peninsular Malaysia.

Studying seed dispersal by elephants in Sundaland's forests is logistically challenging because of the broad temporal and spatial scales involved, elephants' low densities, and the difficulty of traversing through the forest. Additionally, fruiting episodes are infrequent and unpredictable. A way to overcome these difficulties is to conduct long-term monitoring (e.g. Fredriksson et al 2006) and to sample locations that are frequently visited by elephants. In Malaysian rainforests, mineral licks provide key resources for large herbivores and elephants frequently visit them (Hii 2016), hence, they provide an opportunity to find elephant dung.

Here I present a long-term study to understand the ecological role of Asian elephants as agents of seed dispersal in tropical rainforests of the Sundaland. The specific objectives of the study were to describe the quantity, diversity, spatial heterogeneity, and phenology of seeds dispersed by Asian elephants as well as the seed and fruit traits of the plants dispersed. I was

particularly interested in whether elephants in Southeast Asia disperse megafaunal-syndrome plants. I did this by combining monthly dung surveys in two mineral licks and haphazard dung sampling for a period of six years in Temenggor Forest Reserve, Perak and other forests of northern Peninsular Malaysia.

2.0 Study Aims and Objective

As very little is understood about the role of Asian elephants in seed dispersal for tropical plant species in the Sundaland, this study aims at broadening our understanding on the importance of Asian elephants in seed dispersal for Sundaland plant species. Therefore, the objectives of this study are:

1. To identify the diversity of plant species dispersed by elephants in Malaysian rainforests using morphological identification and DNA barcoding techniques.
2. To quantify the number of seeds for each species dispersed by Asian elephants
3. To describe the seasonal patterns of fruit consumption and seed dispersal by Asian elephants.
4. To describe the characteristics of seeds and their corresponding fruits if possible, with focus towards megafaunal-syndrome fruits.

3.0 Materials and Methods

Study area. — This study took place in the forests of northern Peninsular Malaysia, primarily in two mineral licks in Temenggor Forest Reserve, within the Belum-Temenggor Forest Complex (BTFC), in the state of Perak (Lim et al. 2010; Fig. 1). BTFC has an area of ~ 3500 km^2, including the Royal Belum State Park, and four permanent forest reserves in which logging is permitted and ongoing in some areas. BTFC also encompasses a man-made lake that flooded ~150 km^2 of lowland forest, including mineral licks frequently used by wildlife (Lim et al. 2010). Vegetation in BTFC is dominated by hill dipterocarp forest with pockets of lowland mixed dipterocarp and montane forest. Plant families such as Annonaceae, Dipterocarpaceae, Euphorbiaceae, Rubiaceae, and Lauraceae have high tree diversity (Chua et al., 2000). BTFC is home to endangered charismatic megafauna such as Asian elephants, tigers (*Panthera tigrisi*), Malayan tapirs, and others.

Our systematic dung surveys took place in two mineral licks named Sira Gajah and Sira Tersau (*sira* means mineral deposit used by wildlife in local Malay language) located 11.3 km away from each other (Fig. 1). The two licks are quite different, while Sira Gajah (SG) is a dry mineral deposit (i.e. elephants consume soil that they kick from the ground), Sira Tersau (ST) is a sulfur spring (elephants drink the mineral-rich waters; Fig. 2). SG's terrain is an exposed slope pocketed with several mineral rich holes excavated by elephants and ST is an open-flat area with a small stream flowing above the sulphur vents into Temenggor lake (Fig. 2). Previous camera trap studies found Asian elephants frequently visiting both salt licks (Hii 2016).

Seed surveys in dung. — From November 2012 to November 2018, systematic dung surveys were conducted in both mineral licks at a frequency of either once or twice a month. In each survey, I aimed to sample at least 20 elephant dung piles (each dung pile corresponding to a single defecation by a single elephant) to look for seeds, although in some surveys I was unable to find enough dung piles. Sampling for seed was done by hand-searching through dung boli. Seeds retrieved from each dung pile were stored in individual bags, tagged, and taken to a field station for subsequent identification and quantification. Besides the systematic sampling at SG and ST, I conducted opportunistic sampling of elephant dung piles that were found during other field

activities throughout Northern Peninsular Malaysia. Whenever seeds were haphazardly found in elephant dung, seeds were collected, tagged, and stored them for subsequent identification. I did not attempt to quantify the seeds found outside SG and ST. Collected seeds were either stored at -80^{o}C or germinated as living specimens for identification purposes. Besides seeds, I also recorded the presence of seedlings growing from elephant dung.

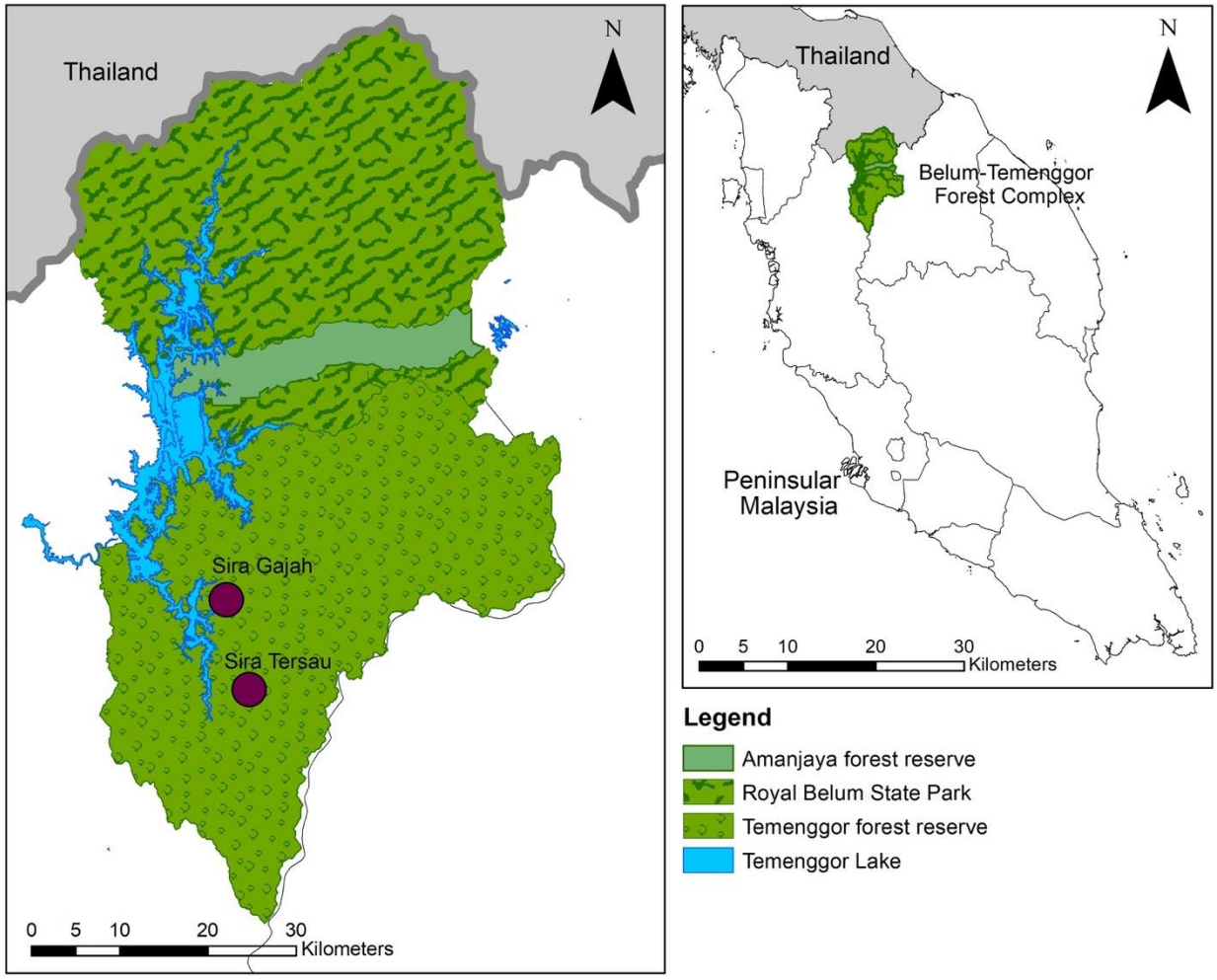


Figure 1: Map of Peninsular Malaysia with location of Belum-Temenggor Forest Complex. Map with breakdown consisting of Royal Belum State Park and Temenggor Forest Reserve with locations of study sites Sira Gajah and Sira Tersau. Please note that the locations of both Sira Gajah and Sira Tersau have been intentionally modified and do not represent their exact location.



Figure 2: Mineral licks. A) Sira Gajah B) Sira Tersau

Seed identification and characterization. — Seeds were categorized into unique morphotypes (hereafter morphospecies) based on their morphological characters. Subsequently I used a combination of approaches – (1) comparing with local herbarium specimens, (2) relying on local ecological knowledge from Orang Asal (indigenous community) from the Temiar community, and (3) using DNA barcoding – to identify seed and seedling specimens to the lowest taxonomic level possible. Additionally, seed dimensions (length, width, and depth) were measured to the nearest 0.1 mm using Vernier calipers and recorded fruit traits (size and color) either through field observations or from literature (Whitmore, 1972).

ENSO data. — Data on El Niño-Southern Oscillation (ENSO) cycles represented through the Oceanic Niño Index (ONI) from November 2012 to August 2018 were obtained from the National Oceanic and Atmospheric Administration (NOAA), United States. El Niño was recorded from November 2014 until May 2016 while two La Niña episodes occurred from August 2016 to December 2016 and October 2017 to March 2018. ENSO data was used to plot and visualise patterns in graphs during data processing and analysis.

Data processing and analysis. - Data analyses were conducted in R version 7 (R Core Team, 2019), *dplyr* (Wickman, 2017) was used for data manipulation and *ggplot2* (Wickham, 2017) for data visualization. Sample completeness (i.e. coverage) and the estimated asymptotic species richness at SG, ST, and both sites together were assessed using package *iNEXT* (Hsieh et al. 2016) for

abundance data, and I calculated Jaccard's dissimilarity index with the function *vegdist* in the package *vegan* (Oksanen et al. 2019). I used ANOVA F to test for interannual differences in the mean number of seeds per pile between SG and ST, Chi square χ^2 to test for differences in morphospecies richness per year.

Megafaunal Syndrome Fruit – Based of literature or personal observations of fruit sizes and traits of morphospecies, those that exhibit megafaunal syndrome traits were characterised based on Guimaraes et al.'s (2008) definition of megafaunal syndrome fruits:

Type 1: Fleshy fruits 4–10 cm in diameter with up to 5 large seeds (generally .2.0 cm diameter).

Type 2: Fleshy fruits 10 cm diameter with numerous (.100) small seeds.

However, several morphospecies with megafaunal syndrome fruits of do not conform with the Guimaraes et al.'s (2008) definition. Thus, in our case, I added a Type 3 – species with large fruits and moderately large (> 1.5 cm) seeds in moderately large numbers (> 15).

4.0 RESULTS

Quantity, diversity, and spatial heterogeneity of seeds in dung. — I conducted 181 visits to the mineral licks (53.7 % of them in SG and 46.3 % in ST) in which I sampled 1,284 elephant dung piles (77.3 % in SG and 22.7 % in ST; Fig S2) and retrieved a total of 4770 seeds (82.6 % in SG and 17.4 % in ST) initially assigned to 33 distinct morphospecies (Table 1). Extrapolated sample coverage for both sites after 73 months of continuous sampling was 0.83 (Fig. 3) and the estimated (extrapolated) species richness for 146 months was 50.8 species (36.6 – 89.6 95 % CI; Fig. 3). Per site, sample coverage and observed and estimated morphospecies richness were 0.89, 21, and 25.5 (22.0 – 42.2 95 % CI) in SG; and 0.83, 10, and 22.3 (11.6 – 102.6 95 % CI; Fig. 3) in ST. Of these 33 morphospecies, 39.4 % were found in both sites, while 42.4 % were found exclusively in SG and 18.2 % exclusively in ST (Table 1). The Jaccard dissimilarity index between SG and ST was 0.45.

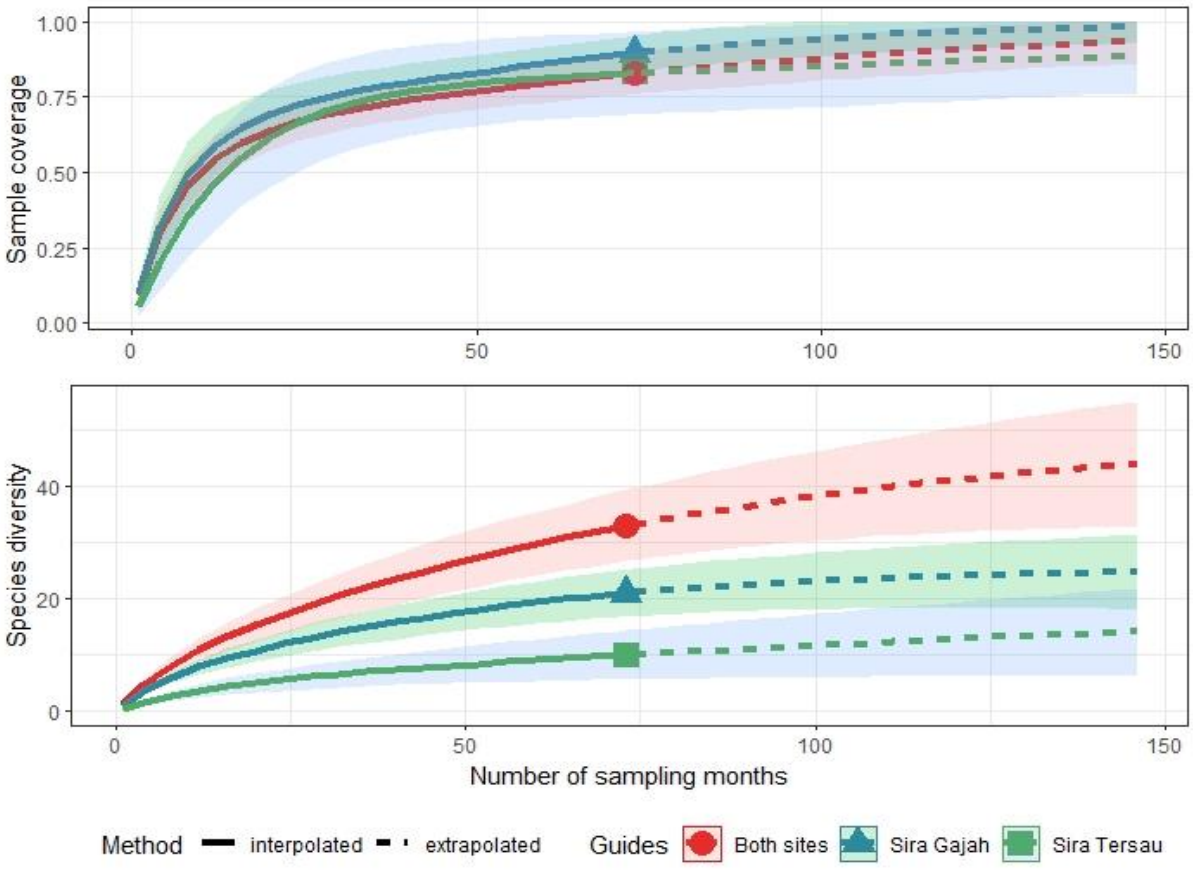


Figure 3: Sample coverage and species diversity (based on iNEXT).

Table 1: Taxonomy, frequency, quantity and other details of species recovered from Asian elephant dung.

ID	Family	Species	Total Months Found	Total No. Seed	Sira Gajah		Sira Tersau		Extra	Mean(mm) n=3			Fruit Colour	Plant Form	Seed Germ.	Megafaunal syndrome Type
					Months Found	No. Seed	Months Found	No. Seed	Presence of Seeds	Len.	Diam.	Wid.				
1	Anacardiaceae	*Bouea* sp.	2	10	2	10	0	0	No	12.00	13.77	18.67	Yellow	T	Yes	
2		*Dracatomelon dao*	1	2	1	2	0	0	No	16.00	14.67	16.67	Yellow	T	No	
3		*Mangifera maingayi*	1	8	1	8	0	0	No	49.00	31.00	21.00	Green	T	Yes	Type 1
4		*Mangifera* sp.1	9	501	7	413	6	88	Yes	51.33	44.33	34.33	NA	T	Yes	Type 1
		Mangifera sp.2														Type 1
5	Annonaceae	*Monocarpia marginalis*	1	1	0	0	0	0	Yes	NA	NA	NA	Brown	T	No	
6		*Mezzettia* sp.	8	43	8	43	0	0	Yes	26.30	18.03	26.33	Green	T	Yes	Type 1
7		*Platymitra macrocarpa*	1	25	1	25	0	0	No	24.67	17.17	5.30	Orange	T	No	Type 1
8		Unknown sp. 1	0	0	0	0	0	0	Yes	1.10	0.70	0.35	NA	U	No	
10		Unknown sp. 2	3	8	3	8	0	0	Yes	16.67	8.33	5.00	NA	U	Yes	
11	Apocynaceae	*Willughbeia* sp.	2	16	1	10	1	6	Yes	21.00	13.67	11.00	Brown	U	No	Type 3
12	Arecaceae	*Borassus flabellifer*	0	0	0	0	0	0	Yes	NA	NA	NA	Black	T	No	Type 1
13		*Orania Sylvicola*	1	3	0	0	1	3	No	30.67	29.67	29.33	Green	T	Yes	
14	Burseraceae	*Caranium littorale*	1	2	1	2	0	0	Yes	56.00	26.33	20.00	Green	T	No	
15	Calophyllaceae	*Calophyllum macrocarpum*	3	38	3	38	0	0	No	49.00	33.67	32.00	Green	T	No	Type 1
16	Chrysobalanaceae	*Parinari oblongifolia*	2	23	1	1	1	22	Yes	61.33	38.33	25.00	Brown	T	No	Type 1
17		*Parinari* sp	1	2	1	2	0	0	No	4.25	2.48	2.16	Brown	T	No	Type 1
18	Clusiaceae	*Garcinia* sp.	1	1	0	0	1	1	Yes	12.67	4.00	6.30	NA	T	No	
19	Dilleniaceae	*Dillenia indica*	12	1663	11	1383	5	280	Yes	4.00	2.67	2.00	Green	T	Yes	Type 2
		Dillenia reticulata														Type 2
20	Euphorbiaceae	*Baccaurea* sp.	1	5	1	5	0	0	No	11.50	9.50	2.50	NA	T	No	
21	Fabaceae	*Intsia palembanica*	8	55	6	49	2	6	No	38.67	27.00	14.67	Green	T	Yes	
22		*Parkia timoriana*	3	17	2	15	1	2	No	17.33	10.67	4.67	Green	T	Yes	
23	Fagaceae	*Lithocarpus kuntsleri*	1	10	1	10	0	0	No	22.67	13.67	15.67	Brown	T	No	
24	Irvingiaceae	*Irvingia malayana*	17	1525	15	1169	7	356	Yes	46.67	29.30	22.00	Green	T	Yes	Type 1
25	Lecythidaceae	*Barringtonia* sp.	0	0	0	0	0	0	Yes	30.00	17.00	16.00	Green	T	No	
26	Loganiaceae	*Strychnos* sp.	2	16	2	16	0	0	No	16.67	12.67	1.30	NA	L	No	

27	Malvaceae	*Durio* sp.	1	1	0	0	1	1	Yes	29.30	16.33	15.67	Green	T	Yes	Type 3
28	Meliaceae	*Sandoricum koetjape*	2	4	0	0	2	4	Yes	32.00	26.00	15.00	Orange	T	Yes	Type 3
29	Moraceae	*Artocarpus cf anisophyllus*	9	186	5	152	4	34	Yes	13.30	10.67	5.67	Yellow	T	Yes	Type 3
		Artocarpus elasticus														Type 3
		Artocarpus cf rigidus														Type 3
		Artocarpus sp.1														Type 3
30		*Artocarpus* sp.2	5	40	3	36	2	4	Yes	14.00	8.30	8.30	Green	T	Yes	Type 3
31		*Artocarpus* integer	1	6	0	0	1	6	No	NA	NA	NA	Green	T	No	Type 3
32	Myrtaceae	*Syzigium* sp.	1	2	1	2	0	0	No	20.25	28.50	28.50	Green	T	Yes	
33	Musaceae	*Musa* sp.	1	1	1	1	0	0	No	NA	NA	NA	Yellow	H	Yes	
34	Polygalaceae	*Xanthophyllum* sp.	5	649	2	581	3	68	Yes	17.67	13.00	11.67	NA	T	Yes	Type 1
35	Sapindaceae	*Nephelium* sp.1	0	0	0	0	0	0	Yes	NA	NA	NA	NA	T	Yes	
36	Sapotaceae	*Chrysophyllum burkilii*	2	11	2	11	0	0	No	17.67	10.67	16.67	Green	T	Yes	Type 1
37		*Diploknema* sp.	4	37	1	15	2	22	Yes	59.00	31.33	30.33	Green	T	Yes	Type 1
38		Unknown sp.1	2	7	1	6	1	1	Yes	19.00	2.00	13.00	Green	T	No	
39	Styracaceae	*Styrax* sp.	0	0	0	0	0	0	Yes	32.00	31.00	30.00	Green	T	Yes	
40	Zingiberaceae	*Alpinia pahangensis*	0	0	0	0	0	0	Yes	NA	NA	NA	Orange	H	Yes	
41		*Etlingera fulgens*	0	0	0	0	0	0	Yes	3.73	3.00	3.00	Red	H	No	
42		*Zingiber* sp.	1	6	0	0	1	6	Yes	6.00	4.00	3.00	NA	H	No	
43	Unknown		0	0	0	0	0	0	Yes	NA	NA	NA	NA	U	Yes	
44	Unknown		0	0	0	0	0	0	Yes	NA	NA	NA	NA	T	Yes	
45	Unknown		0	0	0	0	0	0	Yes	9.00	7.00	5.00	NA	U	No	

Abbreviations: Plant forms: L= Liana, T=Trees, U = unknown, H=Herb

After accounting for additional species that I identified from seedlings (5 species) and species haphazardly recorded outside SG and ST (7 species) I recorded a total of 45 elephant-dispersed morphospecies in northern Peninsular Malaysia (Table 1). Of these 45 morphospecies, I identified 93.3 % to family level, 86.6 % to genus level, and 40 % to species level (Table 1; Figure 5). Of the 45 morphospecies, 13.3 % were monocots and 86.7 % dicots. By plant form, 77.8 % were trees, 2.2 % were lianas, 8.9 % were herbaceous plants, and 8.8 % were unknown (Table 1). The 45 observed morphospecies represented a minimum of 25 plant families, of which the most diversely represented were Moraceae (six morphospecies) and Anacardiaceae and Annonaceae (five morphospecies each; Table 1 and Fig. S2).

I observed seeds of 24 morphospecies germinating in elephant dung (Table 1). The seedlings growing from elephant dung allowed me to distinguish four different species of *Artocarpus*, two species of *Dillenia*, and two species of *Mangifera* (Table 1). I was otherwise unable to distinguish seeds of the species within these three genera, hence for subsequent quantitative analyses we pooled these morphospecies by genus (Table 1).

The mean number of seeds per dung pile was 3.7 and it was not different between SG and ST (5.3 ± 11.6 in SG and 2.6 ± 6.5 in ST; $F_{(1,144)} = 4.13$, $p > 0.05$). By morphospecies, the mean number of seeds per 100 dung piles was 11.1 ± 29.7 (median = 0.9, range = 0.07 – 133.3), although their distribution was highly skewed, with five morphospecies accounting for over 90 % of all the seeds: *Dillenia* spp. = 40.4 %, *Irvingia malayana* = 27.6 % of all seeds, *Xanthophyllum* sp. = 11.3 %, *Mangifera* spp. = 9.2%, and *Artocarpus* spp. = 3.5,% (Table 1;Fig. 5).

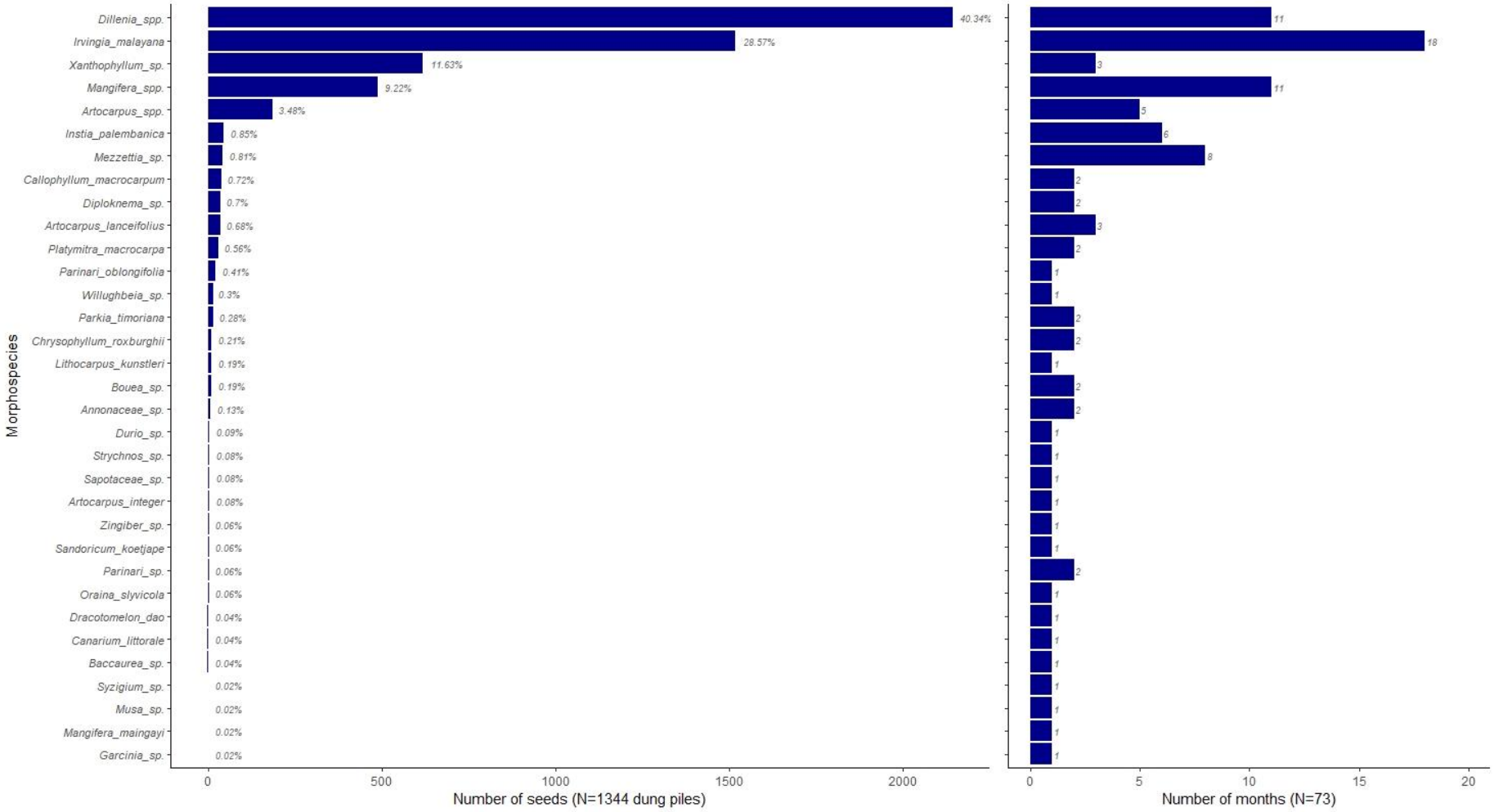


Figure 5: Number of seeds retrieved from elephant dung for each morphospecies (numbers at the right of the bars represent the percentage of the total seeds); Number of months in which I found seeds of each morphospecies in elephant dung.

Phenology of seeds in dung. — I found very marked temporal patterns, with most of seed dispersal by elephants happening at very low frequency and highly irregular events (Fig. 6). Overall, only 19.1 % of the sampled dung piles contained seeds (19 % of piles in SG and 19.2 % in ST), and seeds were present just in 49.3 % of the 73 sampled months (48 % in SG and 26 % in ST; Fig. 6). This means that there were long periods in which elephants did not disperse any seed, including a 16-month (December 2016 to March 2018), a six-month (June to November 2013), and several four-month periods (Fig. 6).

The highest morphospecies richness was in September 2014, when I found 10 different seed morphospecies (Fig. 6c), while on average I found 1.3 ± 2.1 (range: 0 - 10) morphospecies per month, and 10.0 ± 7.6 (range: 1 - 19) morphospecies per year during my sampling period. The number of morphospecies dispersed varied between years (χ^2 = 38.7, df = 6, p << 0.0001; Fig. S3). Even the most frequently dispersed morphospecies appeared in elephant dung in few and generally not overlapping (between species) peaks of abundance (Fig. 7). For example, *Irvingia malayana* was dispersed in five different periods (Fig. 7), *Dillenia* spp. in three (Fig. 7), *Xanthopyllum* sp. in just one (Fig. 7), and *Mangifera* spp. in three periods (Fig. 7) over the total period of six years.

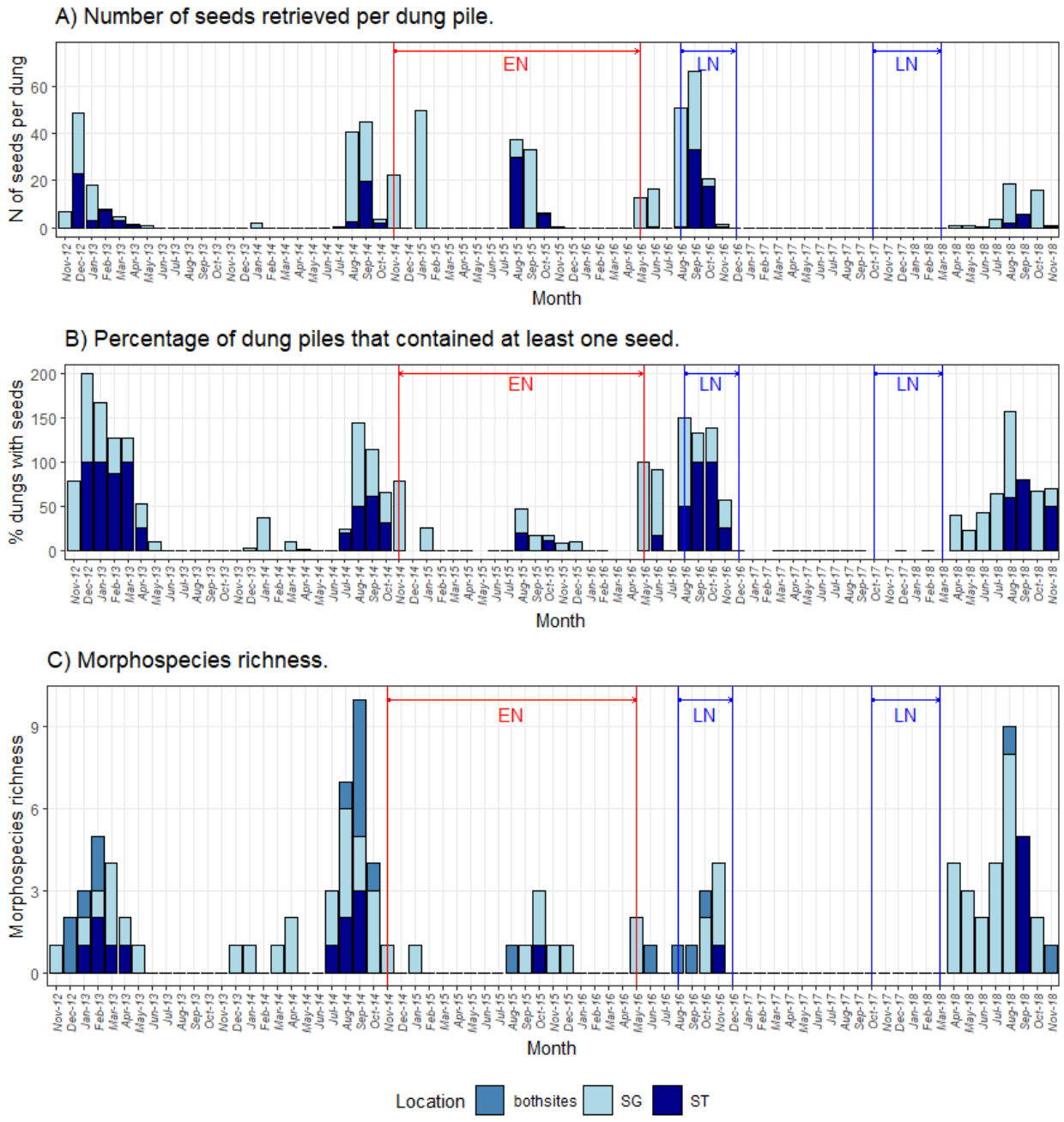


Figure 6: Monthly distribution of (A) number of seeds retrieved per dung pile; (B) percentage of dung piles that contained at least one seed; and (C) morphospecies richness.

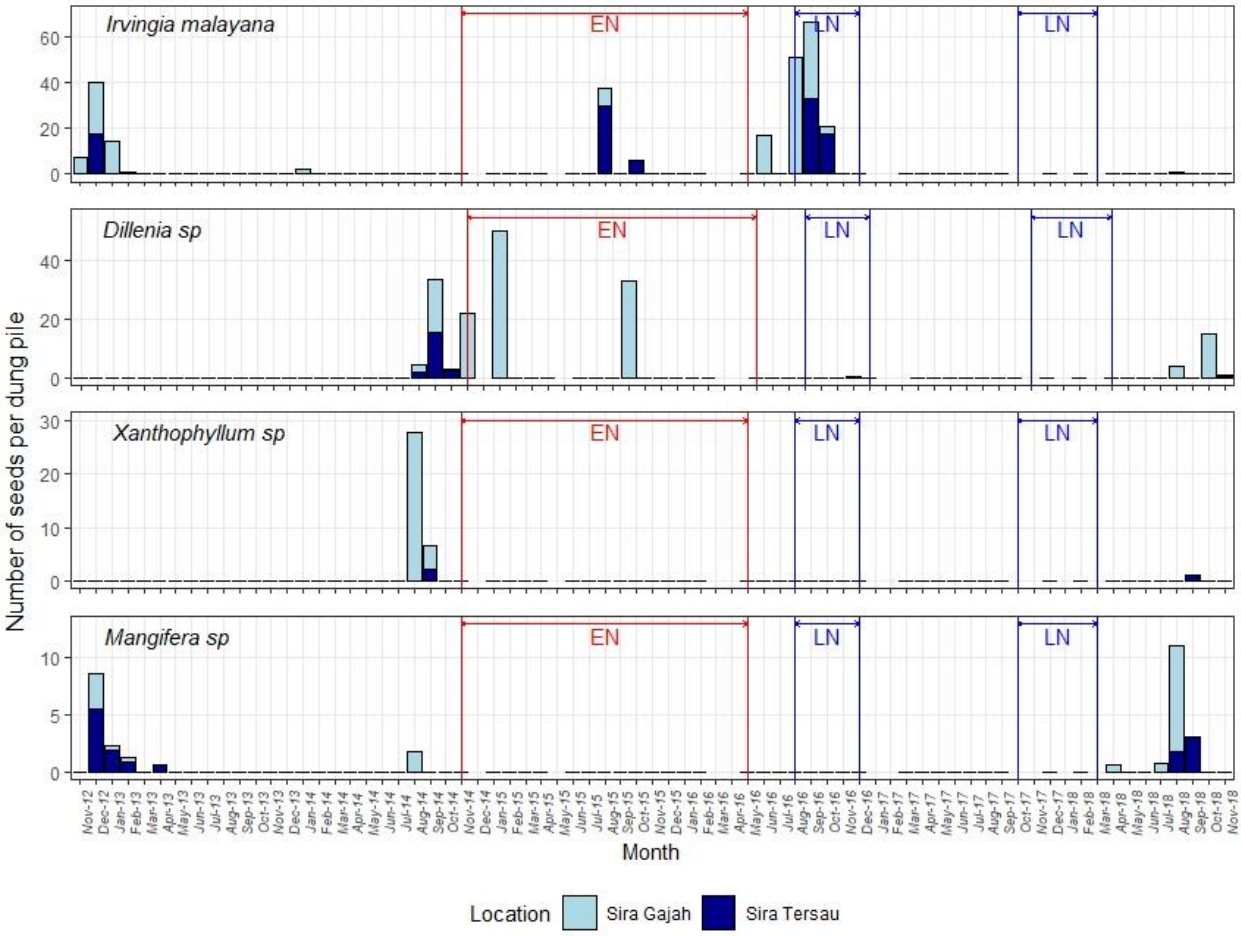


Figure 7: Example of seed temporal patterns in number of seeds per dung pile of four plants commonly dispersed by Asian elephants in our study.

Fruit traits - Based on literature review or field observations, the color for 30 fruits were compared (Table 1; Fig. 8). Green (50% of the fruits) was the most common fruit color, followed by brown (17%%), yellow (17%%), orange (10%), black-purple (3%), and red (3%; Fig. 8). Fruits of blue, white, and other colors were not observed to be eaten by elephants in this study.

Based on Guimarães et al.'s (2008) classification of megafaunal-syndrome fruits, I classified 15 megafaunal species; 13 exhibit Type 1 (mango-type) traits and two exhibit Type 2 (papaya-like) traits. A type 3 megafaunal syndrome trait was observed in nine morphospecies, resulting it a total of 24 megafaunal syndrome morphospecies (Table 1).

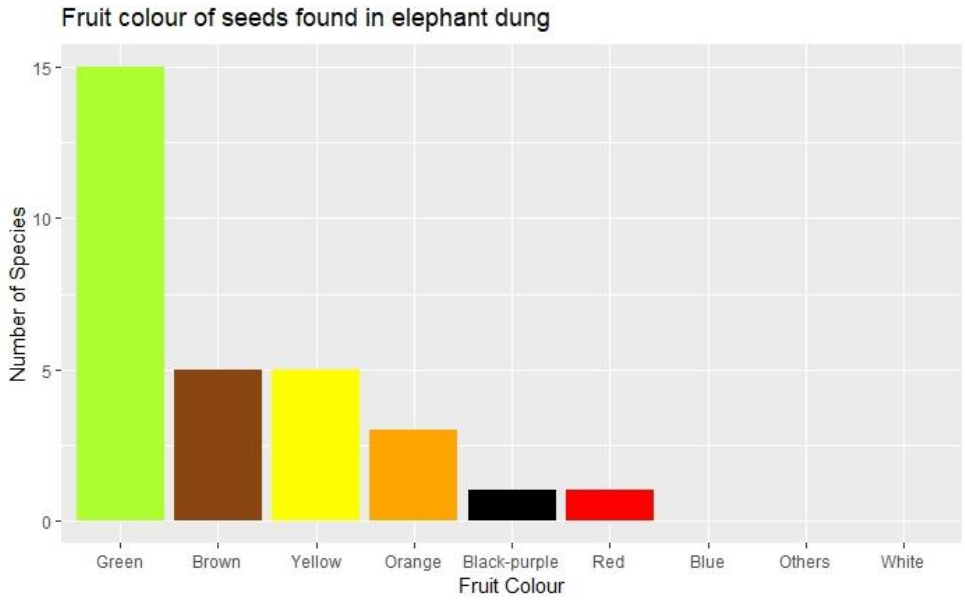


Figure 8: Distribution of fruit colors.

5.0 Discussion

I conducted long-term monitoring of the seeds dispersed by Asian elephants in the rainforests of northern Peninsular Malaysia. Asian elephants were found dispersed seeds of at least 45 different morphospecies from 25 plant families with high spatial heterogeneity and very irregular temporal peaks of frequency and diversity. Furthermore, over 53% of the species that were found to be dispersed can be classified as megafaunal-syndrome plants, suggesting to specialized rather than casual interactions between elephants and the plants they disperse. To my knowledge, this is the first detailed study on the seeds dispersed by a megaherbivore in the forests of the Sundaland.

Asian elephants were found to disperse seeds of a higher number of species than in previous studies, i.e. nine species in Thailand (Chanard et al., 1998; Kitamura et al., 2007), 29 species in central Myanmar (Campos-Arceiz et al. 2008a), 34 species in India's Western Ghats (Baskaran and Desai, 2013; Jothish, 2013), and 20 non-cultivated species in north-western Sri Lanka (Samansiri and Weerakoon, 2008). Some genera (e.g. *Artocarpus*, *Mangifera, Dillenia*; this study, Campos-Arceiz et al. 2008a, Jothish 2013, Sekar & Sukumar 2013, Sekar et al. 2015), and families (e.g. Anacardiaceae, Annonaceae, Arecaeae, Fabaceae, Moraceae, Poaceae; Campos-Arceiz & Blake 2011) seem to be commonly dispersed by elephants throughout the species range. In this study, I provide the first record from the family Polygalaceae were dispersed by elephants, and the first plants (two species) from the family Chrysobalanaceae were dispersed by elephants in Asia (this family was already known to be dispersed by African elephants; Campos-Arceiz & Blake 2011). Contrary to what happens in drier environments (e.g. Samansiri & Weerakoon 2008), in Malaysian rainforests the family Fabaceae accounted just for 4.4% (i.e. two) of the species dispersed by Asian elephants.

The two sampling sites, Sira Gajah and Sira Tersau, were remarkably dissimilar, with just 40% of the dispersed plant species being found in both locations despite being relatively close to each other (11.3 km away in straight-line). Some individual elephants were found to have visited both locations during the study period (Hii 2016). This indicates very high spatial heterogeneity in the seed rain generated by elephants in these forests. As noted by Fitri et al. (2017), the density

of fruit trees is very low in dipterocarp forest and the species composition is highly variable in space.

The temporal pattern of seeds found in Asian elephant dung throughout the 73-month study period reflects the irregular and – sometimes but not always – masting fruiting cycles of many plants in the Sundaic forests (Appanah 1985; Sakai et al. 1999). Similar patterns were observed in the frugivory and seed dispersal of sun bears in Borneo, as the remains of mast fruiting species were only recovered during two mast fruiting events throughout a 52-month study period (Fredriksson et al., 2006). No seeds were found in most (80.9%) of the dung piles and nearly half (49.3%) of the months sampled throughout the 73-month study period. This suggests an asymmetric relationship between elephants and the plants they disperse. I speculate that elephants are more important for these plants, especially those with megafaunal-syndrome, than the plants' fruit is for elephants, since it is a highly unreliable food resource. Some authors report that sun bears lose weight and body condition in the inter-mast periods (Wong et al. 2005). In Malaysia, however, elephants seem to retain a good body condition throughout the year and over the years, do not show seasonal changes in body condition (Campos-Arceiz, personal observation).

Phenology in Sundaland forests is complex and, in our case, it was not apparent what drove the presence of seeds in elephant dung. The presence of the most commonly dispersed morphospecies (e.g. *Dillenia* spp*., Irvingia malayana, Mangifera* spp.) did not seem to be driven by the ENSO phenomenon (Fig. 7). Some other species, however, such as *Xantophyllum* sp. and less commonly dispersed species, appeared to have been associated with El Niño phenomenon in 2014 (Figs. 6 and 7).

My observations on the temporal patterns of seed dispersal by Asian elephants in Malaysia are congruent with Fredriksson et al.'s (2006) stance on the importance of long term frugivory studies to account for the complex cycles and interannual masting episodes of trees in the forests of Sundaland. As the temporal presence of seeds in elephant dung varied substantially over time, any short survey (e.g. less than two years, as common for most postgraduate projects) would result in a misrepresentation of elephant frugivory and seed dispersal in these forests.

Even after 73-months of continuous monitoring, I only achieved 83% of sample completeness (Fig. 3).

According to my classification (Table 1), at least 53% of morphospecies dispersed by Asian elephants in northern Peninsular Malaysia can be considered as megafaunal-syndrome, indicating relatively high level of specialization in elephant-fruit interactions in this environment. This contrasts with the situation in South Asia, where there seems to be less specialized interactions (e.g. Samansiri & Weerakoon 2008). It is important to note that I did not follow Guimaraes et al. (2008) classification of megafaunal-syndrome plants in a strict way. Guimaraes et al. (2008) defined two types of megafaunal syndrome fruits: the mango-like Type I and the papaya-like Type II. In this case I added a Type III – species with large fruits and moderately large (> 1.5 cm) seeds in moderately large numbers (> 15). Examples are *Durio* spp. (durians) and *Artocarpus* spp. (jackfruit, cempedak) in Southeast Asia. Moreover, megafaunal syndrome fruits traits are represent in several unrelated plant families observed as noted in South America. However, the definition by Guimarães et al. (2008) is oversimplified as its only restricted to the physical traits of the fruits. One possible solution would be to revisit Alexandre (1978) description and categorisation of elephant fruits from Africa.

The color of ripe fruits consumed by Asian elephants in my study site were restricted within the ranges of green, orange-yellow, brown, and very few red or black (Fig. 5d). This pattern is consistent with that of fruits consumed by elephants in Thailand (Kitamura, 2007) and megafaunal-syndrome fruits in the Neotropics (Guimaraes et al. 2008). Asian elephants have dichromatic vision during the day and are therefore unable to distinguish red from green and orange from yellow (Yokoyama et al., 2005). This suggests that Asian elephants do not rely on visual cues but on their sensitive olfactory sense (Rizvanovic et al. 2013, Plotnik 2019) to find fruits on the forest floor. Fruits consumed by Asian elephants in Thailand emit a sweet aroma (Kitamura, 2007) and fruits like *Durio* spp., *Artocarpus* spp., *Mangifera* spp. and *Dillenia indica* emit a distinct pungent scent that is perceivable from a considerable distance (author, personal observation).

Although I did not attempt to test seed viability, I often germinated seeds for identification purposes or recorded when I found them germinating in elephant dung in the field. In total, I recorded more than half (24 out of 45) of the morphospecies germinating after elephant dispersal, showing that seeds were frequently viable and able to germinate rapidly after deposition. Some plants, including some dispersed in my study site (*Platymitra macrocapa:* McConkey et al. 2018; *Dillenia indica:* Sekar et al. 2015), have been found to increase their germination rates after passing through Asian elephant guts. Seeds defecated by elephants were invariably free from fruit pulp, a known inhibitor of germination (Traveset et al., 2007). Given that elephants in Peninsular Malaysia have mean daily movement distances of over 5 km (and up to 16 km; Jamie Wadey, unpublished data) I expect seeds to be dispersed on for several km from mother plants (Campos-Arceiz et al. 2008b). Seed viability and long dispersal distances reinforce the idea of elephants providing high-quality seed dispersal services in Sundanland's dipterocarp forests.

Besides the important ecological function, seed dispersal by elephants also provides important ecosystem services for people. At least 55% of the morphospecies dispersed by elephants in my study are of economic significance for timber or agriculture. *Instia palembanica* (merbau, Malaysia's designated national tree in 2019), for example, is a highly valued tropical timber species (Lee et al., 2002). Wild varieties of mango (*Mangifera* spp.), durian (*Durio* spp.), and cempedak (*Artocarpus integer*) provide important genetic resources for crop improvement and diversification of their domesticated relatives. Moreover, several species such as *P. timoriana* (forest petai; Angami et al. 2018), *S. koetjape* (sentul; Narendra et al. 2013), *I. malayana* (wild almond; Cruz-Garcia & Price 2011), *Artocarpus* spp. (jackfruit relatives; Gajaseni & Gajaseni 1999), *D. indica* (elephant apple; Sekar & Sukumar 2013), and *D. dao* (Pacific walnut; Van Hoang et al. 2008) are either cultivated or their wild fruits harvested as a source of income by villagers around Southeast Asia. This shows the intricated relationships between wildlife, plants, and people, especially indigenous communities, in the region.

Seed predation by vertebrates on dung piles were observed on several occasions but were not recorded quantitatively. The large seeds of species like *Irvingia malayana* and *Mangifera* spp. were deposited in large clumps that may attract seed predators (Kitamura et al. 2007; Ong et al.

2019). Based on footprints and bite marks, wild boars (*Sus scrofa*) and porcupines (Family Hystricidae) seemed to have predated on seeds in elephant dung. Large seeds like *I. malayana* and *M. maingayi* were either hollowed or split opened with their kernel consumed. Smaller seeds like *Parkia timoraina* and *Chrysophallum burkilii* were consumed whole. Seed predation by porcupines was also observed in Thailand (Kitamura et al., 2007) while jungle fowl and small carnivores like mongoose were found to break open elephant dung in Sri Lanka (Samansiri and Weerakoon, 2008). Foraging in elephant dung is a widespread phenomenon, with seeds being an important food source for several vertebrates (Magliocca et al., 2003). Moreover, some seeds are likely to be ingested intact or hoarded, resulting in secondary dispersal.

This study has several caveats worth discussing. First, I was unable to identify all the seeds to the species or genus level. This could have been solved by germinating more seeds to identify the seedlings. In our case I started to germinate late in the study (~2016) due to resource limitations earlier in the project. Second, I did not monitor tree fruiting phenology while we surveyed the presence of seeds in elephant dung. For future studies it would be preferable to monitor both phenomena simultaneously (but I realize the logistical challenge of conducting such work in tropical rainforests). Third, given the dissimilarity between sites, I suspect that I would need to sample a higher number of locations, even within a single landscape, to achieve a more complete understanding of the diversity of plant species dispersed by elephants. I sampled for 73 continuous months, to my knowledge the longest continuous study of these characteristics in Asia and reached 83% sample completeness for the both sites I monitored. Future studies could also focus on the effect of elephant consumption on seed viability, seed fate of seeds dispersed by elephants, or the spatial patterns of elephant seed deposition in Sundaic forests.

Given the importance of Asian elephants as seed dispersers for Southeast Asian megafaunal-syndrome trees (e.g. *Platymitra macrocarpa*: McConkey et al. 2018; *Irvingia malayana*: Ong et al. 2019), the ongoing loss of these megaherbivores in many forests will have severe negative cascading effects on these plants (e.g. Pires et al. 2018) and potentially other species. Formerly sympatric megaherbivores like the Javan (*Rhinoceros sondaicus*) and Sumatran rhinos are ecologically extinct in all but a handful of forests (Brook et al. 2012, Brandt et al. 2018), leaving Asian elephants as the only effective megaherbivore seed disperser in the region

(Campos-Arceiz et al. 2012, Sekar et al. 2015). Several studies have demonstrated the inability of other large mammals such as tapirs (Campos-Arceiz et al., 2012) and bovids (Sekar et al., 2015) in effectively replacing Asian elephants as seed dispersers. The loss of key dispersers will have negative cascading effects on plant demography as the reduction in gene flow results with populations becoming increasingly genetically homogenous with their neighbours (Pérez-Méndez et al., 2016) and limits dispersal distance and area (Guimarães et al., 2008). For example, seed recruitment of *Balanites wilsoniana* was very poor in the absences of their sole dispersers, African forest elephants (Babweteera et al., 2007). Protecting and restoring, where appropriate, Asian elephant populations and the non-redundant ecological function they bring to Sundaland forests should therefore be a high priority for conservation scientists, agencies, and donors.

6.0 References

1. Ahmad Fitri, Z., Latiff, A., Nizam, M.S., Abdul Rahman, K., Serafina Christine, F., Shamsudin, I., 2017. Wild fruit trees in an upper hill dipterocarp forest at Temengor Forest Reserve, Perak, Malaysia. Malaysian For. 80, 129–135.
2. Aiken, S.R., Leigh, C.H., 1988. Environment and the federal government in Malaysia. Appl. Geogr. 8, 291–314. https://doi.org/10.1016/0143-6228(88)90037-9
3. Alexandre, D.-Y., 1978. Le role disseminatuer des elephants en Foret de Tai, Cote d'Ivoire. Rev. d'Ecologie (Terre Vie) 32, 47–72.
4. Angami, T., Bhagawati, R., Touthang, L., Makdoh, B., Nirmal, Lungmuana, Bharati, K.A., Silambarasan, R., Ayyanar, M., 2018. Traditional uses, phytochemistry and biological activities of *Parkia timoriana* (DC.) Merr., an underutilized multipurpose tree bean: a review. Genet. Resour. Crop Evol. 65, 679–692. https://doi.org/10.1007/s10722-017-0595-0
5. Appanah, S., 1985. General flowering in the climax rain forests of South-east Asia. J. Trop. Ecol. 1, 225–240. https://doi.org/10.1017/S0266467400000304
6. Ashton, P. S., 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. Ann. Rev. Eco. Syst. 19:1, 347-370. https://doi.org/10.1146/annurev.es.19.110188.002023
7. Babweteera, F., Savill, P., Brown, N., 2007. *Balanites wilsoniana*: Regeneration with and without elephants. Biol. Conserv. 134, 40–47. https://doi.org/10.1016/j.biocon.2006.08.002
8. Baskaran, N., Desai, A.A., 2013. Frugivory and seed dispersal by the Asian elephant *Elephas maximus* in the tropical forests of Nilgiri Biosphere Reserve , southern India. J. Threat. Taxa 5, 4893–4897. https://doi.org/10.11609/JoTT.o2848.4893-7
9. Blake, S., Deem, S.L., Mossimbo, E., Maisels, F., Walsh, P., 2009. Forest elephants: Tree planters of the Congo. Biotropica 41, 459–468. https://doi.org/10.1111/j.1744-7429.2009.00512.x
10. Blake, S., Hedges, S., 2004. Sinking the flagship: the case of forest elephants in Asia and Africa. Conserv. Biol. 18, 1191-1202. https://doi.org/10.1111/j.1523-1739.2004.01860.x

11. Brandt, J.R., De Groot, P.J.V.C., Witt, K.E., Engelbrektsson, P.K., Helgen, K.M., Malhi, R.S., Ryder, O.A., Roca, A.L., 2018. Genetic Structure and Diversity Among Historic and Modern Populations of the Sumatran Rhinoceros (*Dicerorhinus sumatrensis*). J. Hered. 109, 553–565. https://doi.org/10.1093/jhered/esy019
12. Brook, S.M., Dudley, N., Mahood, S.P., Polet, G., Williams, A.C., Duckworth, J.W., Van Ngoc, T., Long, B., 2014. Lessons learned from the loss of a flagship: The extinction of the Javan rhinoceros Rhinoceros sondaicus annamiticus from Vietnam. Biol. Conserv. 174, 21–29. https://doi.org/10.1016/j.biocon.2014.03.014
13. Campos-Arceiz, A., Lin, T.Z., Htun, W., Takatsuki, S., Leimgruber, P., 2008. Working with mahouts to explore the diet of work elephants in Myanmar (Burma). Ecol. Res. 23, 1057–1064. https://doi.org/10.1007/s11284-008-0466-4
14. Campos-Arceiz, A., Traeholt, C., Jaffar, R., Santamaria, L., Corlett, R.T., 2012. Asian tapirs are no elephants when it comes to seed dispersal. Biotropica 44, 220–227. https://doi.org/10.1111/j.1744-7429.2011.00784.x
15. Chanard, T., Posang, T., Wongkalasin, W., 1998. Distribution of wild Asian elephants (*Elephas maximus)* in Phu Luang Wildlife Sanctuary, Thailand. Nat. Hist. Bul. Siam Soc. 46, 17–26.
16. Chen, J., Deng, X.B., Zhang, L., Bai, Z.L., 2006. Diet composition and foraging ecology of Asian elephants in Shangyong, Xishuangbanna, China. Acta Ecol. Sin. 26, 309–316. https://doi.org/10.1016/S1872-2032(06)60006-1
17. Chen, Y.Y., Satake, A., Sun, I.F., Kosugi, Y., Tani, M., Numata, S., Hubbell, S.P., Fletcher, C., Nur Supardi, M.N., Wright, S.J., 2018. Species-specific flowering cues among general flowering Shorea species at the Pasoh Research Forest, Malaysia. J. Ecol. 106, 586–598. https://doi.org/10.1111/1365-2745.12836
18. Chua LSL, Kamarudin S & Damahuri S (2000) A preliminary checklist of seed plants of the Belum Forest Reserve, Perak, Peninsular Malaysia. Malayan Nature Journal, 54(3): 171–186.
19. Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in forest trees. In: Dynamics of Populations (eds Den Boer PJ,

Gradwell GR), pp. 298–312. Centre for Agricultural Publishing and Documentation, Wageningen.

20. Corlett, R.T., 2017. Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. Glob. Ecol. Conserv. 11, 1–22. https://doi.org/10.1016/j.gecco.2017.04.007
21. Cruz-Garcia, G.S., Price, L.L., 2011. Ethnobotanical investigation of "wild" food plants used by rice farmers in Kalasin, Northeast Thailand. J. Ethnobiol. Ethnomed. 7. https://doi.org/10.1186/1746-4269-7-33
22. DWNP. 2012. Laporan Tahunan Jabatan PERHILITAN 2012. Kuala Lumpur: Department of Wildlife and National Parks, Peninsular Malaysia.
23. Feer, F., 1995. Morphology of fruits dispersed by African forest elephants. Afr. J. Ecol. 33, 279–284. https://doi.org/10.1111/j.1365-2028.1995.tb00808.x
24. Fredriksson, G.M., Wich, S.A., Trisno, 2006. Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. Biol. J. Linn. Soc. 89, 489–508. https://doi.org/10.1111/j.1095-8312.2006.00688.x
25. Gajaseni, J., Gajaseni, N., 1999. Ecological rationalities of the traditional homegarden system in the Chao Phraya Basin, Thailand. Agrofor. Syst. 46, 3–23. https://doi.org/10.1023/A:1006188504677
26. Guimarães, P.R., Galetti, M., Jordano, P., 2008. Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. PLoS One 3. https://doi.org/10.1371/journal.pone.0001745
27. Hii, Ning (2017) Asian elephants' social structure and mineral lick usage in a Malaysian rainforest using camera traps. University of Nottingham Malaysia Campus.
28. Howe, H.F., 1985. Gomphothere fruits: A critique. Am. Nat. 125, 853–865. https://doi.org/10.1086/284383
29. Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221
30. Hsieh, T. C., Ma, K. H., Chao, Anne., 2019. iNEXT: iNterpolation and EXTrapolation for

species diversity. R package version 2.0.19 URL: http://chao.stat.nthu.edu.tw/blog/software-download/.

31. Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104, 501–528.
32. Janzen, D.H., Martin, P.S., 1982. Neotropical anachronisms : The fruits the gomphotheres ate. Science (80). 215, 19–27.
33. Jothish, P.S., 2013. Frugivory and seed dispersal of woody species by the Asian elephant (*Elephas maximus*) in a mid-elevation tropical evergreen forest in India. J. Trop. Ecol. 29, 181–185. https://doi.org/10.1017/S0266467413000060
34. Kitamura, S., Yumoto, T., Poonswad, P., Wohandee, P., 2007. Frugivory and seed dispersal by Asian elephants, *Elephas maximus*, in a moist evergreen forest of Thailand. J. Trop. Ecol. 23, 373–376. https://doi.org/10.1017/S0266467407004026
35. Kurten, E.L., Bunyavejchewin, S., Davies, S.J., 2018. Phenology of a dipterocarp forest with seasonal drought: Insights into the origin of general flowering. J. Ecol. 106, 126–136. https://doi.org/10.1111/1365-2745.12858
36. Lee, S.L., Ng, K.K.S., Saw, L.G., Norwati, A., Salwana, M.H.S., Lee, C.T., Norwati, M., 2002. Population genetics of *Intsia palembanica* (Leguminosae) and genetic conservation of Virgin Jungle Reserves in Peninsular Malaysia. Am. J. Bot. 89, 447–459. https://doi.org/10.3732/ajb.89.3.447
37. Lim KC (2010) Belum-Temengor Forest Complex, north Peninsular Malaysia. BirdingAsia, 14, 15–22.
38. Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proc. Natl. Acad. Sci. U. S. A. 113, 838–846. https://doi.org/10.1073/pnas.1502540113
39. Magliocca, F., Queroli, S., Gautier-Hion, A., 2003. Seed eating in elephant dung by two large mammals in the Congo Republic. Rev. d'Ecologie (Terre Vie) 58, 143–149.
40. McConkey, K.R., Brockelman, W.Y., 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. Ecology 92, 1492–1502. https://doi.org/10.1890/10-1255.1

41. McConkey, K.R., Nathalang, A., Brockelman, W.Y., Saralamba, C., Santon, J., Matmoon, U., Somnuk, R., Srinoppawan, K., 2018. Different megafauna vary in their seed dispersal effectiveness of the megafaunal fruit *Platymitra macrocarpa* (Annonaceae). PLoS One 13, 1–18. https://doi.org/10.1371/journal.pone.0198960
42. McKay, George M. 1973. "Behavior and ecology of the Asiatic elephant in southeastern Ceylon." Smithsonian Contributions to Zoology. 1–113. https://doi.org/10.5479/si.00810282.125
43. Medway L. 1972. Phenology of a tropical rain forest in Malaya. Biol J Linn Soc 4: 117–146. https://doi.org/10.1111/j.1095-8312.1972.tb00692.x
44. Miettinen, J., Shi, C., Liew, S.C., 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Glob. Chang. Biol. 17, 2261–2270. https://doi.org/10.1111/j.1365-2486.2011.02398.x
45. Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/doi.org/10.1038/35002501
46. Narendra, B.H., Roshetko, J.M., Tata, H.L., Mulyoutami, E., 2013. Prioritizing underutilized tree species for domestication in smallholder systems of West Java. Small-scale For. 12, 519–538. https://doi.org/10.1007/s11842-012-9227-x
47. Numata, S., Yasuda, M., Suzuki, R.O., Hosaka, T., Noor, N.S.M., Fletcher, C.D., Hashim, M., 2013. Geographical pattern and environmental correlates of regional-scale general flowering in Peninsular Malaysia. PLoS One 8. https://doi.org/10.1371/journal.pone.0079095
48. Oksanen, J., Blanchet, F.J., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan
49. Oliver, R.C.D., 1978. On the ecology of the Asian elephant *Elephas maximus* Linn, with particular reference to Malaya and Sri Lanka. University of Cambridge.

50. Ong, L., McConkey, K., Solana-Mena, A., Campos-Arceiz, A., 2019. Elephant frugivory and wild boar seed predation of irvingia malayana, a large-fruited tree, in a rainforest of peninsular Malaysia. Raffles Bull. Zool. 67, 160–170. https://doi.org/10.26107/RBZ-2019-0013
51. Pérez-Méndez, N., Jordano, P., García, C., Valido, A., 2016. The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. Sci. Rep. 6, 1–9. https://doi.org/10.1038/srep24820
52. Pires, M.M., Guimarães, P.R., Galetti, M., Jordano, P., 2018. Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. Ecography, 41, 153–163. https://doi.org/10.1111/ecog.03163
53. Plotnik, J.M., Brubaker, D. L., Dale, R., Tiller, L. N., Mumby, H. S., Clayton, N. S., 2019. Elephants have a nose for quantity. PNAS 116 (25) 12566-12571; DOI: 10.1073/pnas.1818284116
54. Rizvanovic, A., Amundin, M., Laska, M., 2013. Olfactory discrimination ability of Asian elephants (*Elephas maximus*) for structurally related odorants. Chem. Senses 38, 107–118. https://doi.org/10.1093/chemse/bjs097
55. R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
56. Saaban, S., Othman, N. bin, Yasak, M.N. bin, Nor, B.M., Zafir, A., Campos-Arceiz, A., 2011. Current status of Asian elephants in Peninsular Malaysia. Gajah 35, 67–75. https://doi.org/10.1016/j.ajhg.2012.05.023
57. Samansiri, K. a P., Weerakoon, D.K., 2008. A study on the seed dispersal capability of Asian elephants in the northwestern region of Sri Lanka. Gajah 28, 19–24.
58. Sakai, S., 2002. General flowering in lowland mixed dipterocarp forests of South-east Asia. Biol. J. Linn. Soc. 75, 233–247. https://doi.org/10.1046/j.1095-8312.2002.00016.x
59. Sekar, N., Lee, C.L., Sukumar, R., 2015. In the elephant's seed shadow: the prospects of domestic bovids as replacement dispersers of three tropical Asian trees. Ecology 96, 2093–2105. https://doi.org/10.1890/14-1543.1
60. Sekar, N., Sukumar, R., 2013. Waiting for gajah: An elephant mutualist's contingency

plan for an endangered megafaunal disperser. J. Ecol. 101, 1379–1388. https://doi.org/10.1111/1365-2745.12157

61. Sukumar, R. (1990) “Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns,” *Journal of Tropical Ecology*, 6(1), pp. 33–53. https://doi.org/10.1017/S0266467400004004
62. Surovell, T., Waguespack, N., Brantingham, P.J., 2005. Global archaeological evidence for proboscidean overkill. Proc. Natl. Acad. Sci. U.S.A. 102, 6231e6236.
63. Terborgh, J., Davenport, L.C., Ong, L., Campos-Arceiz, A., 2018. Foraging impacts of Asian megafauna on tropical rain forest structure and biodiversity. Biotropica 50, 84–89. https://doi.org/10.1111/btp.12488
64. Theuerkauf, J., Waitkuwait, W.E., Guiro, Y., Ellenberg, H., Porembski, S., 2000. Diet of forest elephants and their role in seed dispersal in the Bossematié forest reserve, ivory coast. Mammalia 64, 447–460. https://doi.org/10.1515/mamm.2000.64.4.447
65. Traveset, A., Robertson, A.W., Rodríguez-Pérez, J., 2007. A review on the role of endozoochory in seed germination. Seed dispersal theory its application in a changing world. 78–103. https://doi.org/10.1079/9781845931650.0078
66. White, L.J.T., Tutin, C.E., Fernandez, M., 1993. Group composition and diet of forest elephants *Loxodonta africana cyclotis*. Afr. J. Ecol. 31, 181–189.
67. Whitmore, T 1972, *Tree flora of Malaya : a manual for foresters. Volume 1*, Longman Malaysia, Kuala Lumpur
68. Wickham, H., 2017. tidyverse: Easily Install and Load the 'Tidyverse'. R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse
69. Wong, S. Te, Servheen, C., Ambu, L., Ahmad, N., 2005. Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. J. Trop. Ecol. 21, 627–639. https://doi.org/10.1017/S0266467405002622
70. Vancuylenberg, B.W.B., 1977. Feeding behaviour of the Asiatic elephant in Southeast Sri Lanka in relation to conservation. Biol. Conserv. 12, 33-54
71. Van Hoang, S., Baas, P., Keßler, P.J.A., 2008. Uses and conservation of plant species in a national park - A case study of Ben En, Vietnam. Econ. Bot. 62, 574–593.

https://doi.org/10.1007/s12231-008-9056-1

72. Yokoyama, S., Takenaka, N., Agnew, D.W., Shoshani, J., 2005. Elephants and human color-blind deuteranopes have identical sets of visual pigments. Genetics 170, 335–344. https://doi.org/10.1534/genetics.104.039511

7.0 Supplementary Information

7.1 Supplementary Graphs

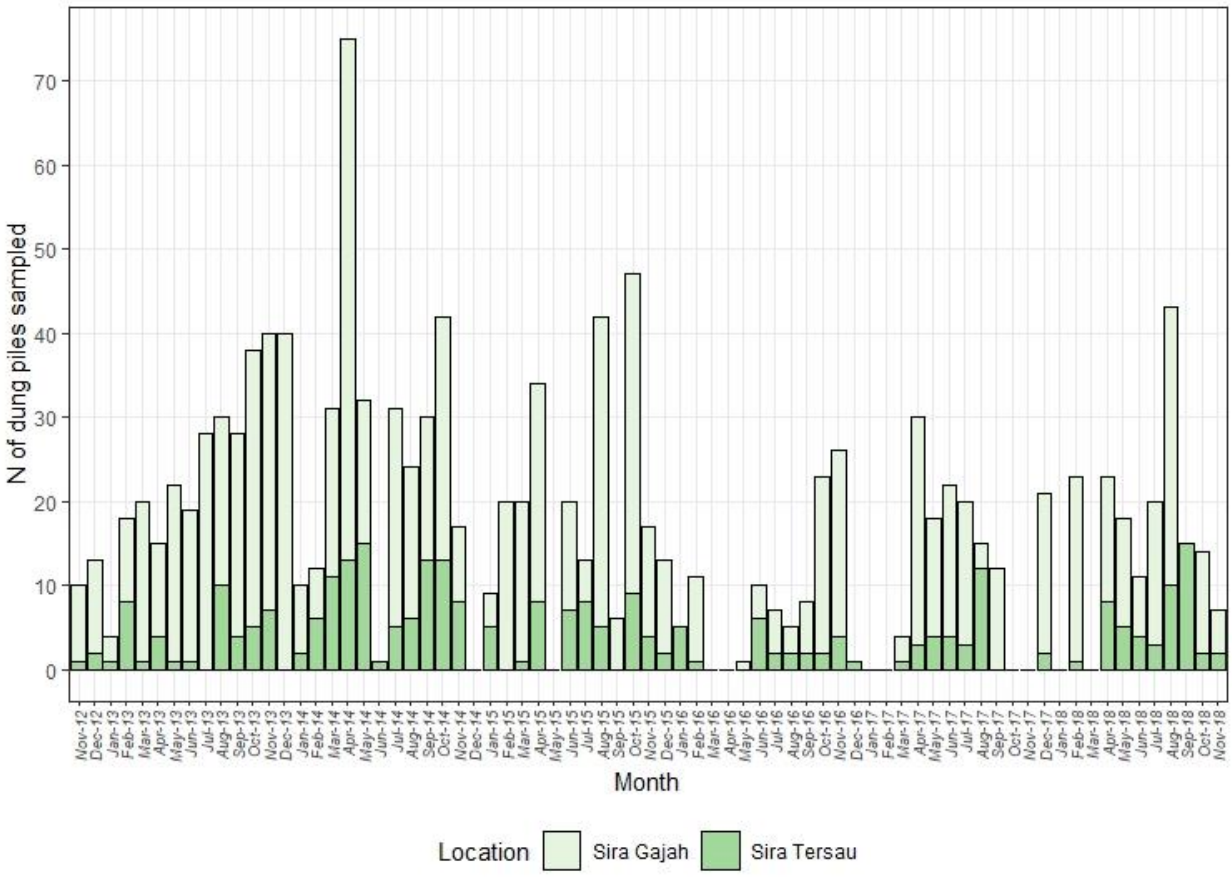


Figure S1: Number of trips per month to Sira Gajah and Sira Tersau.

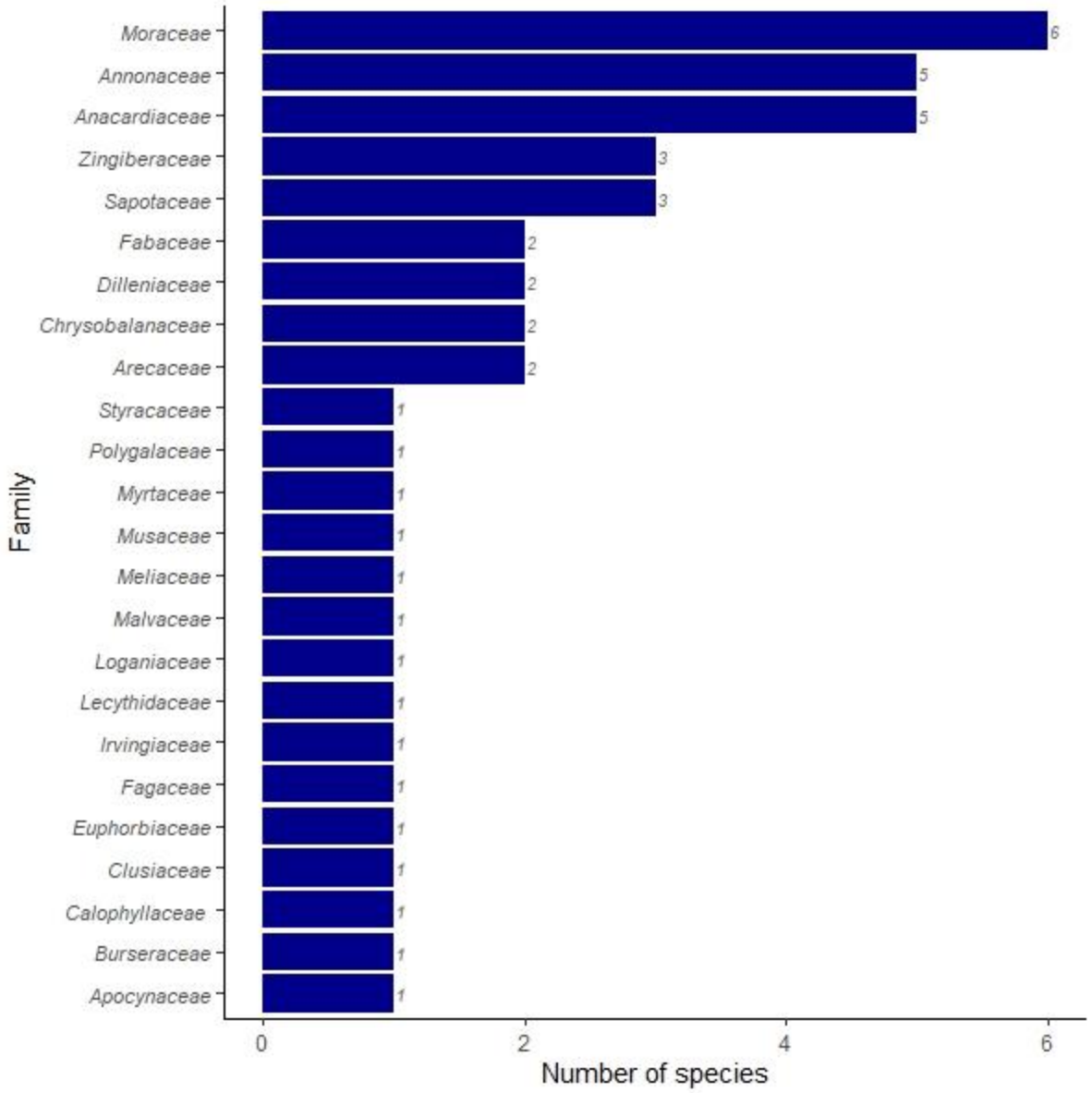


Figure S2: Distribution of species richness per family.

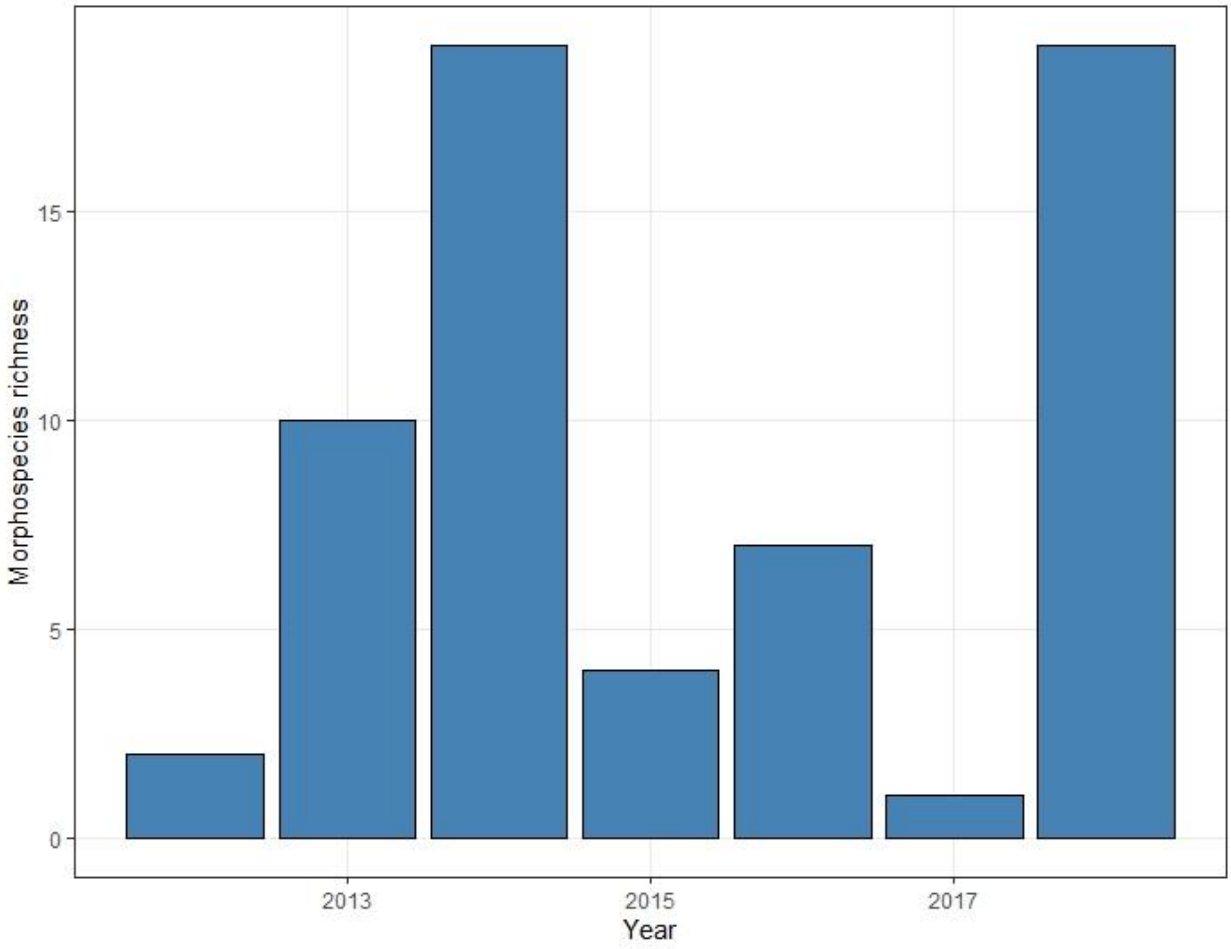


Figure S2: Morphospecies richness per year.

7.2 Sequences

P1- *Diploknema* cf *sebifera*

TTTATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCG
AAGCCATTAGGCCGAGGGCACGCCTGCCTGGGCGTCTCACATCGTGTCGCCCCCCAAACCTGTGCCCGC
AAAGGGTTCTTGGGTTGAGGGGGCGGATTTTGGCCCCCCGTGTGCCCTACTTCGCGGTCGGCCTAAATG
TGTAAGTCCTGGGCAACAAACGTCACGACAAGTGGTGGATGTGTGATACCTTTGCGTCCGTCGTGCACG
TCTTGACCCCCCGGGTTGTTTCGTTTTTGACCCTAAAGCACCGTTTCCACGGAGCCTCGATTGCGACCCCA
GGTCAGGCGGGATTACCCGCTGAGTTTAAGCATATCAATAAGCGGAGGAAAAGAAACTTACAAGGATT
CCCTTAGTAACGGCGAGCGAACCGGGAATAAGCCCAGCTTGAAAATCGTGCGGCCTCGCCGTTCGAATT
GTAGTCTGGAGAAGCGTCAA

P2 – *Xanthophyllum* sp.

TTTATGCGATACTTGTGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCGCCC
GAAGCCTTCGGGCCGAGGGTACGTCTGCCTGGGCGTCACGCACAGTCGTCCCCGTCGCACCGTCTCTGC
GGTGAAGGCGAGGGGCTGGATGTTGGTCTCCCGCGAGCCGCGACTCGCGGATGGCTTAAAATTGTAGT
CCGCGACGCCGTACACCGCGCCGCATGGTGGATGAGTAAACCTCGAGACCCGTGGCGGGTGTTGTCGC
GGTCTGGCACGACCCTGGTGCGCCGTTGGTGGCGCCTTTCGACGCGACCCCAGGTCAGGCGGGACTAC
CCGCTGAGTTTAAGCATATCAATAAGCGGAGGAAAAGAAACTTACGAGGATTCCCCTAGTAACGGCGA
GCGAACCGGGAAGAGCCCACGATGAGAATCGGCNCSTCCTTTCGGCGGTCCGAATTGTAGTCTGGAAG
AAGCGTCAAT

7.3 Species Profile

Anacardiaceae

1. *Bouea* sp.
   Common name: Setar



Plate 1: A) Seed in skin remnant, B) Seedling

2. *Dracotomelon dao*
   Common name: Buah senkuang, Pacific walnut



Plate 2: Seeds

3. *Mangifera maingayi*

Common name: Wild mango

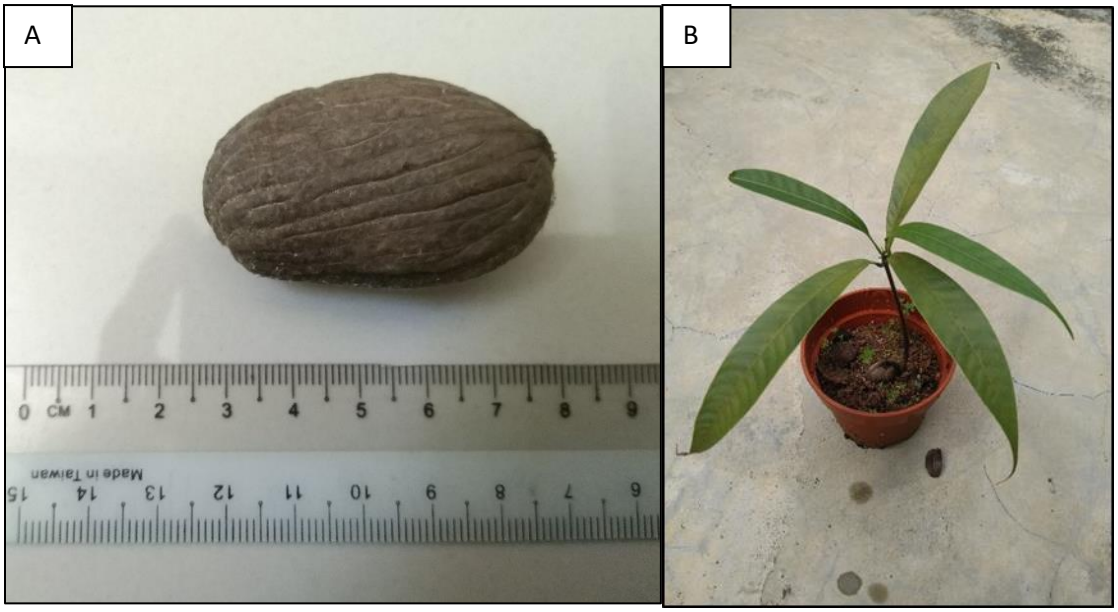


Plate 3: A) Seed; B) Seedling

4. *Mangifera* spp.
   Common name: wild mango

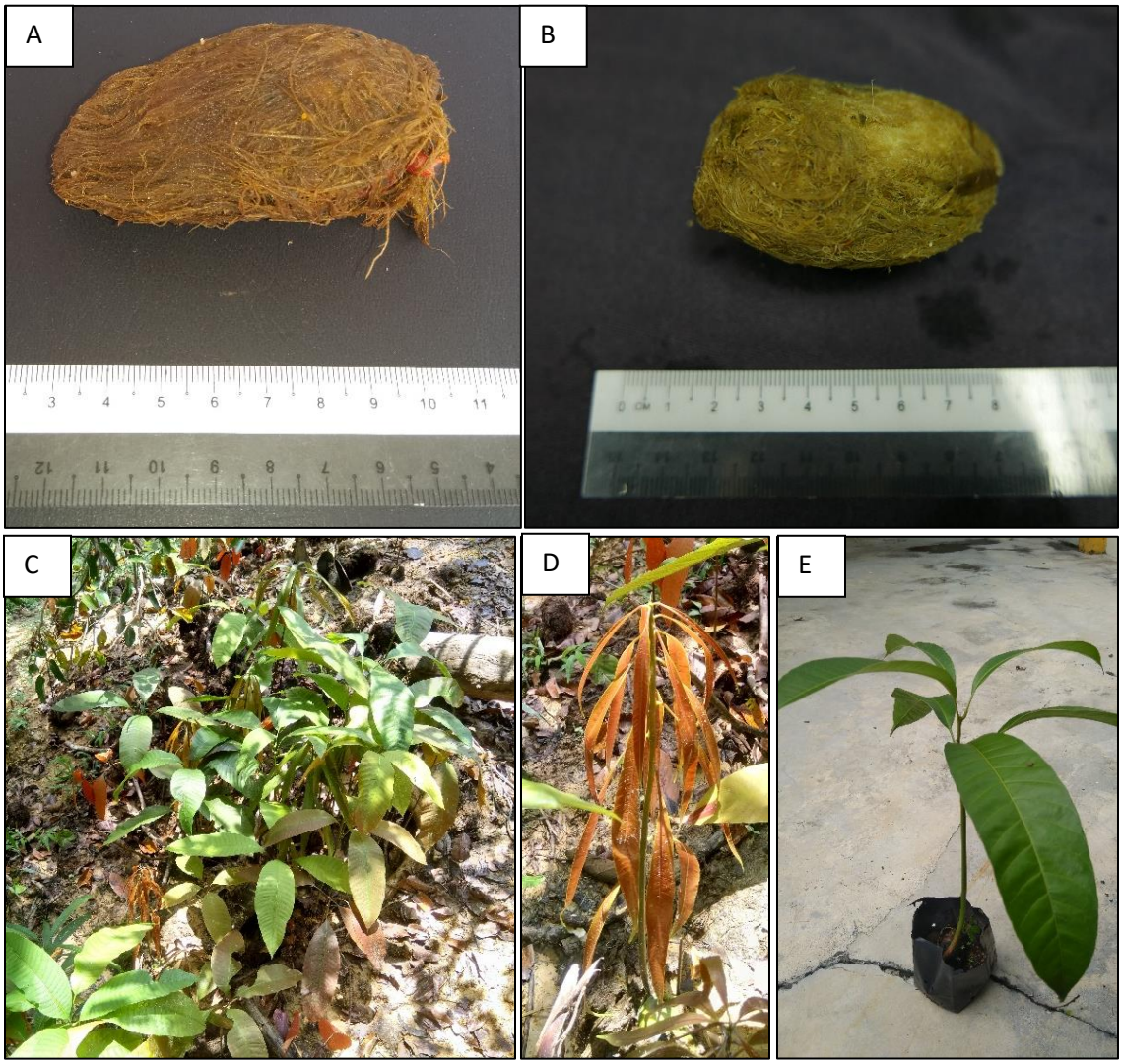


Plate 4: A & B) Seeds of *Mangifera* spp., C) clump of seedlings, C) *Mangifera* sp1, D) Mangifera sp2

Annonaceae

1. Monocarpia marginalis
   Common name: Mempisang tangbai



Plate 5: Seeds

2. *Mezzetia* sp.
   Common name: kemlem



Plate 6: Seeds

3. *Platymitra macrocarpa*

   Common name: Mempisang binak



Plate 7: A) Seed, B) Seeds in fruit

4. Unknown



Plate 8: seed (Photo by Anders)

5. Unknown

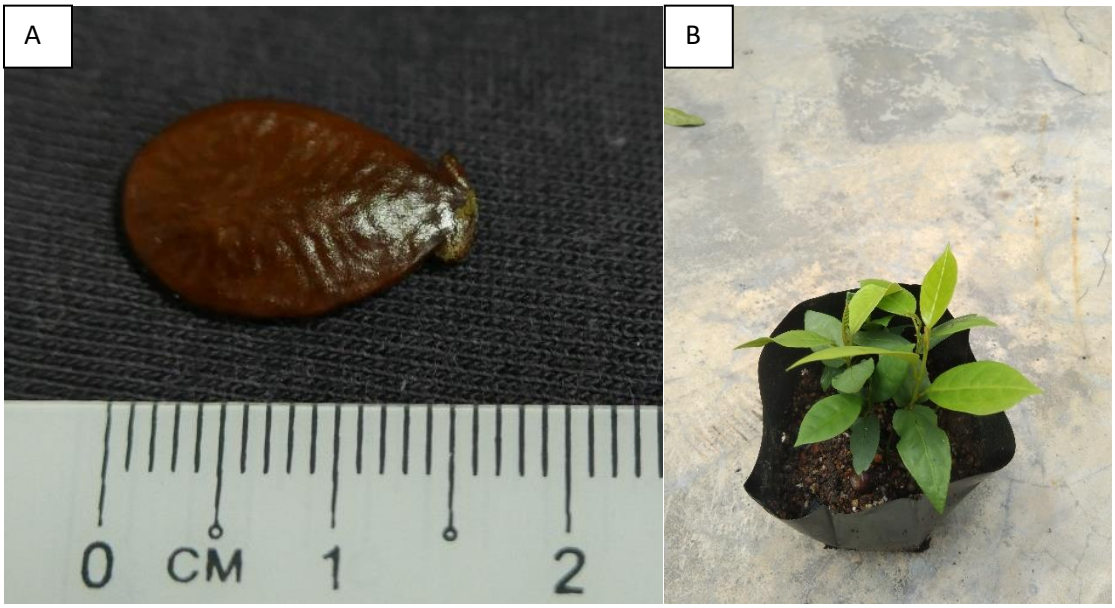


Plate 9: A) Seed, B) Seedlings

Apocynaceae

1. *Willughbeia* sp.
   Common name: none



Plate 9: Seed

Arecaceae

1. *Borassus flabellifer*



Plate 10: A) Seed in dung, B) Seed with scale (Photo credits: Ahimsa)

2. *Orania sylvicola*
   Common name: Ibul



Plate 11: A) Seed, B) Fresh Fruit

Burseraceae

1. *Caranium littorale*
   Common name: kedondong



Plate 12: A) Seed, B) Split seed

Calophyllaceae

1. *Callophyllum macrocarpum*
   Common name: Bintangor



Plate 13: A) Seed, B) whole fruit, C) Halved fruit with intact seed

Chrysobalanaceae

1. *Parinari oblongifolia*
   Common name: Merbatu



Plate 14: Seed

2. *Parinari* sp.



Plate 15: Seeds

Clusiaceae

1. *Garcinia* sp.



Plate 16: Seed

Dilleniaceae

1. *Dillenia* spp.
   Common name: Simpoh, elephant apple

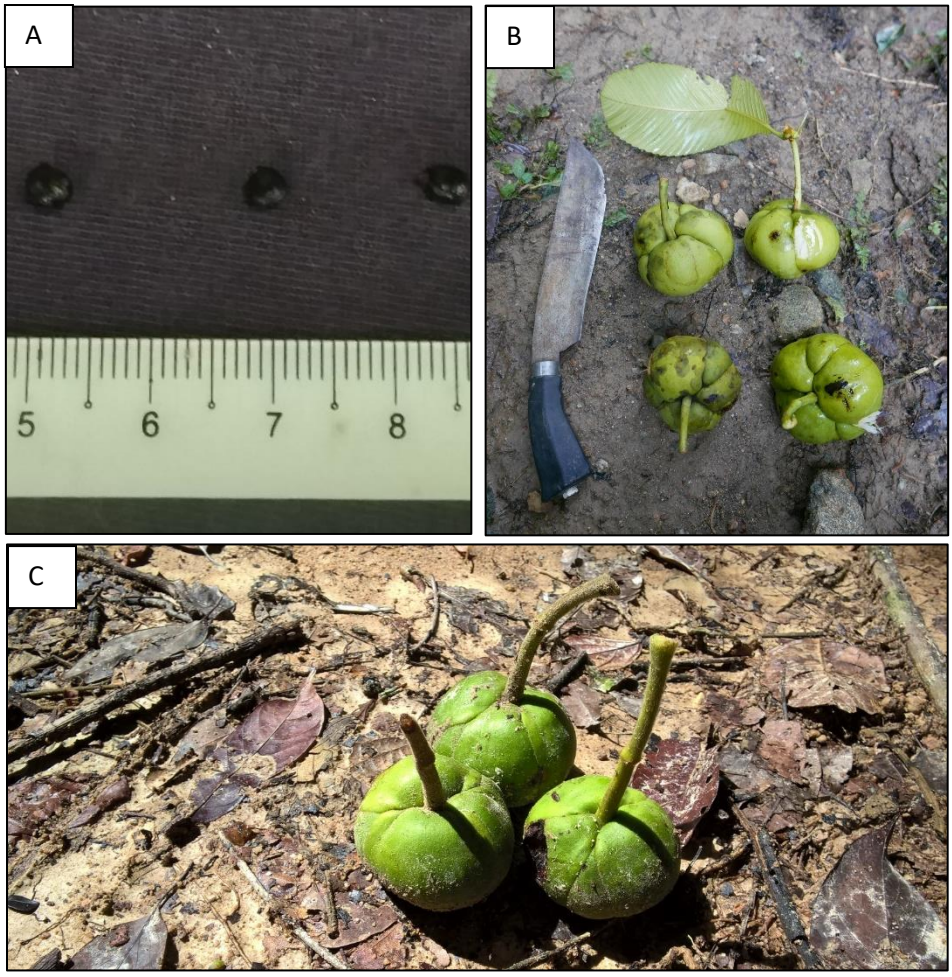


Plate 17: A) Seeds, B) Fruits of *Dillenia indica*, C) Fruits of *Dillenia reticulata*

Euphorbiaceae

1. *Baccaurea* sp.



Plate 18: Seeds and fruit of *Baccaurea* sp.

Fabaceae

1. *Intsia palembanica*
   Common name: Merbau



Plate 19: Seed

2. *Parkia timoriana*
   Common name: Petai hutan

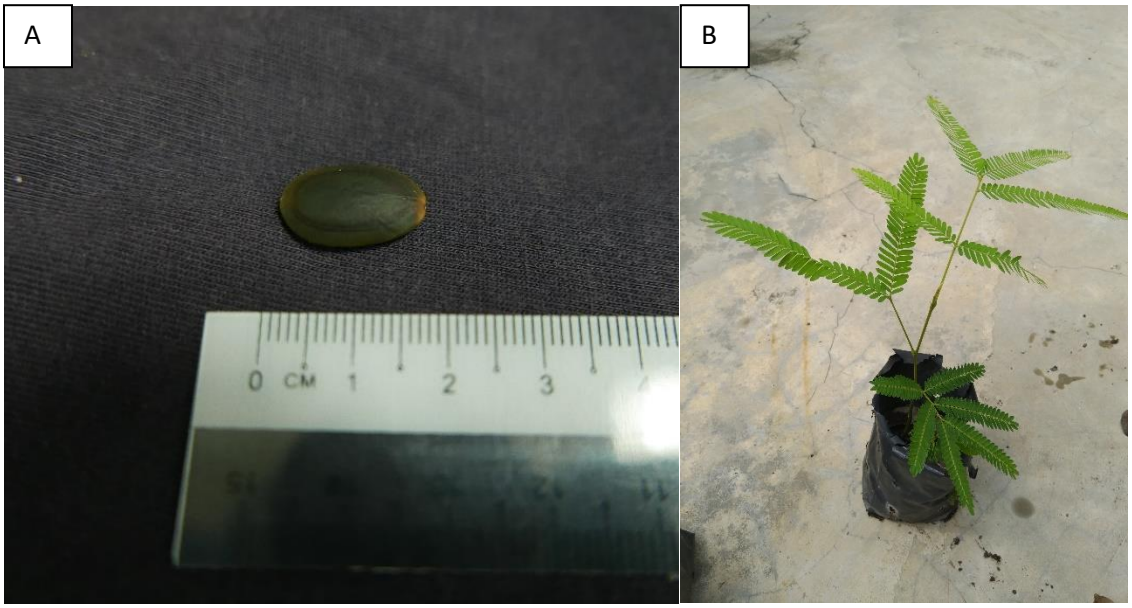


Plate 20: A) Seed B) Seedling

Fagaceae

1. *Lithocarpus kuntsleri*
   Common name: Oak



Plate 21: Acorns

Irvingiaceae

1. *Irvingia malayana*
   Common name: Barking deer's mango, Asian almond

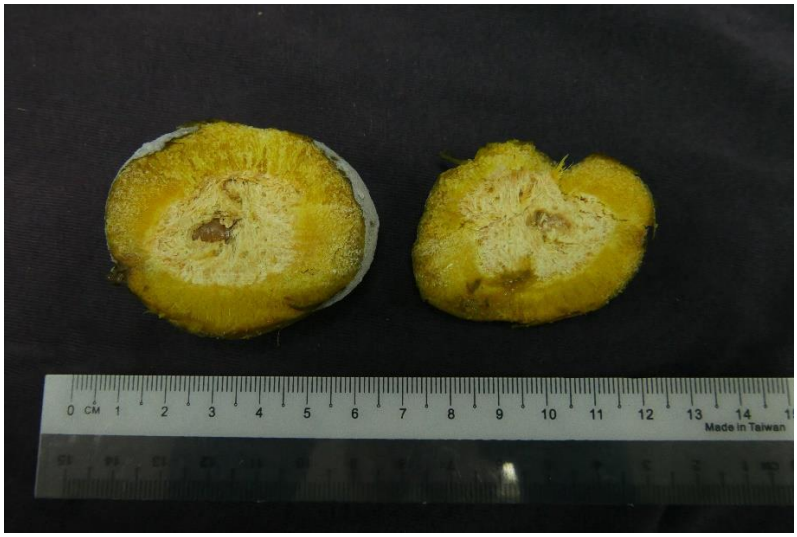


Plate 22: Halved fruit

Lecythidaceae

1. *Barringtonia* sp.



Plate 23: Seed

Loganiaceae

1. *Strynos* sp.



Plate 24: Seed

Malvaceae

1. *Durio* sp.
   Common name: Durian hutan



Plate 25: Germinated seed

Meliaceae

1. Sandoricum koetjape



Plate 26: Seedlings

Moraceae

1. *Arthocarpus* spp.
   Common name: Terap



Plate 27: A) Seeds, B) Different species of seedlings

2. *Artocarpus lanceifolius*



Plate 28: Seed

Myrtaceae

1. *Syzigum* sp.
   Common name: Wild jambu



Plate 29: Fruit

Musaceae

1. *Musa* sp.
   Common name: Wild banana



Plate 30: Seedling

Polygalaceae

1. *Xanthophyllum* sp.

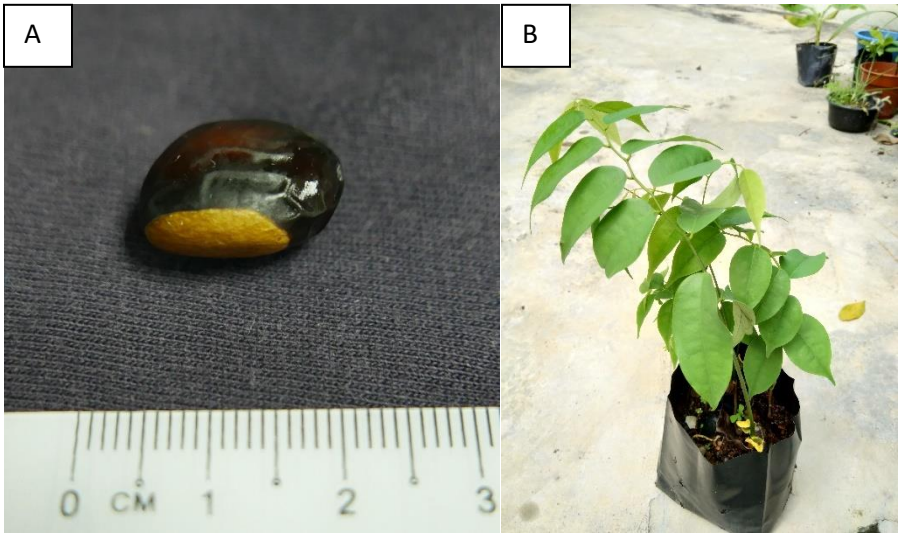


Plate 31: A) Seed, B) Seedling

Sapotaceae

1. *Chrysophyllum burkilii*



Plate 32: Seed

2. Diploknema sp.

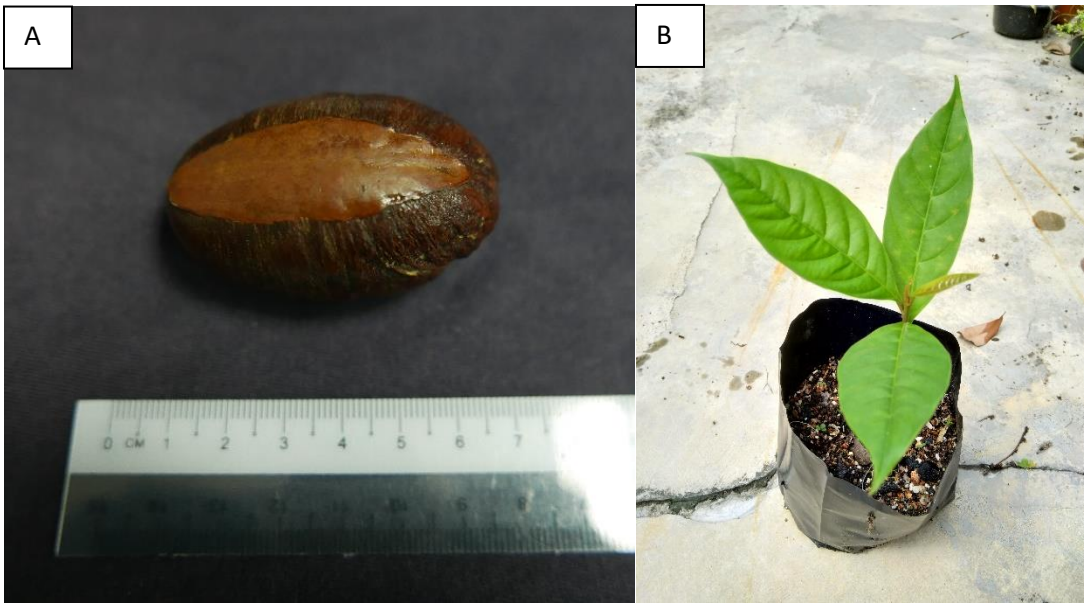


Plate 33: A) Seed B) Seedling

3. Unknown



Plate 34: Seed

Styracaceae

1. *Styrax sp*.



Plate 35: A) Halved fruit, B) Whole fruit (Photo by Anders)

Zingiberaceae

1. *Etlingera* sp.



Plate 37: Fruit

2. *Zingiber* sp.



Plate 38: Seeds

Unknown

1. Sample 41



Plate 39: Seedling

2. Sample 42



Plate 40: A) Crushed Fruit, B) Seeds